Effect of land-use history and site-specific environmental factors on solitary bees and flower beetles in clear-cuts of boreal coniferous forest

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Sammanfattning/Abstract:
Land-use history has been recognized as an important factor in shaping biological communities in clear-cuts. Many solitary bees and flower beetles (Cerambycidae: Lepturinae) are commonly found in clear-cuts, which serve as early successional habitats. I analyzed the effect of land-use history on the abundance and species richness, as well as the preference for land-use history in specific species, of solitary bees and flower beetles in coniferous clear-cuts in southern Sweden. Additionally, the effect of site-specific environmental factors was examined. Insects were caught with blue, white and yellow pan-traps in 48 clear-cuts, of which half were meadow and half were forest in the 1870s. With few exceptions, the species found did not show preference for any land-use history. Furthermore, land-use history had no significant effect on the abundance or species richness of solitary bees or flower beetles. This may be due to pan-traps being less attractive in flower-rich locations, a bias in the sampling method. However, species richness and abundance of solitary bees was higher in young clear-cuts (2-4 years old), probably best explained by more exposed soil and higher frequencies of flowering plants in newer clear-cuts. Abundance of flower beetles was higher in old clear-cuts (6-8 years old). This may be due to larger amounts of more strongly decomposed wood in older clear-cuts, which is used in the flower beetles’ larval development. I conclude that solitary bees are likely to benefit if clear-cuts, particularly with meadow history, are kept more open by introducing disturbance regimes, as suggested by previous studies.

Nyckelord/Keyword:
Abundance, Clear-cut age, Community organization, Early successional habitats, Lepturinae, Pan-traps, Pollinators, Species richness
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1 Abstract

Land-use history has been recognized as an important factor in shaping biological communities in clear-cuts. Many solitary bees and flower beetles (Cerambycidae: Lepturinae) are commonly found in clear-cuts, which serve as early successional habitats. I analyzed the effect of land-use history on the abundance and species richness, as well as the preference for land-use history in specific species, of solitary bees and flower beetles in coniferous clear-cuts in southern Sweden. Additionally, the effect of site-specific environmental factors was examined. Insects were caught with blue, white and yellow pan-traps in 48 clear-cuts, of which half were meadow and half were forest in the 1870s. With few exceptions, the species found did not show preference for any land-use history. Furthermore, land-use history had no significant effect on the abundance or species richness of solitary bees or flower beetles. This may be due to pan-traps being less attractive in flower-rich locations, a bias in the sampling method. However, species richness and abundance of solitary bees was higher in young clear-cuts (2-4 years old), probably best explained by more exposed soil and higher frequencies of flowering plants in newer clear-cuts. Abundance of flower beetles was higher in old clear-cuts (6-8 years old). This may be due to larger amounts of more strongly decomposed wood in older clear-cuts, which is used in the flower beetles’ larval development. I conclude that solitary bees are likely to benefit if clear-cuts, particularly with meadow history, are kept open longer by introducing disturbance regimes, as suggested by previous studies.

2 Introduction

Factors that govern the species composition of biological communities are central to the success of conservation efforts. In this context, land-use history has for a long time been overlooked but is now being recognized as an important factor in shaping biological communities (Foster et al. 2003). Several studies have shown that historical land-use, sometimes more than 200 years ago, can explain the composition of plant communities in grasslands (e.g. Dahlström et al 2006; Gustavsson et al 2007).

Historical land-use has also been shown to have considerable effect on the biological communities on clear-cuts. When compared to clear-cuts with a long history as coniferous forest, clear-cuts managed as meadow in the 1870s (and then reforested) held higher plant species richness.
(Jonason et al. 2014) as well as higher species richness and abundance of butterflies (Ibbe et al. 2011). Additionally, in these studies, the number of butterfly and plant species associated with grasslands were significantly higher in clear-cuts historically managed as meadow.

Many species of solitary bees utilizes clear-cuts (Rubene et al. 2015a), which serve as early successional habitats that are otherwise scarce in landscapes dominated by coniferous production forests. Species richness of solitary bees has been shown to be positively correlated with species richness, diversity and abundance of flowering plants in agricultural land (Steffan-Dewenter & Tscharntke 2001; Potts et al. 2003; Potts et al. 2004). In clear-cuts of boreal coniferous forest, bee species richness is positively correlated with flower richness (Rubene et al. 2015a). As clear-cuts with meadow history are richer in flowering plant species (Jonason et al. 2014), it is reasonable to expect them to also hold more bee species. This expectation has, to my knowledge, never been investigated.

As a group, solitary bees are overrepresented in the Swedish red list (Blank & Svensson 2013), primarily due to changes in land-use practices associated with agriculture (Linkowski et al. 2004). On a global scale, bees are widely recognized as one of the most important groups of pollinators (e.g. Kearns & Inouye 1997; Schoonhoven et al. 2005). In Sweden, solitary bees together with bumble-bees (Bombus spp.) constitute the most important pollinator group (Linkowski et al. 2004). Because of this, their preservation is important, both for conserving biodiversity per se and from an ecosystem service perspective. Therefore, it is important to investigate possible ways to improve their habitats, including clear-cuts.

Some flower beetles (Cerambycidae: Lepturinae) are known to utilize clear-cuts as habitat (Ehnström & Holmer 2007). While most species are associated with forest environments, many are known to frequently visit flowering plants for nectar or pollen (Ehnström & Holmer 2007). Because of this they may show a preference for flower rich clear-cuts, i.e. clear-cuts with a history as meadow.

In this study, I examine if and how differences in land-use history and other site-specific environmental factors affect the species present, species richness and abundance of solitary bees and flower beetles in clear-cuts. I do this using data for insects collected in 48 clear-cuts of coniferous production forest located in southern Sweden. Of the 48 clear-cuts, half were meadow and half were forest in the 1870s. At this time, a shift in land-use practices took place in Swedish agriculture, when large
areas of semi-natural grasslands were abandoned or actively reforested (Dahlström et al. 2006).

The following questions will be addressed:

- Are there differences in the species richness and abundance of solitary bees and flower beetles in clear-cuts with histories either as meadow or as forest?
- Do solitary bees and flower beetles show preference, on species or higher taxon level, for clear-cuts with particular land-use histories?
- How does site specific factors such as clear-cut age, size, amount of exposed soil and woody debris affect the occurrence of solitary bees and flower beetles in clear-cuts?

3 Material & methods

The selection of clear-cuts and the data collection was executed as part of a previous study (see Jonason et al. (2014)). However, for the readability of this report, it is summarized below.

3.1 Selection of the clear-cuts

Forty-eight clear-cuts, two to eight years old, were selected for the study, located near the lake Sommen in the County of Östergötland, Sweden. The landscape is dominated by boreal coniferous forest, with dispersed arable fields, lakes and small areas of semi-natural grasslands. The area has a long history of agriculture. The clear-cuts were selected with regard to their land-use history. In the 1870s, 24 of the clear-cuts were managed as meadow and 24 as coniferous forest. Land-use history was determined by studying historical land-use maps (Häradsekonomiska kartan). For details, see Ibbe et al. (2011) and Jonason et al. (2014).

Clear-cuts were categorized as having meadow history if at least 15 % were meadow on the historical maps. The whole clear-cuts were used, not just the part classified as meadow (Jonason et al. 2014). Before logging, all the clear-cuts were dominated by coniferous trees, predominantly Norway spruce (Picea abies). It is unknown exactly when the clear-cuts earlier managed as meadows were turned into forest, but at least one generation of coniferous trees has passed (Jonason et al. 2014). This means that they have been forested for at least 70-90 years (Skogsstyrelsen 2015). To avoid confounding effects from migration, clear-cuts were chosen with a minimum distance of 300 meters to the nearest grassland.
3.2 Plant inventory and environmental factors

In each clear-cut, plants were inventoried in 100 circular plots (1 m radius) distributed evenly along transects which were placed 25 m apart. This was done on one occasion, between August and October in 2013, for each clear-cut (Jonason et al. 2014). In each plot, all present plant species were noted. From this data, an occurrence frequency for each species and clear-cut (defined as the number of plots, out of 100, where the species was present) was calculated.

At the location of every third plant inventory plot, a range of environmental factors was registered within a circular area (radius 5.64 m) to control for possible differences between the clear-cut categories; basal area and tree species identity before logging, percentage exposed rock, mineral soil and logging residues. No significant differences were found that could not be explained by land-use history. For details, see Jonason et al. (2014).

3.3 Insect collection

Insects were collected using pan-traps (diameter 8.7 cm) painted with blue, yellow or white UV-paint (Soppec, Sylva mark fluo marker, Nersac, France). Pan-traps were mounted in groups of three, one of each colour, on steel sticks. Three sticks with pan-traps were placed in each clear-cut (Berglund 2014). The height of the traps were adjusted to match the height of the nearby vegetation and the traps were placed as to represent the vegetation on each clear-cut in the best possible way (pers. comm. Dennis Jonason, IFM, Linköping University). The pan-traps were filled with equal amounts of propylene glycol and water. Traps were emptied on two occasions (on 11/7 and 25/7, 2013) after being active for one week. Collected insects were placed in 70 % ethanol, separated by pan-trap colour and clear-cut (Berglund 2014).

3.4 Insect identification and nomenclature

Insects were identified to species level except for the flower beetle species *Anastrangalia sanguinolenta* and *Anastrangalia reyi*, which were lumped together due to difficulties in separating these species. Since their ecological traits are very similar (e.g. preferred habitat, substrate for larval development; Ehnström & Holmer 2007), separation was deemed unnecessary. For the identification of the solitary bees, an expert was consulted. Nomenclature follows Ehnström & Holmer (2007) for the flower beetles. Authors for bee species are given in Appendix 1.
3.5 Statistical analyses

For the analyses, insects caught in a clear-cut were treated together, regardless of pan-trap colour.

Species richness and abundance in clear-cuts with different land-use histories were compared using the 95 % confidence intervals of the means, using the statistical program SPSS 22 (IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp.). In figures for species richness and abundance, adjoining, but not overlapping error bars indicate p=0.01. Confidence intervals overlapping by one half of an error bar indicate p=0.05 (Cumming et al. 2007).

Odds ratios (OR) and their 95 % confidence intervals were used to determine whether individual species show preference for clear-cuts with particular land-use histories. Odds ratios were calculated using equation (1):

\[
\text{Odds ratio} = \frac{a/b}{c/d}
\]  

(1)

In this case “a” is the number of times a particular species was present in meadow clear-cuts and “b” is the number of times it was not present in meadow clear-cuts. In the same manner, “c” is the number of times the species was present in forest clear-cuts, and “d” the number of times it was not. As suggested by the name, this gives an estimate of the odds of finding a particular species in clear-cuts with a particular land-use history in relation to finding it in clear-cuts with the other land-use history. By taking the natural log of the odds ratio, zero was set as the midpoint. That is, zero is the value representing equal occurrence on both clear-cut types (suggesting no preference in land-use history). Positive values indicate a preference for meadow clear-cuts whereas negative values indicate a preference for forest clear-cuts. Confidence intervals, for odds ratios on log-scale, that does not include zero indicate p<0.05 (Körner & Wahlgren 2006).

Odds ratios can be used when samples are small, which is useful when analyzing datasets that contains many zeros, such as when analyzing occurrences of rare species. The software Comprehensive meta-analysis was used to calculate odds ratios and confidence intervals. For correction in samples (clear-cuts) where one or more cell count was zero, Gart adjusted logit was used. That is, for species where any of the presence/absence values were zero, 0.5 was added (to all four values) before the calculation of the odds ratio or confidence interval.
Principal component analysis (PCA) with environmental factors as supplemental variables was used to investigate if the environmental factors could explain the variation in species composition between clear-cuts. Redundancy analysis (RDA) with 9999 permutations was used to test the explanatory value of land-use history and clear-cut age regarding species composition. Linear methods were used because of the relatively short gradient (SD<2) of the species composition. Multivariate analyses were performed in CANOCO 5. The environmental factors were the recorded percentage of exposed soil and rock, the amount of logging residues (woody debris), time since logging and size of the clear-cuts, and the occurrence frequencies of plants in different configurations grouped by ecological or taxonomical properties. The occurrence frequency for a plant species was defined as the number of plots (out of 100) where the plant was present. Occurrence frequencies for plant configurations were calculated by summing the occurrence frequencies for all the included plants. As the found flower beetle species are often encountered visiting some plant species: *Leucanthemum vulgare*, *Angelica sylvestris*, *Aegopodium podagraria*, *Anthriscus sylvestris*, *Chamerion angustifolium*, *Rubus idaeus* and *Viburnum* sp. (Ehnström & Holmer 2007), frequencies for these species were summed in a “flower beetle plant frequency”.

### 4 Results

#### 4.1 Summary of found species

For the abundance of flower beetles there was a relatively small difference between clear-cut types (table 1). Two more species of flower beetles were found on clear-cuts with a history as meadow: *Pachyta lamed* and *Judolia sexmaculata*. However, these species were represented by only one and two individuals, respectively. Otherwise, the same flower beetle species were found in clear-cuts with both land-use histories. *Alosterna tabaciclor* and *Gaurotes virginea* were only represented by three and two individuals, respectively. Thus, together with *J. sexmaculata* and *P. lamed* they constituted less than 0.1 % of the collected flower beetles. *Stenurella melanura* was, by far, the most abundant species, constituting almost 74 % of the collected flower beetles, followed by *Anastrangalia sanguinolenta/reyi* (16.9 %) and *Stictoleptura maculicornis* (3.8 %). These three were present on all clear-cuts. The three remaining species were *Stictoleptura rubra* (3.4 %), *Leptura quadrifasciata* (1.3 %) and *Pedostrangalia pubescens* (0.7 %).

In total, 59 bee species were found (table 1), belonging to six families: *Andrenidae*, *Apidae*, *Colletidae*, *Halictidae*, *Megachilidae* and *Melittidae*. The most abundant species was *Hylaeus confusus*, constituting 24.8 % of
the collected bees. This can be compared with the second and third most abundant species: *Andrena fulvida* (8.6 %) and *Lasioglossum albipes* (5.8 %). Five more bee species were found in clear-cuts with forest history than in clear-cuts with meadow history. The species found differed more between clear-cut types than for the flower beetles: 33 species occurred in only one clear-cut category. However, 22 of these species was represented only by singletons. The majority of these, 17 species, were found in clear-cuts historically managed as forest.

Table 1. Summary of the number of species and individuals of insects caught in pan-traps in 48 clear-cuts of which 24 were meadow and 24 were coniferous forest in the 1870s. There were no significant differences (α=5 %) in mean species richness or abundance in clear-cuts with different land-use histories.

<table>
<thead>
<tr>
<th></th>
<th>Solitary bees</th>
<th>Flower beetles</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Individuals</td>
<td>Species</td>
<td>Individuals</td>
</tr>
<tr>
<td>Meadow</td>
<td>171</td>
<td>40</td>
<td>5134</td>
</tr>
<tr>
<td>Forest</td>
<td>224</td>
<td>45</td>
<td>5391</td>
</tr>
<tr>
<td>Total</td>
<td>395</td>
<td>59</td>
<td>10525</td>
</tr>
</tbody>
</table>

* Flower beetles *A. sanguinolenta* and *A. reyi* are treated as one species

4.2 Effects of land-use history

4.2.1 Species richness and abundance

Mean species richness and abundance for both solitary bees and flower beetles, as well as for the insect groups combined, were slightly higher in clear-cuts with a history as forest. However, differences were far from statistically significant for α=5 %, which is shown by the error bars (95 % CI) in figure 1.
4.2.2 Occurrences of specific taxa

One species (the bee *Lasioglossum albipes*), out of 69, showed significant preference for clear-cuts with a history as meadow (fig 2) (ln OR= 1.266, CI$_{95\%}$: 0.066-2.60, p=0.039). A few species showed near-significant preference for clear-cuts with a history as forest. These were *Andrena fulvida* (ln OR= -1.05, CI$_{95\%}$: -2.25-0.14, p=0.083), *Andrena subopaca* (ln OR= -2.62, CI$_{95\%}$: -5.58-0.33, p=0.082) and *Sphecodes hyalinatus* (ln OR= -2.04, CI$_{95\%}$: -4.24-0.17, p=0.070). The weighted mean for the bee species in family Andrenidae indicates a significant preference for forest clear-cuts (fig 2) (weighted mean of ln OR= -1.69, CI$_{95\%}$: -1.69-(-0.28), p=0.006) in this species-group.
Figure 2. Natural log of the odds ratios and 95% CI calculated from species presence/absence data in clear-cuts (n=48) with histories as meadow or forest. Odds ratios indicate preference for clear-cuts with a history as meadow (positive values) or forest (negative values). Confidence intervals that do not include zero indicate a significant effect of land-use history (α=5%). Values for higher taxa (family or subfamily) are weighted means (random model). The
flower beetles A. sanguinolenta/reyi, S. melanura and S. maculicornis occurred in all clear-cuts. Because of this they were excluded from the weighted mean for Lepturinae.

4.3 Effects of other environmental factors

4.3.1 Multivariate analyses

Approximately 3% of the variation in species composition in the clear-cuts could be explained by land-use histories according to the RDA. However, the test was found nonsignificant (RDA, 9999 permutations, pseudo-F=1.5, p=0.1204).

Most environmental factors varied independently of land-use history. However, higher frequencies of flowering plants and herb species richness were associated with the species composition in clear-cuts historically managed as meadow. The species composition of bees and flower beetles associated with clear-cuts with forest history, was also positively associated with the frequency of Ericaceous plants (mostly Calluna vulgaris) and the amount of woody debris (figure 3) (although there were no significant differences in the amount of woody debris between clear-cuts with different land-use histories (Jonason et al. 2014)).

Older clear-cuts tended to have lower values for flowering plant frequencies, less herb species and less exposed soil. Instead, the frequency of the fern Pteridium aquilinum was higher (figure 3b). Clear-cut age category (new/old, figure 3) explained 5.1% of the variation in species composition of solitary bees and flower beetles in different clear-cuts (RDA, 9999 permutations, pseudo-F=2.5, p=0.0091).

The three most abundant flower beetle species (Stenurella melanura, Anastrangalia sanguinolenta/reyi and Stictoleptura maculicornis) tended to be more abundant in older clear-cuts (figure 3). Together with Stictoleptura rubra they had the biggest impact on the species composition model, as shown by the arrow lengths in figure 3c.
Figure 3. Ordination diagrams (PCA) showing species composition of bees and flower beetles on clear-cuts (n=48) of which half were meadow and half were forest in the 1870s. Eigenvalues are 0.2596 for the horizontal axis (PC1) and 0.1098 for the vertical axis (PC2).

a) Samples (i.e. clear-cuts) plotted along PC1 and PC2 with regard to dissimilarity in species composition, M – meadow history, F – forest history.

b) Shows environmental (supplementary) factors. Arrows indicate the direction of the steepest increase for the variable. Freq – frequency (number of plots out of 100 per clear-cut with presence of plant group or taxon). FB plant freq – flower beetle plant frequency, New – clear-cuts 2-4 years old, Old – clear-cuts 6-8 years old.

c) Shows the 15 species with the highest impact on the model, arrows indicate the direction of the steepest increase in abundance for the species.
4.3.2 Effects of clear-cut age on species richness and abundance

Species richness and abundance of solitary bees were significantly higher in new (2-4 years after logging) than in old (6-8 years after logging) clear-cuts (figure 4a and b). On average, two more species and about 53 % more individuals were found in new clear-cuts. Flower beetles were significantly more abundant in old than in new clear-cuts (figure 4c), with a mean difference of 118 individuals. Thus, on average flower beetles were about 74 % more abundant in old clear-cuts. There was no difference in the species richness of flower beetles (figure 4d).

![Graphs showing mean abundance and species richness](image)

Figure 4. Mean abundance (white bars) and species richness (grey bars) per clear-cut, for solitary bees (a and b) and flower beetles (c and d) caught in pan-traps in clear-cuts (n=48) at different times after logging. In new clear-cuts insects were caught 2-4 years after logging, in old clear-cuts after 6-8 years. Error bars show 95 % CI.

5 Discussion

There were no differences in mean species richness or abundance of either solitary bees or flower beetles between clear-cuts with a history as meadow or as forest. One bee species showed significant preference for clear-cuts with a history as meadow while three showed almost significant preference for clear-cuts with forest history. However, the vast majority of flower beetle and solitary bee species that were found in the clear-cuts seemed to be unaffected by land-use history. This indicates that land-use history is a poor predictor of the species richness and abundance.
of solitary bees and flower beetles in clear-cuts. This was corroborated by a RDA, which indicated a low explanatory value for land-use history. The PCA showed that the variation in species composition between clear-cuts could not be easily explained with a few variables. However, age of the clear-cuts had higher explanatory value than land-use history, which was reflected in species richness and abundance. In newer clear-cuts (2-4 years old) the species richness and abundance of bees were higher and abundance of flower beetles was lower, than in older (6-8 years) clear-cuts. Furthermore, the amount of exposed soil, herb species richness and frequency of flowering plants were able to explain some of the variation in species composition.

The flower beetle species present in the clear-cuts were largely the same, regardless of land-use history. All except one of the species found utilizes coniferous trees (dead wood, roots or living trees) for their larval development (although some of the species may use other tree species as well) (Ehnström & Axelsson 2002). They are also frequently encountered on flowers, eating pollen or nectar (Ehnström & Holmer 2007). Thus, the relative richness of flowering plants and the presence of coniferous trees seem to be plausible explanations for the great abundance of flower beetles in clear-cuts. The remarkable dominance of *Stenurella melanura* is probably best explained by its utilization of relatively thin branches of wood of different species for larval development (Ehnström & Axelsson 2002), which makes clear-cuts a suitable habitat.

No flower beetle species was significantly associated with a particular land-use history (figure 2), although *Stictoleptura rubra* showed almost significant preference for clear-cuts with a history as forest. This is not very surprising, since all species found are associated with forest environments rather than meadows (Ehnström & Holmer 2007). They are also associated with plant species that were equally common in both clear-cut categories, i.e. the plants of the “flower beetle plant frequency” (figure 3). All but two of the species are considered common in Sweden, and for several species clear-cuts are known habitats (Ehnström & Holmer 2007). However, *Pedostrangalia pubescens* is red-listed as near threatened (NT) in Sweden (Artdatabanken 2015) and is subject to a national conservation program. Its larval development occurs in old dead wood of *Pinus sylvestris*. It has been known to occur sparsely in clear-cuts. However, based on the ecological traits listed in Ehnström & Holmer (2007) the presence of this species is probably best explained by some unknown factor in the surrounding landscape, such as occurrence of old-growth forest.
For solitary bees, the species richness was expected to be higher in clear-cuts with a history as meadow than in clear-cuts with forest history. In grasslands, species richness and in some cases abundance of wild bees has been shown to be positively correlated to flowering plant diversity (Potts et al. 2003) and species richness (Steffan-Dewenter & Tscharntke 2001; Potts et al 2004; Ebeling et al 2008). Flower richness has also been shown to be positively correlated with the number of bee and wasp species present in clear-cuts (Rubene et al. 2015a). Species richness of flowering plants and flower richness has been shown to be higher in clear-cuts historically managed as meadow than as forest (Jonason et al. 2014; Jonason et al. unpublished data). Thus, it is reasonable to expect clear-cuts historically managed as meadow to hold more bee species than clear-cuts managed as forest. In this study, no such differences were found. This result differs from that of Ibbe et al. (2011), in which clear-cuts historically managed as meadow held higher abundance and species richness of butterflies.

This could indicate that there is no effect of land-use history on the abundance and species richness of bees. However, another plausible explanation is a potential bias in the sampling method, pan-trapping. Pan-traps are meant to, in the eyes of an insect, look like a flower. In locations with low floral abundance, pan-traps are likely to be very attractive to flower-visiting insects. More so than in locations with high floral abundance. This introduces a sampling bias that results in proportionally more individuals or species (or both) being caught in traps in locations with lower, than with higher, floral abundances (e.g. clear-cuts historically managed as meadows). This kind of bias has been discussed and documented by Cane et al. (2000) and Baum & Wallen (2011). According to Baum & Wallen (2011) the sampling effectiveness of pan-traps decreases with increased floral abundance, but only with regard to species richness, not abundance. However, Rubene et al. (2015b) argues that pan-trapping is the most efficient choice for sampling pollinator, but not wood-nesting (for which window-traps are more efficient), bee species in clear-cuts. This is after excluding sweep-netting for practical reasons (Rubene et al. 2015b).

In this study, the sampling bias discussed above could mask the effect of land-use history. That is if, as hypothesized, the mechanism behind differences in the insect community “due to” land-use history is floral abundance or diversity. Since this is likely the case, more studies are required to determine whether there actually is a difference due to land-use history.
Age category (2-4 years or 6-8 years old) of the clear-cuts had a significant effect on the species richness and abundance of solitary bees, and the abundance but not species richness of flower beetles. The higher flower beetle abundance in older clear-cuts (6-8 years) was suggested by the PCA (figure 3) as the three most abundant species, constituting almost 95% of the flower beetles, were clearly associated with older clear-cuts. Older clear-cuts were associated with lower frequencies of flowering plants (including those associated with flower beetles; Ehnström & Holmer 2007) and higher frequencies of Pteridium aquilinum (figure 3). This, combined with the lack of effect of land-use history, may reflect that the abundance of flowering plants is not limiting for the abundance of flower beetles in the clear-cuts. It could also result from the fact that the most abundant species, Stenurella melanura, primarily uses rather strongly decomposed wood for its larval development (Ehnström & Axelsson 2002). Older clear-cuts likely hold larger quantities of more strongly decomposed wood simply because of their age. However, the greater abundance of flower beetles may also reflect the bias in pan-trapping discussed above, due to the lower frequencies of flowering plants in older clear-cuts (figure 3).

For solitary bees, abundance and species richness was significantly higher in younger clear-cuts (2-4 years old) than in older clear-cuts (6-8 years old). This indicates a clear preference for early successional stages after a disturbance, and a rapid decline in abundance and species richness afterwards. This type of pattern has been observed in other studies. In a study on successional patterns in temperate forests both species richness and abundance of solitary bees was highest after a disturbance and then rapidly declined as succession proceeded (Taki et al. 2013). Steffan-Dewenter & Tscharntke (2001) found that species richness of both bees and flowering plants on set-aside agricultural fields in Germany peaked after two years.

A likely explanation for the higher species richness of solitary bees in newer clear-cuts is the higher frequencies of flowering plants and herb species richness associated with them (figure 3). As mentioned above bee species richness and abundance is positively correlated with the richness and abundance of flowering plants (e.g. Potts et al. 2003; Ebeling et al. 2008; Rubene et al. 2015a), and a temporal correlation between the peaks of plant and bee species richness has been observed on set-aside agricultural fields (Steffan-Dewenter & Tscharntke 2001). Regarding the potential sampling bias in pan-traps discussed above, it would in this case result in more species being caught in older clear-cuts. Therefore, if the
bias is present, it would counteract the observed pattern, and indicate that
the difference between newer and older clear-cuts is even greater.

Another likely explanation for the pattern observed in this study is that
most solitary bees are dependent on exposed soil (for nesting) (Linkowski
et al. 2004), which was positively associated with younger clear-cuts
(figure 3), making them suitable habitats. Older clear-cuts tended to have
higher frequencies of *Pteridium aquilinum* (figure 3) which form dense
aggregations (Mossberg & Stenberg 2010). High and dense vegetation
makes the microclimate on the ground colder and wetter (Linkowski et al.
2004), and therefore less suitable for solitary bees requiring warm and
dry soil.

The effects of flowering plants and the amount of exposed mineral soil
are confounded. Also, other factors are likely important, that are
unaccounted for. Thus, no clear conclusions regarding the mechanism
behind the discussed differences may be drawn. However, age of clear-
cuts clearly affects abundance and species richness of solitary bees.

Many habitats suitable for solitary bees have become scarce, primarily
due to rationalization in the agricultural landscape (Linkowski et al.
2004). Thus, restoration of more traditional habitats or general
improvement of matrix habitats (preferably both) is important for the
preservation of bees (Linkowski et al. 2004; Blank & Svensson 2013) and
the ecosystem services they provide. This study underlines that solitary
bees in clear-cuts are associated with early successional stages with more
exposed soil and higher floral frequencies. Thus, keeping clear-cuts open
longer by introducing grazing or other disturbance regimes would likely
benefit the solitary bees in clear-cuts. This is also the conclusion reached
by Rubene et al. (2015a). Although solitary bees appeared unaffected by
land-use history in this study, they are likely to benefit from the higher
flower species richness in clear-cuts with meadow history if grassland
management were to be continued in these clear-cuts, as suggested in
Ibbe et al. (2011) and Jonason et al. (2014).

5.1 Civil & ethical aspects
As pollinators are declining, and especially since they are crucial for
agriculture, knowledge about them is important. The results has
implications for the management of clear-cuts and possibly for the
restoration of semi-natural grasslands. Pan-traps kill insects, potentially
including rare species. This may increase the extinction risk for sensitive
species. In this study two red-listed species were caught; flower beetle
*Pedostrangalia pubescens* (NT, 77 individuals) and the bee *Andrena*
nitida (VU, 3 individuals). However, the pan-traps were only set for two weeks, which limits the potential damage to the sampled populations. Furthermore, the study aimed to improve our understanding of the insect groups, and the results may be used to improve their habitats and avoid extinctions.

6 Acknowledgments

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7 References


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8 Appendix

8.1 Appendix 1

Authors for bee species caught in the clear-cuts

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