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Does the solitary bee *Andrena lapponica* show sex-specific responses to habitat change?

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Summary

Aim Land use alterations are a serious challenge for solitary bees. This is especially so for specialized bees that rely on a single plant species when collecting pollen for their larvae. Moreover, the sex ratio within bee populations may change with habitat quality because females are costlier to produce than males. However, gender is a rarely considered trait, and potential sex-specific responses to habitat loss and habitat change are poorly understood. I used populations of the solitary bee species *Andrena lapponica* as a model organism to test if the spatial and bi-annual (2013-2014yr) variation in population sizes was related to the sex ratio within populations as well as the availability of foraging resources.

Location Three experimental plots, mimicking different habitat management practices, replicated across 19 power-line clearings in south-eastern Norway. Sampled in both 2013 and 2014.

Methods I tested if the relationships between *A. lapponica* abundance and habitat quality differed between male and female bees at the inter-population level. Because bee populations show inter-annual fluctuations, I also tested if differences in the increase in population sizes between power-line clearings were related to habitat quality. Finally, at the intra-population level, I tested if the occurrence of bees differed among three experimental plots, and if this difference depended on habitat quality. The three treatments were: (1) Cut: All trees were cut and all biomass was left to decay in the plot; (2) Uncut: No trees were cut and the plot remained uncleared; (3) Cut & remove: All biomass was removed after cutting.

Results The sex ratio was female biased, I found no statistically significant difference in habitat use between males and females. The abundance of bees was most strongly associated with *V. myrtillus* availability, which was the main explanatory variable for presence of bees. The number of bees was four times higher in sites where the level of *V. myrtillus* was high compared to sites with low levels of *V. myrtillus*. When including the cut & remove treatment in combination with the high levels of *V. myrtillus* the probability of observing a bee was high. The likelihood of observing a bee in any of the treatment plots without *V. myrtillus* was low.

Conclusions *V. myrtillus* is the main driver for habitat choice for *A. lapponica*, but open sites with direct sunlight and a higher probability of appropriate nest sites are likely important as well. To ensure good habitats for ground nesters like *A. lapponica* it is important to focus on areas that have high food resource levels, but they also need to be combined with open areas with exposed soil or sand resources. For management practices to be efficient, they should ensure and enhance both food and nesting resources for wild bees. Furthermore, the absence of sex-specific responses to habitat change may be due to a short sampling period, as fluctuations in population and sex ratio are normal between years. Longer lasting studies may therefore be necessary when studying wild bees' sex-specific responses.

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1. Introduction

Habitat loss or land use alterations may result in changes in species composition. The number of specialist species might decrease while the generalists persist or even increase, which can have consequences for the ecosystem where the species are located (Díaz et al. 2006; Warren et al. 2001). However, it depends on the degree of alteration. Land moderately altered by humans have proved to be good habitats for some bees and butterflies, and have increased the species richness (Hogsden & Hutchinson 2004; Sydenham et al. 2016a; Westrich 1996). Nevertheless, to prevent the loss of more species and destruction of ecosystems, it is important to find a way to protect what is left of their original habitats, a task that will be a vast challenge with a predicted human population growth of 4 billion within 2100 (Sakschewski et al. 2014; Tilman et al. 2002; United Nations 2015). This challenge becomes even greater knowing that many species depend on several habitats of high quality to survive and reproduce (Westrich 1996). The male capercaillie (*Tetrao urogallus*) for instance prefers old natural forests in general, while the female prefers humid habitats rich in bilberries (*Vaccinium myrtillus*) when raising her chicks, and a denser younger forest during the summer (Rolstad et al. 1988; Wegge et al. 2007). The Atlantic salmon (*Salmo salar*) is another example. The larvae utilize a different habitat than a young of the year, which again use a different habitat than an older parr (Bardonnet & Bagliniere 2000; Heggenes 1990). Animals like the capercaillie and the Atlantic salmon have been a part of our culture for centuries as important food sources. Consequently, a lot of research has been done on these species, which enables knowledge-based management decisions. In contrast, our knowledge about smaller and less conspicuous animals, such as insects - which traditionally have been considered to be of less economic and cultural importance - is generally poor. Considering the number of insect species that exist, relatively few studies exist on insects and their habitat preferences, despite them being fundamental for ecosystem function and ecosystem services like pest control, decomposition of organic matter and pollination (Losey & Vaughan 2006).

A great number of insect species are pollinators and are essential for the world's biodiversity as well as our economy. 87.5% of wild angiosperm plants depend on pollination, and 35% of the world's food crop is largely or to some extent dependent on pollination (Klein et al. 2007; Ollerton et al. 2011). A key pollinator group are bees (*Hymenoptera: Apiformes*), where the domesticated honeybee (*Apis mellifera*) has received most attention. In contrast, wild bees

have received relatively little attention, even though some species may be more effective pollinators than domesticated honeybees (Klein et al. 2007). They have also been shown to improve honeybees' pollination performance (Greenleaf & Kremen 2006). Since pollinators play such an important part in our ecosystems, the fact that 9.2% of wild bees are threatened and an additional 5.2% are considered threatened in Europe (Nieto et al. 2014) is of great concern. Furthermore, 7.7% of the European species are decreasing in numbers while only 0.7% are increasing (Nieto et al. 2014). The main reasons for the decline in numbers are shortage of nest sites and food sources caused by agriculture, roadways and insecticides, but competition from the honeybee may also be a problem for some species of wild bees (Herbertsson et al. 2016; Lindström et al. 2016; Michener 2007).

To what degree wild bees are affected by habitat loss depend on the species' functional response traits and probably also gender, and both population level and community level responses can occur. With respect to community level responses, Williams et al. (2010) found that nest site location, i.e. whether they nest in the ground or above, is an important trait for how wild bees are affected by habitat change. Disturbance affected the species nesting above ground considerably more than species who nest in the ground and the reduction of species nesting above ground were on average six times higher than the species nesting in the ground. Different sized species may also respond differently to habitat loss and fragmentation because bee foraging ranges are related to body size. Body size and diet specialization are traits determining the species foraging range (Gathmann & Tschardtke 2002; Jauker et al. 2013). A higher amount of pollen is needed by the larger species, which means that they may have to travel further to collect enough food resources. Thus, they have larger foraging ranges and may see a separate fragment of habitat as an island of resources. The same fragment can host a whole population of smaller bees who have smaller foraging ranges and lower pollen requirements (Cane et al. 2006; Greenleaf et al. 2007; Müller et al. 2006). Consequently, habitat loss affects small generalists more than large. However, because the typical foraging range of bees is only 150-600 m and that it is related to body size (Gathmann & Tschardtke 2002), small bees may not be able to migrate to new habitats when their current habitat is being destroyed (Bommarco et al. 2010). Indeed, Bommarco et al. (2010) found that the larger species of diet generalists seemed to be more resilient to habitat loss than the small generalists. Differences between generalists and specialists have also been observed. Williams et al. (2010) found that increased agricultural intensity and increased tilling affected the specialists more negatively than the generalists, the generalists even increased when the tilling

intensified. Moreover, Biesmeijer et al. (2006) found evidence that bees specialized in habitat or diet, or bees that have slower mobility and have fewer generations a year, decline more than generalist species who reproduce faster and move further from their nests.

At the intra-population level, habitat alteration may lead to physical changes of a species because of the habitat selecting for individuals within the population based on their functional traits. Warzecha et al. (2016), for instance, found that medium sized species of solitary bees increased in size when they experienced habitat fragmentation, while small and large bee species did not change. Steffan-Dewenter et al. (2002) had similar findings, where the mean body size of solitary bees increased as a result of a decrease in proportion of suitable habitats. However, a study by Oliveira et al (2016) showed that the size of females of larger species of wild bees in the Netherlands decreased by 6.5% between 1900 and 2010. Male bees did not change noticeably. A decline in the size and number of larger wild bee species can lead to changes in species composition of an ecosystem. Different plants are adapted to different sized bees and a decrease in the size of larger bee species may lead to pollen limitation since fewer bees will visit the plant (Ashman et al. 2004; Schweiger et al. 2010). A possible outcome of this is a shift to autogamous species in the plant community (Ashman et al. 2004).

A rarely considered trait is gender, and consequently, potential sex-specific responses to habitat loss and habitat change is poorly understood. Females and males may be affected differently by habitat loss if they have different habitat requirements. Females need pollen and nectar, nesting sites and nesting materials to reproduce, while male bees only need nectar to feed on (Oliveira et al. 2016; Westrich 1996). Female bees could therefore be expected to show a stronger affinity to high quality habitats than male bees. Moreover, because bees are haplodiploid, females can choose to lay fertilized female eggs, or non-fertilized male eggs. As females are generally larger than males, and therefore may require more pollen to sire I therefore expected that the sex ratio within solitary bee populations would become skewed towards more females as foraging availability increases. I used populations of the specialized wild bee species *Andrena lapponica* sampled in power-line clearings in south-eastern Norway as a model system to test if the relationships between *A. lapponica* abundance and habitat quality differed between male and female bees. Power-line clearings have previously been shown to host diverse wild bee assemblages where the clearings provide stable habitats for nesting and feeding (Russell et al. 2005; Sydenham et al. 2016a). Moreover, as power-line clearings transect landscapes with a wide variety of environmental conditions this study

system allowed me to assess the influence of habitat quality of the bees on a wider scale. I tested potential differences between female and male *A. lapponica* abundance and habitat quality at the inter-population level. Because bee populations show inter-annual fluctuations I also tested if differences in the increase in population sizes between power-line clearings was related to habitat quality. Finally, at the intra-population level, I tested if the occurrence of bees differed among the three experimental plots and if this difference depended on habitat quality.

I hypothesized that:

- (1) Inter-population level - spatial scale: The female:male sex ratio of *A. lapponica* increases as habitat quality increases.

My prediction is that there will be relatively more females in sites that are dominated by ericaceous plants and relatively more males in sites at higher altitudes which tend to be colder and less fertile.

- (2) Inter-population level - temporal scale: The change in population size between 2013 and 2014 can be explained by the number of females in 2013.
- (3) Intra-population level: There is a relatively higher number of female than male bees in high-quality habitats, and relatively more males than females in habitats of lower quality. I also tested which of the three treatment plots the bees in general was most abundant in.

2. Materials and methods

2.1. Study area

Data used in this thesis comes from an ongoing project on biological diversity in power-line clearings. The project was carried out by researchers from the Faculty of Environmental Sciences and Natural Resource Management at the Norwegian University of Life Sciences in collaboration with Statnett, ending in 2016. Data was collected in sites in power-line clearings located in the southeast of Norway between 2013 and 2014. Sites were located between latitudes 59.33 - 61.12°N and longitudes 08.95-11.36°E at 48-536 m.a.s.l. The study sites were surrounded by forests of Norway spruce (*Picea abies*) and Scots Pine (*Pinus sylvestris*).

Covering the ground level, species in the Ericaceae family dominated the unproductive sites and herbal species the more productive sites.

2.2. Study species

A. lapponica is an oligolectic solitary bee, which is common in Fennoscandia. It forages mainly on flowers of *Vaccinium myrtillus* and is a boreo-alpine species (Bees, wasps & ants recording society 2005). It is mostly active during May and June when *V. myrtillus* is in bloom (Artsdatabanken n.d.). It prefers open coniferous forests, edges of forests, heath land and mountainous areas. The bee is sexually dimorphic; the female measures 12-13 mm while the male measures 9-11 mm. It is univoltine, i.e. it only flies with one generation per year, and nests in the ground in vegetation-free areas, normally close to conspecifics (Wildbienen.de n.d.). Since this bee is an oligolectic and common species, it makes it a good model organism for studies on how sex ratios and the availability of foraging resources drive the spatiotemporal variation in wild bee population sizes.



Figure 1. *A. lapponica* (Female). Photo taken by Markus Sydenham, summer 2013

2.3. Data collection

Within the main power line grid 19 sites were used for collecting insects. The width of the clearings ranged from 40 to 80m, and there was originally at least 200m of young forest regrowth below the aerial power lines. The distance between the sites was at least 5.5km, ensuring that multiple sites were not reachable by the same individuals, as the foraging distances are considerably shorter than 5.5km (Zurbuchen et al. 2010). Three rectangular plots

were set up at every site with a minimum 20m distance between them, extending 30m along the power line clearing and the full width of the clearing. In late autumn 2012, 16 sites were randomly assigned one of these treatments: (1) Cut: all trees were cut and all biomass was left to decay in the plot; (2) Uncut: No trees were cut and the plot remained uncleared; (3) Cut & remove: All biomass was removed after cutting (Figure 2). The same procedure was carried out on three more sites in early spring of 2013. All the 19 sites had previously been subjected to manual clear-cutting of all woody vegetation every 5-10 years, and trees that were cut were left on site. *V. myrtilus* was registered in 9 plant subplots in each treatment plot (Figure 2). Each subplot measured 1m² and were uniformly organized in a grid pattern with a 5m distance between them.

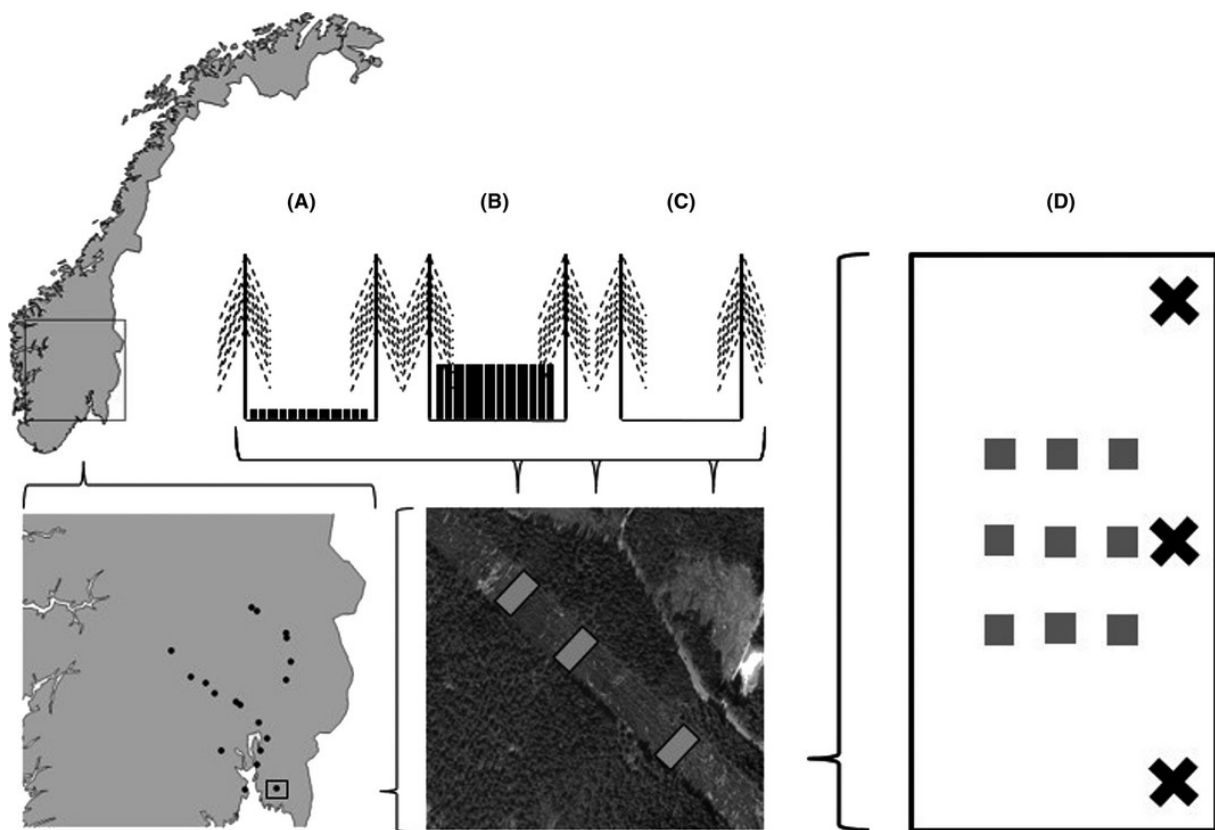


Figure 2. The 19 study sites were located in the eastern part of Norway within power line clearings. The treatment plots are shown as cross-sections of the power-line clearing: (A) Cut: all trees were cut and all biomass were left to deteriorate in the plot; (B) Uncut: No trees were cut and the plot remained uncleared; (C) Cut & remove: All biomass was removed after cutting. Interception traps, marked as black crosses, were used for collecting bees. They were placed in each treatment area (D). All treatment plots had 9 subplots marked as grey squares, that were used for registering of plant species (D) (Figure from Sydenham et al. 2016a).

Bees were collected throughout the flowering season from snowmelt to September by using three flight interception traps within each treatment plot. The trap was made of two rectangular plates of plexiglass measuring 370x210 mm forming a cross. A plastic funnel was attached under the plexiglass that lead the insects down in to a bottle filled with preservation liquid, a mix of a 50/50 green propylene glycol and a drop of detergent. The bottle had small 2mm holes at the top to prevent rainwater filling the bottle. The holes were too small for insects to escape.

The traps were emptied once a month and instantly replaced by new bottles. The bottles filled with insects were brought back to the laboratory and the contents were sieved through a fine meshed-net. The insects were then transferred to marked containers of glass that were filled with 80% ethanol. The collected bees were separated from the other insects, washed in 80% ethanol and blow-dried or carefully dried with tissues before they were pinned. The solitary bees were identified by Markus Sydenham.

2.4. Data analysis

2.4.1. Data preparation

I analyzed factors influencing the sex ratio of *A. lapponica* populations on two levels; inter-population level and intra-population level. As explanatory variables I used:

1. Food resource availability - the cover of *V. myrtillus*. On inter-population level the number of plant subplots that had *V. myrtillus* registered in them on each site was estimated. The highest number of plant subplots being 27. On intra-population level the cover of *V. myrtillus* was estimated by converting the numeric variables to factors and dividing them into two groups; a lower level where there were less than 4 out of 9 plant subplots containing *V. myrtillus* in one treatment area, and a higher level, where more than 4 out of 9 plant subplots contained *V. myrtillus*.
2. Year - 2013 and 2014, which was treated as factor variables
3. Elevation of sites - 36–568 m.a.s.l.
4. Sites – 19 different sites with 3 treatment plots (Fig.2).

All analyses were conducted using R version 3.2.2. (R Core Team 2015).

To see if there was any correlation between the explanatory variables I used the Pairs function to make a scatterplot matrix (Crawley 2007). There were no dependencies between the candidate explanatory variables so all of them could be used as explanatory variables in the statistical models.

2.4.2. Prediction 1:

The female:male sex ratio increases as habitat quality increases.

In order to assess if the sex ratio changed when habitat quality improved, I tested if the abundance of *A. lapponica* within power line clearings (i.e. population size) differed between male and female bees by analysing the interaction between sex and elevation, sex and *V. myrtillus* cover, and sex and year. I first used a generalized linear mixed-effects model (GLMM) with log link function and Poisson error distribution to analyse the response variables. However, the Poisson regression models were underdispersed and using a negative binomial distribution improved the distribution of residuals. I therefore re-fitted the GLMM model with negative binomial distribution.

I used the negative binomial regression GLMM to analyse the influence of the explanatory variables on the response variable (abundance of bees). I tested if the abundance of bees on the inter-population level was related to *V. myrtillus* cover and elevation and their interactions with sex. I first carried out a separate likelihood ratio test (LRT) on each explanatory variable to see if it affected the response variable. There was no significant interaction between sex and altitude (DF=1, LRT=0.40, P=0.53), so I dropped this interaction from the model. Bee abundance was related to sex, food resource availability and year as these variables all had a p-value < 0.05. These variables were all included in a full model. The full model was then simplified by using backward variable selection. The backward variable selection was conducted, using the LRT, to sequentially eliminate insignificant explanation variables with a p-value above 0.05 to create the final model (Crawley 2007).

2.4.3. Prediction 2:

The change in population size between 2013 and 2014 can be explained by the number of females in 2013.

I tested if differences in *A. lapponica* population sizes between 2013 and 2014 was related to the number of females in 2013 or whether it was other factors that could explain the increase in number of bees. I used the number of females within power line clearings in 2013, cover of *V. myrtillus*, and elevation as explanatory variables. A normal linear regression was used to test this hypothesis. I used a forward selection of variables ($p < 0.1$) to build a full model which was thereafter simplified through backward elimination of variables ($p < 0.05$).

2.4.4. Prediction 3:

There is a relatively higher number of female than male bees in high-quality habitats, and relatively more males than females in habitats of lower quality.

To test if the female:male sex ratio was related to local habitat quality I used food resource availability (cover of *V. myrtillus*) but due to the low variation in *V. myrtillus* cover at the treatment level (maximum possible range: 0 to 9) I chose to convert the variable *V. myrtillus* cover from numeric to factor. I divided the *V. myrtillus* cover into two groups; a lower level, where there were less than 4 plant subplots containing *V. myrtillus* in one treatment area, and a higher level, where more than 4 plant subplots contained *V. myrtillus*. Year, elevation and treatment plots were the other explanatory variables used in this site-level analysis. I included site as random effect to account for the variation among the sites.

The residual plots I made for the models at the intra-population level had a clear fan shape and were thus not satisfactory for the negative binomial model used to model bee abundances at the inter-population level. The reason for the fan shaped plot was lack of variation in the number of bees and that many of the treatment plots did not have any bees registered in them. Moreover, because the interactions between sex and *V. myrtillus* cover (DF = 1, LRT = 2.43, P = 0.12) and sex and treatment (DF=2, LRT=0.34, P= 0.85) were not significant on intra-population level I could combine the females and the males into one response variable i.e. bee abundance. However, the resulting negative binomial model on bee abundances within treatments was still zero inflated. I therefore re-classified the response variable to presence vs. absence of *A. lapponica* within treatment plots, which allowed me to include sex as a grouping factor. This response variable was then used to calculate the probability of the

presence/absence of an individual in the treatment plot. Sex, food resource availability, year, treatment plots, and the interaction between treatment plots and high level of *V. myrtillus* cover had a p-value below 0.05 and were further used to make the final model. I added year as a second random effect to account for between year variations in the probability of bees occurring within treatment plots. I used backward elimination of variables to select variables for the final model.

3. Results

The total number of *A. lapponica* sampled was 160 of which 101 were female and 59 were male. The number of individuals increased by 67% from 60 to 100 from 2013 to 2014. The number of females increased from 40 to 61 individuals (+ 52.5%) and males increased from 20 to 39 individuals (+ 95%).

3.1. Inter-population level

The number of females was significantly larger than the number of males, hence there was a female-biased sex ratio in the sites (Fig. 3a, Table 1). Significantly more bees were sampled in 2014 than in 2013 (Fig. 3b). The abundance of bees was most strongly associated with *V. myrtillus* availability ($P < 0.001$), which was the main explanatory variable for presence of bees (Table 1). When the cover of *V. myrtillus* (i.e. number of plant plots where *V. myrtillus* was recorded) increased, the number of bees in a site also increased (Fig. 3c). When *V. myrtillus* was found in all the plots the number of bees were four times higher than in sites where seven or less plots were registered with *V. myrtillus*.

Table 1. Driver on the spatial variation in the population size of *A. lapponica*. Final model output from negative binomial GLMMs on the inter-population level of *A. lapponica* in 19 sites with site identity as random effect. Explanatory variables were sex, *V. myrtillus* cover and year.

	β	SE	z	P
Intercept (Female)	0.48	0.20	2.39	0.017
Sex (Male)	-0.52	0.21	-2.4	0.016
<i>V. myrtillus</i>	0.69	0.12	4.86	<0.001
Year	0.51	0.21	2.36	0.018
Random effects	σ	SD	Obs.	Sites
Site	0.044	0.21	76	19

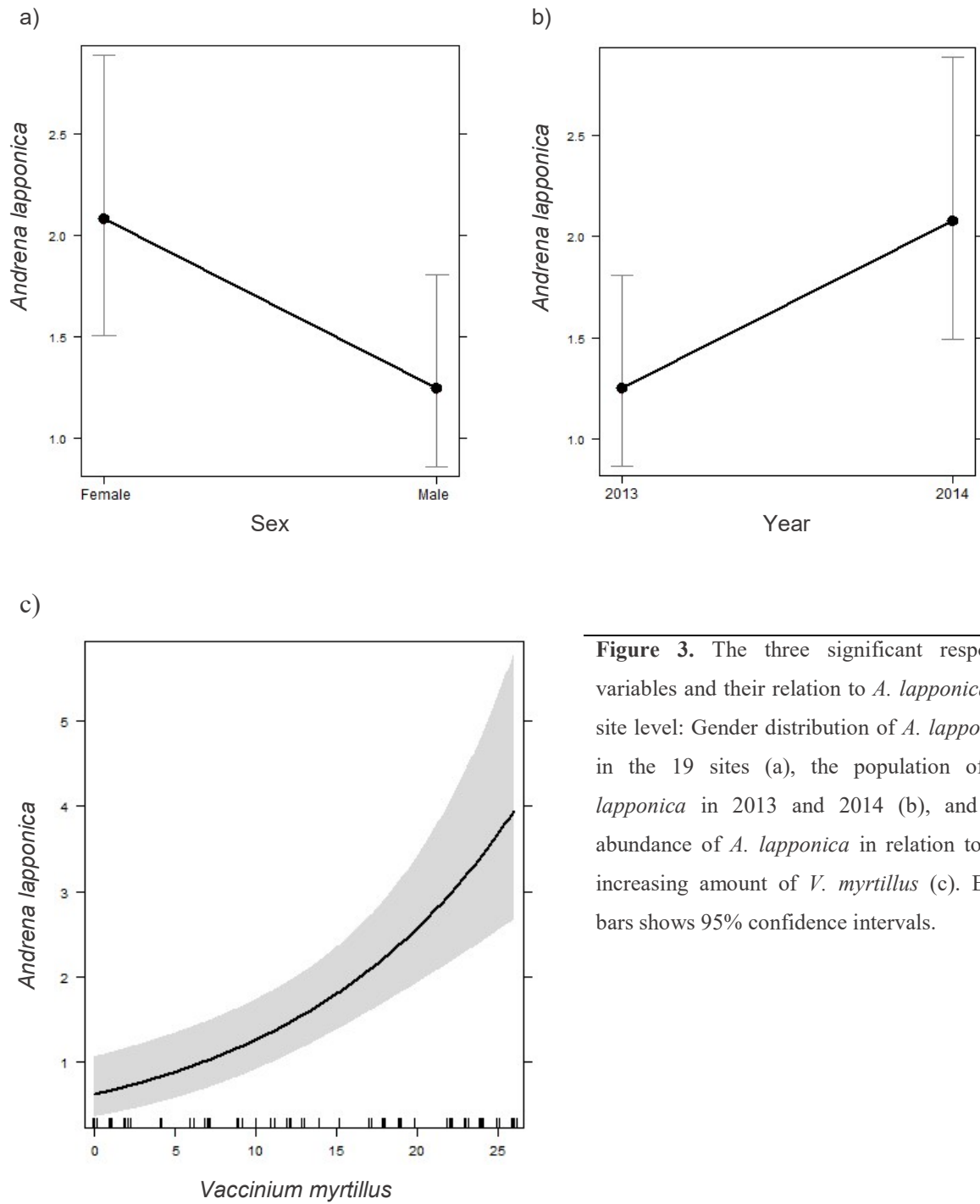


Figure 3. The three significant response variables and their relation to *A. lapponica* on site level: Gender distribution of *A. lapponica* in the 19 sites (a), the population of *A. lapponica* in 2013 and 2014 (b), and the abundance of *A. lapponica* in relation to the increasing amount of *V. myrtillus* (c). Error bars shows 95% confidence intervals.

Despite a large between-year variation in population sizes I found little evidence that the increase was associated with any of the candidate explanatory variables included in my analysis. I found a very weak relationship between *A. lapponica* and *V. myrtillus* cover but this was not statistically significant ($P = 0.088$), but no relationship between *A. lapponica* and the number of females in 2013 ($P = 0.42$) or *A. lapponica* and elevation ($P = 0.70$) (Fig. 4a-c).

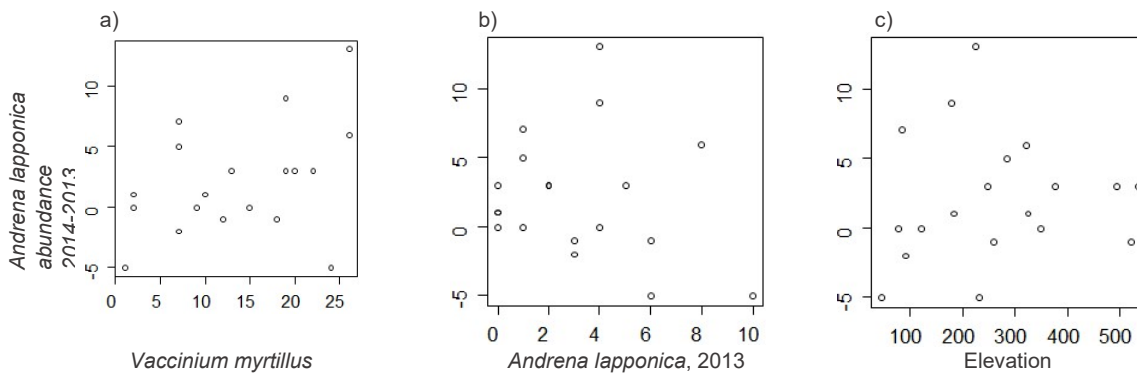


Figure 4. The difference between the year 2014 and 2013 in the number of *A. lapponica*. Figure a) shows the effect *V. myrtillus* in 2013 had on the populations in 2014. Figure b) shows whether the number of bees in 2014 had the largest increase where the number of female bees was highest in 2013. Figure c) shows whether climate in 2013 had any effect on the bee population in 2014.

3.2. Intra-population level

I found a significant interaction between treatment type and *V. myrtillus* cover which showed that the probability of occurrence was highest in the cut & remove treatment, but only in plots with a high level of *V. myrtillus* cover (Fig. 5, Table 2). The probability for hosting a bee in the cut & remove plots with a low level of *V. myrtillus* cover was not significant and therefore low. The cut plots and the uncut plots did not show any significant change between low and high level of *V. myrtillus* cover and the probability of observing a bee. (Fig. 5). The likelihood of observing a bee in any of the treatment plots without *V. myrtillus* was also low. There was no interaction between sex and other explanatory variables on intra-population level.

Table 2. The probability of the presence/absence of an individual of *A. lapponica* on three treatment levels with site and year as random effects. Table shows final model outputs from negative binomial distribution in the GLMMs. Explanatory variables were treatment plots, *V. myrtillus* cover and the interaction between treatment plots and high level of *V. myrtillus*.

<i>A. lapponica</i>	β	SE	z	P
Intercept (Uncut)	-0.023	0.59	-0.045	0.96
<i>V. myrtillus</i> - high	-0.17	0.79	-0.22	0.83
Cut & remove	-0.70	0.75	-0.94	0.35
Cut	0.18	0.71	0.25	0.81
<i>V. myrtillus</i> - high: Cut & remove	3.73	1.39	2.68	0.007
<i>V. myrtillus</i> - high: Cut	1.48	1.12	1.32	0.19
Random effects	σ	SD	Obs.	Sites
Site identity	6.45E-01	0.80	114	19
Year	2.20E-07	0.00047	114	19

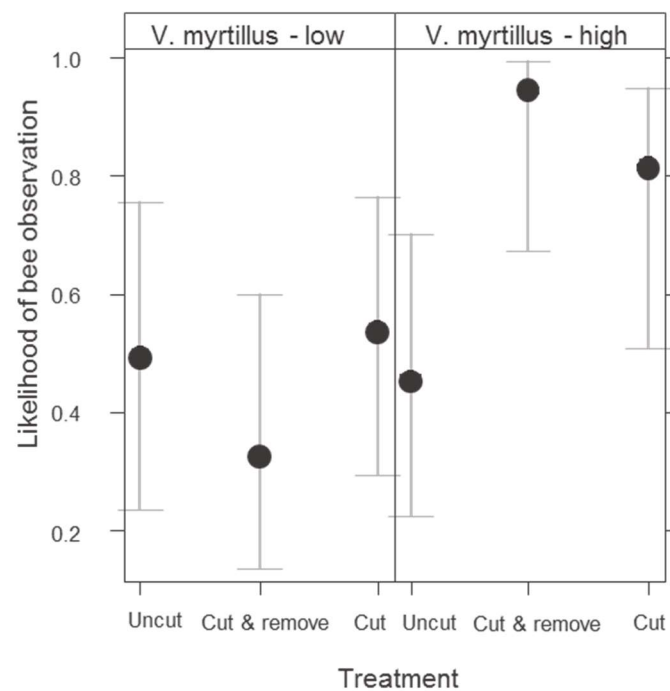


Figure 5. The likelihood of observing an individual of *A. lapponica* in the different treatment plots with two levels of *V. myrtillus*. The difference in uncut and cut plots with low levels of *V. myrtillus* cover and uncut and cut plots with high levels of *V. myrtillus* cover was not significant. The likelihood of observing an individual in the cut & remove plots with a high level of *V. myrtillus* cover was significantly higher than in cut & remove treatment plots with low levels of *V. myrtillus* cover. Error bars shows 95% confidence intervals.

4. Discussion

Contrary to my predictions, I found no difference between the sexes when it came to habitat choice. Males and females both occurred most frequently in sites that had a high cover of *V. myrtillus* and the abundance of bees was strongly associated with *V. myrtillus* availability. However, the sex ratio was female biased even though the increase in the number of males was higher than that of females. The number of bees increased significantly between the year 2013 and 2014, but what caused the increase of bees is uncertain. The increase seemed to happen in areas rich in *V. myrtillus*, but there may be other factors that caused the increase. Population growth did not happen in areas where there was a high number of female bees in 2013. Elevation did not affect the bee population, neither on inter-population level nor on intra-population level. There was no interaction between sex and other explanatory variables on intra-population level. This was most likely due to data shortage. Since there was not enough data to investigate further if there was any difference between the sexes when it came to treatment preference, I have to discuss the species in general on intra-population level. *A. lapponica* occurred most frequently in the cut & remove treatment plots more than the cut and uncut plots, but this potential habitat preference was only significant when the interaction between treatment type and high levels of *V. myrtillus* cover was included in the model.

The sex ratio in the sites was female biased. According to Trivers and Willard (1973), a habitat of poor quality will favour production of the cheaper sex which may lead to a skewed sex ratio towards the less expensive sex, while in habitats of higher quality, production of the more expensive sex is favoured. As haplodiploid organisms, female bees will prioritize differently when it comes to choosing what sex she wants her offspring to be if the habitat changes to one of lower quality (Ulbrich & Seidelmann 2001). When studying *Calliopsis persimilis* (Andrenidae) Danforth (1990) found that the female bees used 1.3-1.5 times more energy on their female offspring than their male, generally making more trips to collect pollen for the females. A female progeny is more expensive to produce than the male and are therefore prioritized when food resource availability is high (Frank 1995). A larger number of females may be an indication that the sites in general provide habitats of high quality but another possible explanation for female bias in a habitat is the establishment of new groups by foundresses who will prioritize reproduction of females. In newly established areas there is a limited number of bees. To make sure that all of the female's offspring reproduce she will

therefore produce more daughters, since only a few sons are needed to mate with all the females (Werren 1987). However, the increase of male bees between the years was very high (95%) compared to females that had a lower increase (52.5 %). A foundress effect is thus not very likely in this case. Moreover, a potential foundress effect in the sites would be difficult to assert, since there was no clear evidence that the increase in numbers was in areas with a high cover of *V. myrtillus*, which could be an indication on this effect. What caused the increase in male offspring could be an indication of a decrease in food resources, but sex ratios can fluctuate within seasons (Frohlich & Tepedino 1986; Torchio & Tepedino 1980) and between years (Tepedino & Torchio 1982). To understand the fluctuations better, more studies over a longer period are needed.

There was a significant increase of the bee populations between 2013 and 2014. The increase seemed to be somewhat affiliated with *V. myrtillus* cover, but I found no clear evidence on what caused the increase. Still, the abundance of bees was four times higher in sites where all the subplots contained *V. myrtillus* compared to sites where *V. myrtillus* was only found in seven or less subplots (Fig. 3c). According to Roulston & Goodell (2011) food resource availability is the main driver for regulating bee population abundance. Studies done on the oligolectic *Andrena hattorfiana* and *Dieunomia triangulife* both showed a clear correlation with the available pollen resources and the population size of the bees (Larsson & Franzén 2007; Minckley et al. 1994). Thus, a fourfold increase of bees between the sites may be an indication of *V. myrtillus* availability being the main driver of the population size of *A. lapponica*. There are several other external factors that can affect population growth besides access to high quality food resources. The number of sunny days and high temperatures may also be an explanation. May of 2013 was abnormally warm with a monthly temperature of 2.6°C above average (Hole et al. 2013) which could have a positive effect when it comes to pollen collecting which again affects the number of cells a female can produce. The following winter and spring of 2014 was mild with temperatures above average (Hole et al. 2014). This, combined with a mild climate during the foraging period in 2013 may have been a contributing factor for the higher number of bees caught that year. *Andrena* species hibernates in their cells as adults, coming out in spring to mate and build nests (Michener 2007), so a mild winter and spring would increase the survival rate of the adults.

Other species may also limit or enhance bees' population growth. Sydenham et al. (2016b), found that the number of large wood boring beetles influenced the number of cavity nesting

bees, increasing the number of bees when their population increased. This is not the case for *A. lapponica* since it is not a cavity nester. However, honeybees and parasites may have an impact on the population growth. Honeybees may be a limiting factor for solitary bees by competing for resources (Cane & Tepedino 2016), and if food availability is low, there is an increasing risk of open cell parasitism because of the longer time used on collecting pollen and constructing each brood cell (Ulbrich & Seidelmann 2001). Since the population increased between the years, competition with honeybees, and the level of parasitism is probably low. Moreover, fluctuations in numbers are common in bee communities (Williams et al. 2001), and some bee populations have been observed to half or double in one year intervals (Roubik 2001) which means that the increase between the years could be arbitrary. I expected that the increase would be in areas where there were a high number of females in 2013, but this was not the case, which means that external factors may be the drivers of the population growth.

I also expected elevation to be related to the sex ratio, but found no evidence to support this hypothesis. On average the monthly temperature decreases by 0.7 ° C between March and August per 100 meters, and elevation has previously been proven to affect the number of species negatively (Sydenham et al. 2015). However, *A. lapponica* have been found at 1500 m.a.s.l. (Hoiss et al. 2012), which could make an elevation of less than 600 meters unlikely to affect the species' numbers or sex ratio noticeably. However, if habitat quality first starts to decrease at higher elevations (e.g. through phenological mismatches between *A. lapponica* and the flowering time of *V. myrtillus*) it is possible that the sex ratio may change accordingly.

A probable explanation for not seeing any difference between the sexes on intra-population level was the lack of data. Yet, even with a larger sample size, I would not necessarily have detected a substantial difference on the habitat choice between the sexes because there simply was no difference. The solitary male bee's main focus in life is to mate and he is dependent on sustaining a high energy level when chasing females (Paxton 2005). This means that males most likely will stay close to females for mating purposes and to save energy. Since females seek habitats where *V. myrtillus* is plentiful, choosing to be near females will heighten his chances of being able to mate as well as getting access to food of high quality. Moreover, it is also important to account for the trapping efficiency. I used a passive sampling technique for collecting insects, which means they did not attract bees particularly. The number of bees

caught is therefore only an estimate of the population size and sex ratio, which can vary significantly because of random factors like precipitation and wind, that affect the number of individuals flying into the traps.

The abundance of bees was highest in the cut & remove plots on intra-population level. This may be because these plots offered the right environment for reproduction with more direct sunlight and more exposed soil to dig nests in (Sydenham et al. 2016a). It was only in combination with a high *V. myrtillus* cover that the bees were most abundant in the cut & remove plots. When the cover of *V. myrtillus* was low in these plots, there was no difference between the cut & remove plots and the cut and uncut plots. This indicates that *V. myrtillus* is the main driver for habitat choice for *A. lapponica*, but that open sites that have direct sunlight and a higher probability of appropriate nest sites may be important as well. More sunlight can have a positive effect on a bee population, for instance clean cut areas after small-scale logging seem to attract wild bees more than areas where some trees are left, because of direct sunlight and increased plant growth (Romey et al. 2007). The number of warm sunny days can influence the number of cells a female bee can produce, as nicer weather can improve the female's efficiency when it comes to collecting pollen and nectar (Larsson & Franzén 2007; Stone 1994). I did not account for nest availability, a potentially important factor for population growth (Cane et al. 2006). Steffan-Dewenter and Schiele (2008) concluded through their study on the generalist mason bee *Osmia rufa* (syn. = *bicornis*) and its population dynamics that scarcity of nest sites were the main limiting factor for population increase followed by food resource availability. A study of Mediterranean landscapes regenerating after fire executed by Potts et al. (2005) showed that the abundance of bees was highest in the habitats that had most recently burned, partly because of easier soil access. The density of ground-nesting bees is negatively affected by increasing vegetation cover (Steffan-Dewenter & Tscharrntke 2000), and numerous soil nesting bees have been proven to avoid a ground surface that is covered by a relatively thick layer of organic matter, since it most likely makes it difficult for them to puncture it (Osgood Jr 1972). *A. lapponica* nests in the ground so increased soil availability, where sources of organic matter are reduced, may be a contributing factor for why they were most abundant in the cut & remove plots. Since I did not have data for nest sites, my measure of habitat quality may have been limited by this constraint.

It is important to preserve habitats of high quality for bees. Low levels of food resources may not only lead to a male biased sex ratio but it can also generate smaller offspring (Peterson et al. 2006), which can result in smaller individuals within species (Oliveira et al. 2016). Ulbrich and Seidelmann (2001) argues that smaller females will lay more male eggs as this takes less energy, since they need less food to grow. This could decrease the population size over time since the sex ratio shifts towards males and the number of females declines over generations (Ulbrich & Seidelmann 2001). Inadequate food resources may also affect the bees' fecundity negatively. If the nectar availability is too low the female's egg production rate may be reduced, which contributes to fewer individuals in the population (Minckley et al. 1994). This trend is possible to reverse if the amount of desirable pollen sources and habitat increases (Carvalho et al. 2013; Steffan-Dewenter & Schiele 2008), but the population's growth rate is the key to how soon it will occur. This again depends on the species' traits and external factors.

5. Conclusions

V. myrtillus is the main driver for habitat choice for *A. lapponica*, but, as indicated by the high occurrence rates in the cut & remove treatments, open sites with direct sunlight and a higher probability of appropriate nest sites is likely important as well. To ensure good habitats for bees that nest in the ground, like *A. lapponica*, it is important to focus on areas that have high food resource levels, but these areas needs to be open with exposed soil or sand resources. Only focusing on one or the other may not have an optimal conservational effect on a bee population. Furthermore, *A. lapponica* showed no sex-specific responses to habitat change. This may be due to a short sampling period as fluctuations in population and sex ratio are normal between years. Longer lasting studies may therefore be necessary when studying wild bees' sex-specific responses.

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