Living on the Edge
the value of field edges as resource patches for solitary bees (Hymenoptera: Apiformes)

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Preface

In my view studying is as much a matter of finding a platform for maturation of thought as of gaining knowledge. Thanks to its egalitarian structure and the short distance between students and internationally renowned researchers the Norwegian University of Life Sciences has provided an excellent basis for both. Studying there allowed me to pursue my interest in conservation biology and entomology, as well as creating a platform from which I have become able to dwell upon and ask questions about the intricacies of species-landscape interactions.

Work on my thesis has involved many people I am grateful to have met. Ørjan Totland had his hands full but still found time and interest to supervise and facilitate my work. Thank you also for your excellent introduction to pollination biology. Eline Benestad Hågvars introduced me to entomology. Thank you for always having had your door open but thank you first and foremost for motivating me to study solitary bees. Bee specialist Mike Edwards kindly opened his door and volunteered to verify my bee identifications. Graham Collins, David Baldock and Jan Stenløkk also assisted with verifications. Post doc Katrine Eldegard and PhD student Sam Steyaert helped with the GIS-analysis. Celin Hoel Olsen, David Sydenham and Håkon Celius joined me for long nights of bee collecting. Britt Hoel kindly lent me her car for field work.

I could not have written this thesis had it not been for the love and support of friends and family. Mum and Dad, thank you for always encouraging me and for all your visits to Norway. Celin, thank you for thinking that insects are sexy. Christian, thank you for making He-man relevant to conservation ecology.

Ås, 24.04.2012

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Abstract

Current patterns of anthropogenic land-use are reducing the diversity of pollinators through habitat destruction, degradation and landscape simplification. This may adversely affect both wild and domesticated flowering plants through pollen limitation. These concerns are supported in the parallel declines in solitary bees and wild plants observed in Europe.

Solitary bees vary in their requirements to nesting, mating and forage sites. In addition, bee assemblages fluctuate over years. Successful management of remnant habitat patches therefore requires both the consideration of autecological traits and temporal patterns in bee diversity.

In this study I sampled bees to evaluate the potential value of field edges in the Norwegian agricultural matrix. I found that bee species were not randomly distributed in the landscape. Furthermore, the solitary bee assemblages were relatively stable between years but could be grouped by monthly affiliations. I isolated two groups of bee assemblages, one consisting of spring active bees and one of summer active bees. Furthermore I found group-specific responses to habitat conditions. The species richness and abundance of the spring-active group was negatively related to the proportion of agricultural land around the field edge, whereas the summer-active group preferred sun-exposed field edges with short vegetation and a high floral richness.

The group-specific responses reflect seasonal changes in the predominant bee species phenology. The spring group was mainly composed of *Andrena* species which burrow nests in the ground and find forage in spring blossoming trees such as *Salix caprea* Linnaeus. which are common in non-agricultural landscape types. In contrast, the

summer group was more diverse in phenology and occurred at a time when the floral resources were more diverse.

These results suggest that field edges can provide an important asset in the conservation of solitary bees. The success of such management does however call for more research on the temporal variation in the autecology of bees.

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1. Introduction

The diversity of pollinators is declining worldwide (FAO 2008; Murray et al. 2009) due to the intensification of agriculture and habitat loss and degradation (Potts et al. 2010). The absence of pollinators may threaten the integrity of plant communities, directly by reducing the fecundity of flowering plants, and indirectly by increasing inbreeding (Kearns et al. 1998). These effects are conceptualized in the term "pollen limitation". In a meta-analysis Burd (1994) found that 62% of the 258 studied plant species failed to fertilize all available ovules. In addition to increasing the seed set in wild plants, pollinators provide an important ecosystem service with an estimated annual value of €153 billion, our most valuable crops being most dependant on pollinators (Gallai et al. 2009).

Because bees (Hymenoptera: Apiformes) are the most important pollinators (Klein et al. 2007) they should be given conservation priority. The recent decline of the domesticated honey bee (*Apis melifera* Linnaeus) (FAO 2008) has inspired increased interest in wild bees as alternative pollinators of commercial crops. Solitary bees may be more efficient pollinators than the honey bee (Kevan 1999; Klein et al. 2003) but are also more vulnerable to anthropogenic land use (Williams et al. 2010). Documenting the status of bees is challenging because few long-term data records exist. However, due to large communities of amateurs, extensive records exist in both the Netherlands and the UK. Detailed analysis of changes in these records showed that both wild bees and bee pollinated plants have declined during the past century (Biesmeijer et al. 2006).

The bees are a monophyletic group with approximately 20,000 species catalogued so far. It is a highly varied group displaying a large variety of life histories with important implications for conservation (Murray et al. 2009). Polylectic bees collect pollen from unrelated plants,

whereas oligolectic bees rely on the pollen from plants belonging to the same genus or family. Bees also vary in nest locations. Endogeic species build nests below ground, whereas hypergeic species find or create cavities above ground. Bees may also vary from being strictly social to eusocial (Michener 2007). But all bees are central place foragers and depend upon floral resources around the nest site for larval provision (Westrich 1996).

One third of the approximately 200 bee species found in Norway are currently red listed according to the IUCN criteria. Their decline is assumed to be caused mainly by changes in the agricultural landscape over the last 100 years (Hansen et al. 2010). Moreover Biesmeijer et al. (2006) found that oligolectic bees with low mobility have declined the most during the last century as would be expected in fragmented landscapes.

In fragmented landscapes the home range of solitary bees is often composed of partial habitats where resources for foraging, nesting and mating occur. If the quality or availability of one such partial habitat is reduced, it may adversely affect local bee populations (Westrich 1996). Several landscape ecological studies have shown that wild bee species richness increases with the proportion of semi-natural areas in the agricultural matrix (Hendrickx et al. 2007; Williams et al. 2010). Semi-natural landscapes may provide forage resources not found in the matrix and thereby contribute to increase offspring production in solitary bees (Williams & Kremen 2007; Zurbuchen et al. 2010a). In addition, linear elements such as road sides (Sjödin et al. 2008), power line corridors (Russell et al. 2005) and hedgerows (Hannon & Sisk 2009) have been shown to provide important resources for bees in fragmented landscapes. Thus, successful management and conservation of solitary bees require knowledge of the most valuable remnant resource patches in typical agricultural areas.

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The aim of this study was to evaluate the potential value of field edges for the conservation of solitary bees in an agricultural matrix. The study was conducted in South Eastern Norway, which has landscapes dominated by a mixture of intensive cereal production and coniferous forests. Since bee species composition has been shown to vary over seasons and months (Cane & Payne 1993; Kearns et al. 1998) and since the monthly variation is connected to bee phenology, temporal patterns should be included in ecological studies of bees (Oertli et al. 2005). However, to my knowledge this is rarely the case, since most studies focus on species richness, abundance or diversity indexes pooled across the entire season (Steffan-Dewenter et al. 2002; Morandin et al. 2007; Carre et al. 2009; Holzschuh et al. 2010; Le Feon et al. 2010; Samnegard et al. 2011) but see Hopwood (2008) and Hannon & Sisk (2009). In this study, I analyzed the contribution of field edges to bee species richness and abundance on both annual and seasonal scales. To account for the seasonal variation in bee phenology, I also investigated how temporally distinct bee assemblages relate to factors inherent to field edges on different spatial scales. To address these issues I tested the four predictions below:

1. The solitary bee communities in field edges are stable between years.

2. Field edges vary in their contribution to species richness throughout the season.

3. The species turnover between field edges is related to their proximity.

4. Bee assemblages are affected by local habitat and landscape characteristics.

2. Methods

2.1 Study area

The study was conducted in and around the municipality of Ås (approx: 59˚66'N, 10˚79'E) in south-eastern Norway. The landscape is dominated by Common wheat (*Triticum aestivum* L.) fields and Norway spruce (*Picea abies* (L.) H. Karst) forests intermixed by small farms and urbanized areas. Semi-natural areas appear in the forms of field edges, road verges, cleared forests and strips of land surrounding lakes. The area typifies a Norwegian intensive agricultural landscape. The field work was carried out during the summers (April-September) of 2010 and 2011. The average monthly precipitation and temperature during these months is 70.1mm and 11.8˚C, respectively (the Norwegian Meteorological Institute: www.met.no).

2.2 Site selection

I defined field edges as the non-cultivated part of the field margin, bordering forests or cleared forests. I selected 11 field edges (sites) in 2010 and added seven in 2011 (Fig. 1). I selected field edges non-randomly to ensure that the inter-site distances were at least 800 meters, which is farther than the typical foraging distances of most solitary bees (Gathmann & Tscharntke 2002; Zurbuchen et al. 2010b). Large bees may forage at distances greater than 800 meters, and sampling within this range may cause re-sampling of the regional species pool. Nevertheless, I chose to ignore this factor since the aim of this study was to evaluate the value of field edges for the local solitary bee fauna. I therefore accepted the possible presence of a low degree of pseudo-replication in order to achieve an ample sample size. Furthermore the non-random selection ensured that both north and south facing field edges were sampled so that the effect of sun exposure could be tested. Study sites consisted of 30 meters of the selected field edges, with varying widths.
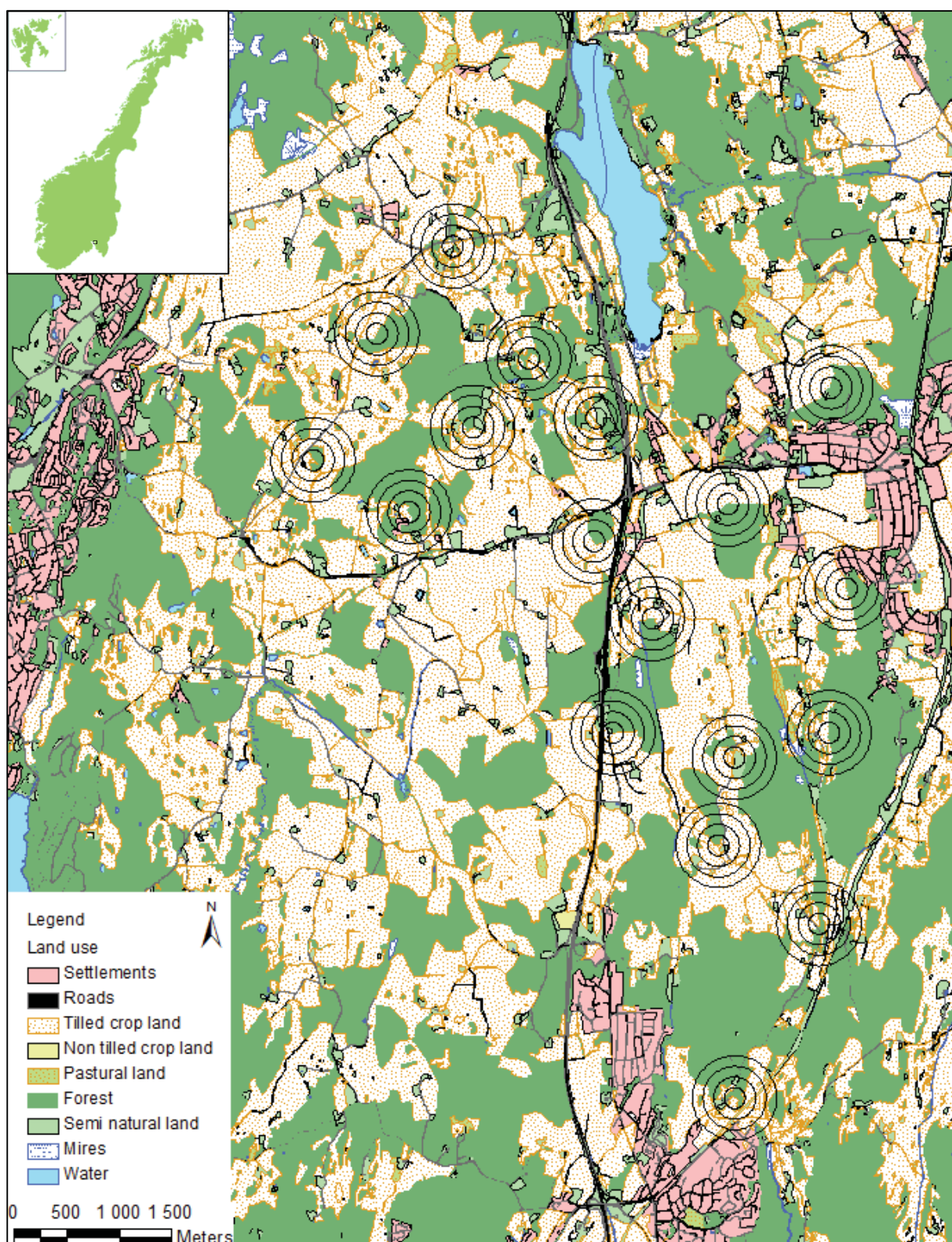
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Figure 1. Digital map (AR5 ^{©Geovekst}) of the study area in Ås, Norway. Selected sites are surrounded by circles with 100, 200, 300 and 400 m radii. Eleven of the sites were sampled in 2010; eighteen were sampled in 2011.

2.3 Bee sampling

I sampled bees with pan traps, which is an efficient way of sampling bee communities with little bias due to collector experience (Westphal et al. 2008). Each set of traps consisted of six plastic soup bowls pairs sprayed with florescent white, yellow or blue paint (Sparvar Leuchfarbe, Spray-color GmbH, Merzenich, Germany). Bowls were filled with 125ml water with a drop of detergent (Zalo Ultra, Lilleborg, Norway) to break the surface tension. Bees are attracted by the colored bowls and drown in the water. Pan traps were placed five meters apart to avoid inter-trap competition (Droege et al. 2010). Since the vegetation was relatively sparse, I placed pan traps on the ground in each field edge. If necessary I cleared the vegetation within one square meter around traps to ensure their visibility to bees, following Calabuig (2000).

Pan traps were deployed four times in 2010 and 2011, from April to September. I deployed and emptied traps between 1700 and 0500 hours to ensure that all traps were active (i.e. received sun-light) in the same time period. All traps were active for at least 48 hours, depending on season and year. Due to variable weather conditions it was challenging to sample on consecutive sunny days with low wind (<5m/s). However, since all traps in all field edges were active during the same period of time they received the same treatment, allowing for direct comparisons between sites (Gotelli & Colwell 2001). See appendix 1 for sampling dates and climate information.

Wild bees include all bees except the domesticated honey bee (*Apis mellifera* L.). I follow the often-encountered definition of solitary bees (Steffan-Dewenter et al. 2002; Le Feon et al. 2010), which excludes the honey bee and all *Bombus* Latreille species but does include facultative social sweat bees (Halictidae). Captured bees were stored in 80% ethanol before

pinning and identification using regional keys (Schmid-Egger & Scheuchl 1997; Amiet et al. 1999; Amiet 2001; Amiet 2004; Amiet 2007; Baldock & Collins 2008). After my own identifications, bees were sent to solitary bee specialists Mike Edwards (UK), Graham Collins (UK), David Baldock (UK) and Jan Stenløkk (NO) for verification. The nomenclature follows Ascher and Pickering (2010).

2.4 Local field edge characteristics

2.4.1 Plant survey

I conducted plant surveys four times during the 2011 growing season (April-August) at the same time as pan traps were active (see appendix 1). The plant surveys were conducted within 6 rectangles measuring 2·1 meters within every field edge. The rectangles were placed 3 meters apart, parallel to the field edge. I estimated the floral abundance as the number of flowers or inflorescences per plant species in each rectangle (see appendix 2 for a full list of plant species and measurements). Since the surveys were conducted while the pan-trans were active, I used monthly plant species richness and monthly floral abundance per square meter as estimates of resource diversity and abundance, respectively. The total floral abundance per square meter and total plant species richness per square meter, pooled throughout the entire season, was used to indicate habitat integrity, assuming that rich plant communities reflected continuity in the environmental conditions in field edges, in a long-term perspective.

2.4.2 Plant heights

I measured plant heights once in July at the peak of the growing season. Measurements were done three times along the lengths of the rectangles by placing a ruler vertically and noting the highest point where a stem or straw of an annual plant met the ruler. To achieve random samples, measurements were taken one meter apart. The average plant height per field edge was used as an estimate for vegetation height in that field edge.

2.4.3 Site area

I defined site area as the distance between the two most distant pan-traps (i.e. 30 meters) multiplied by the average field edge width. Field edges are often characterized by a sharp edge formed through tilling of the neighboring arable land. I measured the distance from this edge perpendicularly through each pan trap sampling point to the first wooded stem and used the six measurements to calculate the average width of each study site.

2.4.4 Sun exposure

I estimated sun-exposure at field edges based on the orientation of the forest edge, if present, bordering the field edge. Values were within the range of zero to 180 degrees. I let zero degrees (North) represent minimum sun-exposure, and 180 degrees (South) represent maximum sun-exposure. A forest edge running from East to West and facing the field edge in a southern direction in this way gave the field edge the value of maximum sun-exposure. Field edges without connected forest edges were also given the maximum value. Forest edges running from North to South thereby gave the field edge intermediate sun-exposure (90 degrees).

2.5 Landscape context

I used a GIS program (ArcGIS10) to create a nested dataset of the landscape context within radii of 100, 200, 300 and 400 meters around each study site (Fig. 1). Landscape features were based on digital maps (AR5[©Geovekst]) with a spatial resolution of 2 m, provided by The Norwegian Forest and Landscape Institute (Bjørdal & Bjørkeklo 2006). Maps were updated using aerial photos from 2008 (Follo 2009) and my own observations to account for the most recent landscape changes. The AR5 maps contain information such as forest type and age. However, I focused on landscape types at the resolution often encountered in landscape

ecological studies of pollinating insects, such as arable land, semi-natural areas, forests, human settlements and linear elements (Steffan-Dewenter et al. 2002; Kleijn & van Langevelde 2006; Holzschuh et al. 2010). I used the ACCRU toolbox (Nielsen 2010) to calculate the percentage cover for all area-based habitat measures. Linear elements such as lengths of roads, field edge length and forest edge length and inter-site distances were calculated with the standard toolbox available in ArcGIS10. I treated forests as a specific landscape type and not as part of semi-natural habitats since the majority of Norwegian bees find their habitats in the non-forested agricultural land (Hansen et al. 2010). I therefore defined semi-natural habitats as ditches, road verges, grassy areas and clear cut forests (see appendix 3 for a full list of landscape parameters, descriptive statistics and abbreviations used in this thesis).

3. Data analysis

3.1 Sampling efficiency

I ran a quadratic and a simple linear regression on the annual relationship between species richness and abundance to assess whether a satisfying gradient in bee species richness and abundance in field edges had been sampled. I could not construct sample-based rare-faction curves for individual field edges due to low sample numbers within sites and because the sample protocol included different colours of pan traps varying in efficiency (Kwaiser & Hendrix 2008). Different colours may over- or under-sample some taxa, and thereby violate the assumption of random occurrences of species within samples (Gotelli & Colwell 2001). Instead, I assumed that adequate sampling was achieved if the number of identified species reached a plateau as the number of individuals sampled within field edges increased.

A total of 127 and 285 individuals of wild bees were captured in 2010 and 2011, respectively. *Bombus* Latr. was the most abundant genus accounting for 41% of the total sample in 2010 and 45% in 2011. These were excluded from all analysis since the aim of this thesis was to study solitary bees. Pan-traps yielded 74 and 157 solitary bee individuals in 2010 and 2011, respectively. In 2011, field edges sampled the previous year had 104 individuals. I identified 34 solitary bee species, 25 of which were caught in 2010 and 29 in 2011. Sixteen species occurred exclusively in one of the two years, and these species consistently had a low abundance (<2 individuals). *Andrena* Fabricius was the most abundant genus of solitary bees in both years, accounting for 51% and 45% of individuals in 2010 and 2011, respectively. Other relatively abundant genuses were *Hylaeus* F., *Lasioglossum* Curtis and *Halictus* Latr.
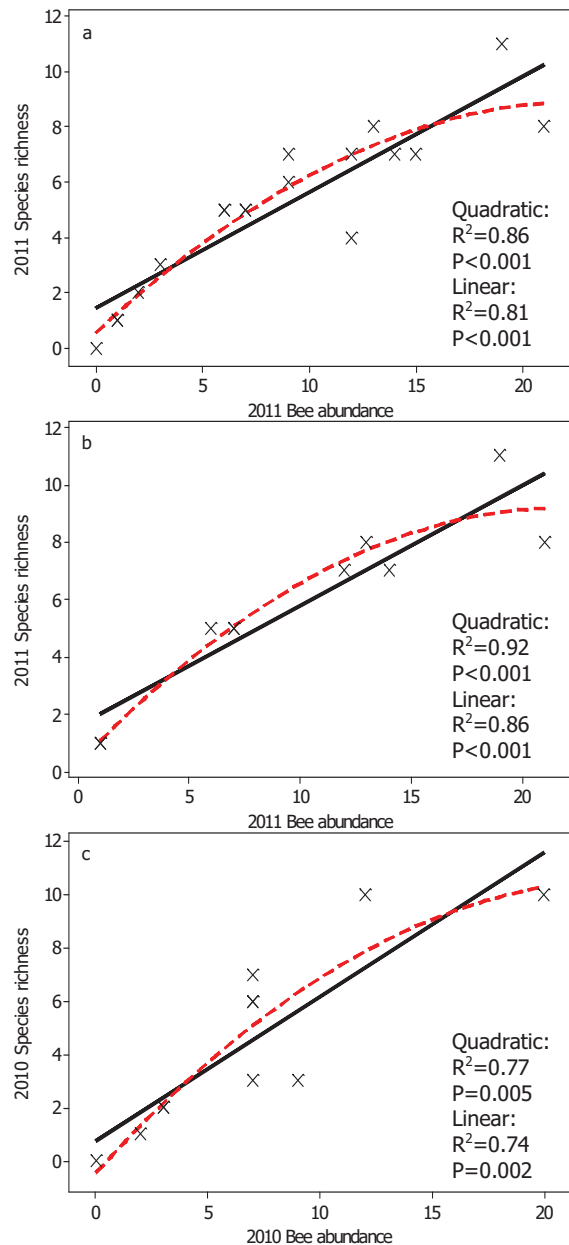
Figure 2a-c. Quadratic and linear regressions on the species richness and abundance in field edges sampled in Ås, Norway, 2011 and 2010. a: All 18 sites from 2011, b: 10 Sites from 2011, sampled also in the previous year, c; sites sampled in 2010. The quadratic predictor was not significant (P=0.265) in c.

In 2011 the species richness tended to level of at 15-20 individuals (Fig. 2a-b) suggesting that a full gradient in field edge quality, in terms of bee species richness and abundance, had been

sampled. Due to lower capture rates, this was not the case in 2010 (Fig. 2c: quadratic predictor P=0.265). See appendix 4 for a full species inventory of the solitary bees.

The capture rates in my study were relatively low compared to other studies on solitary bees where pan traps have also been used. However most of these studies have been conducted in regions with higher bee abundance and diversity, such as Central Europe (Westphal et al. 2008), and they are therefore not directly comparable to my study. One study on semi dry pastures in Sweden reported a total of 73 bee species, including bumble bees and the honey bee (Westphal et al. 2008). However, since landscapes with high proportions of pastural land (>15%) harbor more abundant wild bee communities than areas with less pastoral land (Morandin et al. 2007), and since my study area falls within the latter category, my low capture rates may indicate a low diversity of solitary bees in the Norwegian wheat dominated agricultural landscape.

However, in addition to possibly underestimating the species pool by relying solely on pan traps (Richards et al. 2011) and not including other complementary methods (Westphal et al. 2008), I sampled from field edges with a range of contrasting environmental conditions. My sample protocol may therefore also have added to an underestimation of the local species pool since pan traps in field edges little suited to bees would decrease the capture rate. Despite these potential drawbacks my capture rates were comparable to those by Samnegard et al. (2011) from an agriculturally dominated landscape in southern Sweden, suggesting that field edges in my study were adequately sampled.

3.2 Species turnover

I defined species turnover as dissimilarity between field edges. The dissimilarities in community composition were measured in two ways based on samples from 2011. I ran a

Principal Coordinates Analysis (PCoA) with Bray-Curtis distances using the PrCoord program available from CANOCO 4.5 (ter Braak & Smilauer 2002). In one of the field edges the pan traps captured no bees. This field edge had to be removed from the analysis since it provided no information in the weighted algorithms. All species occurring in less than two samples were also removed from the analysis, resulting in 14 species. I did not log-transform the data or use correction for negative eigenvalues. The first four axes had relatively similar Eigenvalues (λ_1=0.171, λ_2=0.155, λ_3=0.142, λ_4=0.122). I therefore based my estimate of site dissimilarities on the average of distances measured between every two sites on the first four axes. Since this method is based on both the presence and abundance of species within sites it may mask dissimilarities caused by rare species (Leps & Smilauer 2003). I therefore also used the online calculator program by Brzustowski (2002) to calculate a Jaccard dissimilarity index, which is based on the presence or absence of species among sites (Cha 2007). For both methods I applied simple linear and quadratic regressions to fit the species turnover against physical distance. I split the data into smaller components along the physical distance axis to examine the R^2-values and correlation coefficients values at spatial scales ranging up to 3000 m to account for the maximum foraging range of solitary bees (Zurbuchen et al. 2010b).

3.3 Annual variation

I compared species richness and abundances in 2010 and 2011, with simple linear regressions. I did not standardize for unequal sampling since all sites had received the same treatment within a year. Forest bordering one field edge in 2010 had been cleared during winter 2011. Since this clearing increased the sun exposure I excluded this site from the between year comparisons. 10 field edges were included in the analysis.

3.4 Monthly variation

To determine whether the bee community was composed of temporally distinct species groups, I ran an ordination analysis in a two-step process. I only included data from 2011 to avoid pseudo-replication, which could follow from sampling different generations the same population twice. In the first step, I ran a detrended correspondence analysis (DCA) on all species captured in 2011 with trapping periods (April, May, June, August) as samples. This method removes some of the unimodality in the ordination which is created as a statistical artefact while running the mathematical algorithms (Leps & Smilauer 2003). The DCA thereby forces the information onto the primary axes. The length of the primary gradient can thereby be used to infer whether the species data reflect a bell shaped response to the environment or if only either side of the unimodal response is reflected in the data. A primary gradient shorter than 3 SD is generally assumed to indicate a linear response of the species. Since the length of the primary gradient was >3 SD, I assumed the data to fit a unimodal response model (Leps & Smilauer 2003).

In the second step I re-ran the data through a correspondence analysis (CA) centring on species and down-weighing rare species and otherwise using the default settings in Canoco 4.5. To further investigate if field edges varied in their richness and abundance of solitary bee species during the season I ran a single-factor experiment with repeated measures on all treatments, using a Generalized Linear Model (GLM) on monthly species richness and abundance as responses, sampling period as a fixed effect and field edge as random effect.

3.5 Effects of habitat and landscape characteristics on solitary bees

I conducted an initial screening for multi-colinearity by applying a Pearson's correlation matrix on all landscape variables (appendix 5). I selected 3 landscape variables to be

included in the analysis: percentage semi-natural habitats, percentage arable land and total length of forest within each of the four radii. I selected arable land since it was the most dominant landscape type, semi-natural areas because they have been shown to be of importance to bees, and total forest edge length since I assumed that increasing the area of forest edges than of field edges would entail fewer conflicts between local authorities and land owners under a management regimen aimed at improving bee habitat quality.

All selected variables were tested for deviations from normality using the Anderson-Darling test against $P<0.05$, employing Minitab 16. All percentage based variables were square root-transformed to achieve normality. Site area and forest edge lengths were log10 transformed. Since I was unable to achieve normal distribution for forest edge length and percentage semi-natural habitats at 100m radius, these variables were omitted from all analyses at this spatial scale. Due to the nested nature of the landscape measurements there was a high degree of correlation between the landscape variables at the different spatial scales (appendix 5). I did not correct for this since the aim of the analysis was to find the environmental characteristics that consistently explained the species distributions at different scales.

I ran a stepwise regression analysis with forward-backwards selection, setting alpha-values at 0.1 to enter and remove, to find the environmental variables that most consistently (i.e. at more than one spatial scale) explained the pooled and monthly species richness and abundance of solitary bees. I classified the environmental variables into two groups according to their spatial scale. The first group consisted of variables that were measured within individual field margins, defined as local variables, whereas the second group consisted of landscape variables. I ran the step-wise regression analysis hierarchically by first screening for local variables. The selected local variables were included in the four subsequent analyses on the landscape context at respective spatial scales. I evaluated the

results following the approach of Kleijn & van Langevelde (2006) by assessing variables based on the models R^2 and p-value and the p-value of the variables selected through the stepwise analysis. I did not use Bonferroni adjustment for P-values since this may inflate the chance of type-II errors (Moran 2003). I applied a Pearson's correlation matrix to isolate any strong correlations between the environmental variables which might help interpreting the results (Appendix 6). I detected no multi-colinearity between the variables included in the selected models (i.e. no Variation Inflation Factors were above 5).

Following the regression-analysis, I ran an ordination analysis to further analyse if the temporal activity pattern of solitary bee species would separate them along environmental gradients. I included all local habitat and previously selected landscape variables at the 400 m radius as explanatory variables. I added four indicator plants to the explanatory variables, since ordination of bee species might provide a finer resolution than regression analysis on species richness or abundance. Indicator plants were selected by running a DCA on all plant species present in more than 50% of the studied field edges (λ_1=0.713, λ_2=0.291, λ_3=0.166, λ_4=0.03). I then selected four plants accounting for most of the variation along the two primary axes: *Melampyrum pratense* L. scored 3.43 on the first axis while *Galeopsis bifida* Boenn. scored -0.67. *Hypericum maculatum* Crantz scored 3.23 on the second axis, whereas *Ranunculus acris* L. scored -0.31.

To ascertain whether the solitary bee data would fit a linear or unimodal response model I ran a DCA on the raw abundance of solitary bee species. I did not use any post-transformation other than down-weighing rare species. The species ordination showed a unimodal response since the length of the first axis was >3 SD. I therefore ran a CCA with bi-plot scaling. I used $\log_{10}(1+y)$-transformation to standardize species abundances and also down-weighed rare species. I selected variables blindly using a step-wise forward selection with 499 Monte

Carlo Permutations, including only variables with P<0.1. No multi co-linearity between selected variables was detected (VIF<5). Since raw data may mask the response of less abundant species, I re-ran the analysis using present-absence data.

4. Results

4.1 Species turnover

The species turnover of solitary bees between field edges increased with the physical distance between them (Fig. 3). Linear regression with quadratic predictors did not fit the data (P>0.1). Instead the species turnover increased linearly with physical distance up to about 1500 m (R^2=0.23, P=0.023 and R^2=0.34, P=0.004 for Bray-curtis and Jaccard indexes, respectively) after which it fluctuated and the explanatory power of distance *per se* decreased but remained significant (P<0.05) up to 1800 m, for Bray-Curtis (R^2=0.20, P=0.018) and up to 1900 m for the Jaccard index (R^2=0.14, P=0.029).
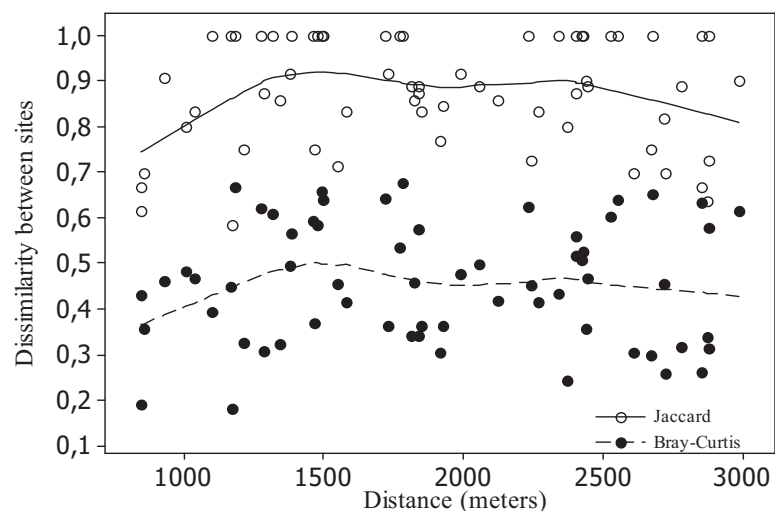
Figure 3. Bray-Curtis and Jaccard dissimilarity indexes on solitary bees, from Ås, Norway in 2011, against physical distance between sites. Linear regression on Bray-Curtis scores vs. physical distance is significant at distances ranging from 1500 to 1800 meters (P<0.05). Linear regression on Jaccard scores vs. physical distance is significant at all distances except at 1200 and 3000 meters (P>0.05). Lowess smoother with 2 steps and 0.5 degrees of smoothing.

Linear regressions on Bray Curtis dissimilarities vs. physical distance yielded four significant regression coefficients whereas Jaccard dissimilarities vs. physical distance between sites yielded six. The six regression coefficients showed a linear decrease in relation to increased

physical distance (R^2=0.83, P=0.011), suggesting that the species turnover between sites levels of with increased distance between them (Fig. 4).

4.2 Annual variation

Bee species richness in 2011 was related to the abundance of bees in 2010 (Fig. 5a: R^2=0.46, P=0.03) and close to significantly related to the

Figure 4. Rate of solitary bee species turnover between sites in Ås, Norway in 2011 with increased inter-site distance. Regression coefficients were extracted from linear regression on Jaccard-index in vs. physical distance (Fig. 3).

species richness in 2010 (Fig. 5b: R^2=0.31, P=0.094). The bee abundance in 2011 was not explained by the abundance of bees in the same site in 2010 (Fig. 5c: R^2=0.19, P=0.204). The lack of explanatory power was due to a large variation between years at one site. In 2010 pan traps at this site yielded only 2 individuals of the solitary bee *Andrena haemorrhoa* F., whereas the pan traps yielded eight species in 2011 including six individuals of *A. haemorrhoa* F. If this site was removed from the analysis (n=9) the bee abundance in 2011, was related to the abundance of bees in 2010 (Fig. 5c: R^2=0.64, P=0.01).

Figure 5a-c. The stability of bee assemblages in field edges across two years in Ås, Norway. Regressions excluding outlier (marked in red); (a) R^2=0.7, P=0.005, (b) R^2=0.52, P=0.027, (c) R^2=0.64, P=0.010.

4.3 Monthly variation

The species composition of the solitary bee community changes through the season (Fig. 6). The first axis of the correspondence analysis (CA) accounted for 76% of the variation in the data and separated the spring-active (April) and summer-active species (May-August). The second axis accounted for 37.7% of the variation and partitioned the summer-active species into three groups. One group consisted of species active throughout the remaining summer (whole summer), and another consisting of species mainly active in early summer (June). The May and August groups were largely composed of singletons and did not show clear patterns.
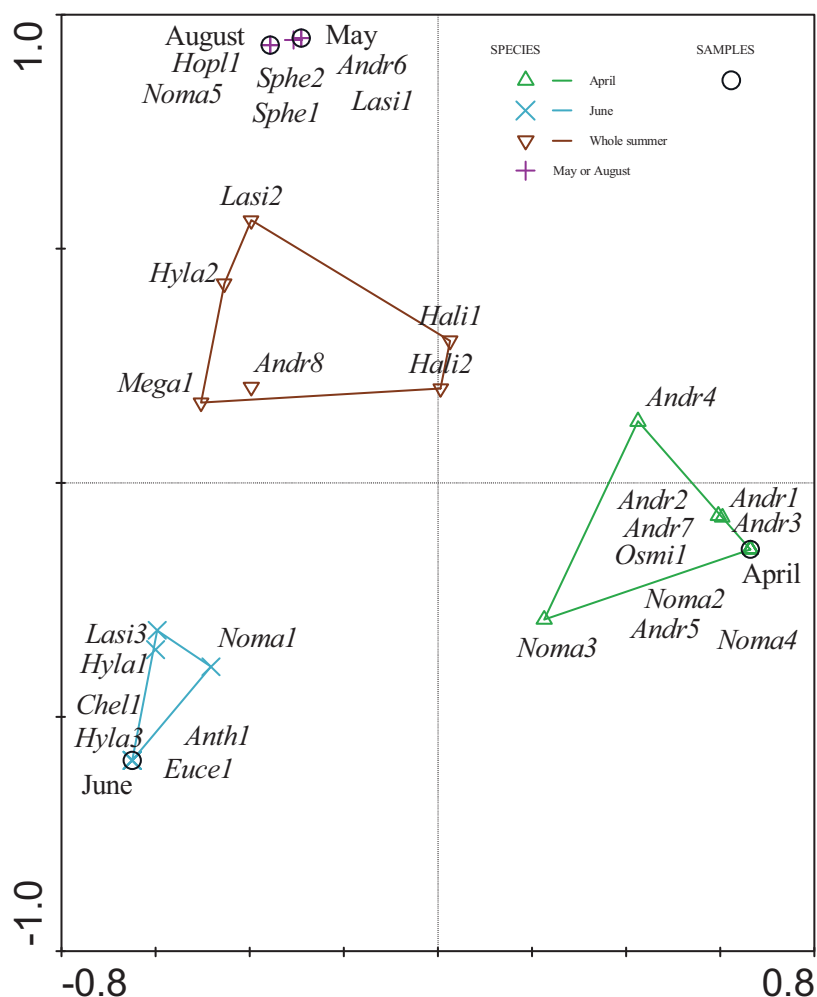
Figure 6. Correspondance Analysis axes 1 & 2. The seasonal affiliations of solitary bees in 2011 from Ås, Norway. Species are enveloped according to temporal distribution. Eigenvalues: λ_1=0.761, λ_2=0.377, λ_3=0.268, λ_4=0.000. Note that some species names were moved due to overlapping. See appendix 4 for abbreviations.

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The solitary bee species richness in field edges was close to significantly different between months (Fig. 7a: P=0.052). Although no month had significantly more species than the others, there was a tendency for more species in April and in June than in May and August. Average bee abundance did however vary among months (ANOVA: P=0.015). Pan traps caught more bees in April than May and August, but not June, when pan trap yields did not differ from any other month (Fig. 7b).
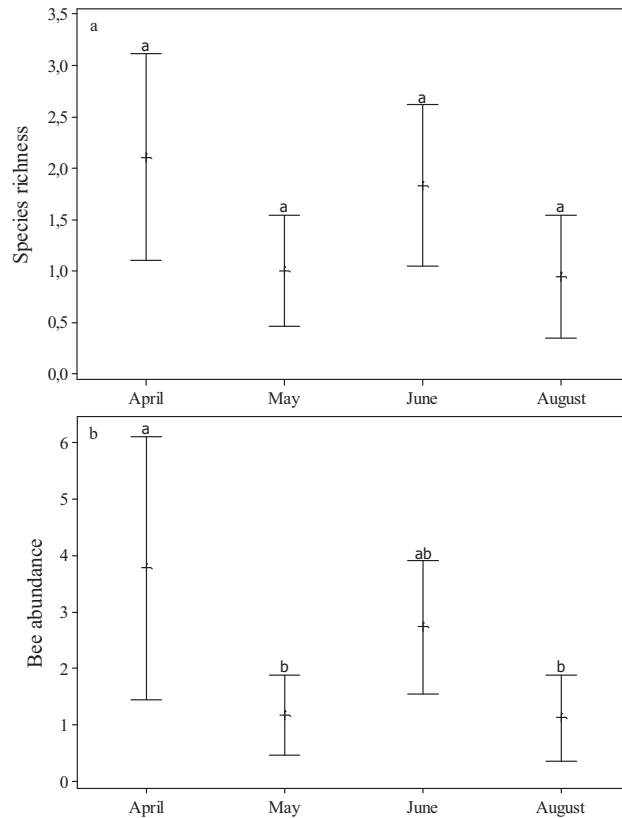
Figure 7a-b. The average monthly solitary bee species richness and abundance in field edges in Ås, Norway in 2011. Vertical bars are 95% CI. a: One-way ANOVA on species richness vs. months (P=0.052), b: Bee abundance vs. months (P=0.015) monthly abundances with different letters are significantly different (Tukeys test).

The contribution of individual field edges to the overall species richness varied throughout the summer (GLM: R^2=0.47, Site; P=0.022, Month; P=0.024). Especially two field edges (1 and 12) mainly hosted species-rich spring communities, largely composed of *Andrena* F. sp. and their cuckoo bees from the genus *Nomada* Scopoli. One field edge (8) mainly hosted June active species. Field edges 17 and 18 were the most balanced and hosted species from all the sample periods. The remaining sites did not show any clear patterns (Fig. 8).
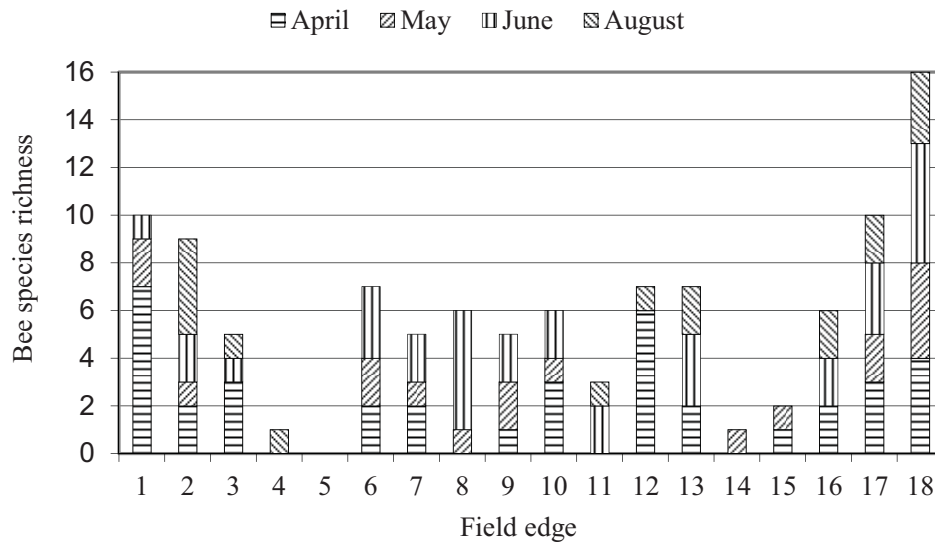
Figure 8. Monthly species richness in field edges in Ås, Norway in 2011. Note that the same species may occur in >1 month. General Linear Model (GLM) on monthly species richness vs. month (fixed effect) and site (random effect): $R^2=0.47$, site; P=0.022, month; P=0.0024.

4.4 Effects of habitat and landscape characteristics on solitary bees

Species richness of solitary bees was related to both local habitat characteristics and the landscape context (Table 1). The pooled species richness from the entire season was best explained by sun exposure ($R^2=0.43$, P=0.003). In April, species richness showed a consistent negative response to the area of arable land. This relationship was strongest at a 200 m radius ($R^2=0.39$, P=0.006). At a local scale, the monthly plant species richness explained 25.5% of the variation in April bee species richness (P=0.032). When the marginally significant (P=0.062) negative relationship with the seasonal plant species richness was added, the local habitat explained 41% of the variation. The variation in both May and June species richness was best explained by local habitat characteristics. In May, 38% of the variation in species richness (P-model=0.028) was explained by a positive significant relationship with the pooled plant species richness (P=0.018) and a marginally significant relationship to sun exposure (P=0.057). The June species richness was best explained by floral resource abundance (P=0.049), sun exposure (P=0.003) and area of arable

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land at 200 m radius (P=0.030), together accounting for 61.5% of the variation (P-model=0.003). However, when testing at other spatial scales only the local predictors were significant. The most consistent model for June species richness consisted of seasonal floral abundance (P=0.075) and sun exposure (P=0.017), which together explained 45% of the variation in bee species richness (P-model=0.011). Variation in August species richness could not be explained by any variable at any spatial scale.

Total bee abundance was negatively related to the area of arable land within a 100 m radius (R^2=0.37, P=0.007). At other spatial scales the landscape context had no explanatory power whereas sun exposure did (R^2=0.27, P=0.027). The abundance of bees in April showed a consistently negative relationship to the area of arable land (R^2=0.39, P=0.005 at 200 m). No predictors significantly explained variation in May abundance. The abundance of bees in June was positively related to plant species richness in June (P=0.001), negatively related to plant height (P=0.014), positively related to sun exposure (P<0.001) and arable land at 200 m (P=0.019). Together, these variables accounted for 82% of the variation in June bee abundance (P<0.001). June bee abundance was positively related to the area of semi-natural habitat at 300 m (P=0.085) and 400 m (P=0.044) radii. However, only local habitat characteristics remained in the model at all spatial scales and explained 73% of the variation in the abundance of bees in June (P-model<0.001). There was no significant predictors for bee abundance in August, presumably due to the low capture rates this month, despite increased sampling effort (see appendix 1 for sampling dates).

Table 1. Regression coefficients from stepwise regression on species richness and abundance of solitary bees (responses) and environmental variables (predictors). Based on data from 2011. The analysis was run on species counts pooled throughout the season (Tot. Sp. and Tot Ab.), and counts from individual sampling periods (April, May, June and August). Sp. is species richness, Ab. is abundance and Co. is cover. Plant species richness was assessed within sampling periods (Plant Sp. (Month)) and pooled throughout the entire season (Plant Sp. (pooled)), as were floral abundance per m^2 (Plant Co. (Month) and Plant Co. (pooled)).

Predictors		Bee species richness					Bee abundance				
Spatial scale		Tot. Sp.	Apr Sp.	May Sp.	Jun Sp.	Aug Sp.	Tot. Ab.	Apr Ab.	May Ab.	Jun Ab.	Aug Ab.
Local	Plant Sp. (month)		2.81***							0.65***	
	Plant Co.(month)				0.046(*)						
	Plant Sp. (pooled)		-0.176(*)	0.128**							
	Plant Co.(pooled)							0.07(*)			
	Plant He.									-0.055*	
	Sun Ex.	0.0338***		0.0083(*)	0.0145**		0.057*			0.0258***	
	R^2	0,4343	0,4144	0,379	0,4534	NS	0,2709	0,18	NS	0,7325	NS
	P-model	0,003	0,018	0,028	0,011	NS	0,027	0,074	NS	0	NS
100 m	Plant Sp. (month)									0.65***	
	Plant Co.(month)				0.046(*)						
	Plant Sp. (pooled)			0.128**							
	Plant He.									-0.055*	
	Sun Ex.	0.0338***		0.0083(*)	0.0145**					0.0258***	
	Arbl La.		-1.72**				-6***	-3.7*			
	R^2	0,4343	0,2895	0,379	0,4534	NS	0,37	0,244	NS	0,73	NS
	P-model	0,003	0,021	0,028	0,011	NS	0,007	0,037	NS	0,00	NS
200 m	Plant Sp. (month)									0.59***	
	Plant Co.(month)				0.045*						
	Plant Sp. (pooled)			0.128**							
	Plant He.									-0.055**	
	Sun Ex.	0.0338***		0.0083(*)	0.0176***		0.057*			0.0294***	
	Arbl La.		-1.2***		0.63*			-2.80***		0.73**	
	R^2	0,4343	0,3868	0,379	0,615	NS	0,2709	0,3928	NS	0,827	
	P-model	0,003	0,006	0,028	0,003	NS	0,027	0,005	NS	0	
300 m	Plant Sp. (month)									0.64***	
	Plant Co.(month)				0.046(*)						
	Plant Sp. (pooled)			0.128**							
	Plant He.									-0.047(*)	
	Sun Ex.	0.0338***		0.0083(*)	0.0145**		0.057*			0.0203***	
	Semi Nt.									0.71(*)	
	Arbl La.		-1.06**					-2.58***			
	R^2	0,4343	0,3325	0,379	0,4534	NS	0,2709	0,3653	NS	0,789	NS
	P-model	0,003	0,012	0,028	0,011	NS	0,027	0,008	NS	0	NS
400 m	Plant Sp. (month)									0.71***	
	Plant Co.(month)				0.046(*)						
	Plant Sp. (pooled)			0.128**							
	Plant Co.(pooled)							0.065*			
	Plant He.									-0.042(*)	
	Sun Ex.	0.0338***		0.0083(*)	0.0145**		0.057*			0.0207***	
	Semi Nt.							-3.2**		1.01*	
	Arbl La.		-0.95**					-1.43(*)			
	R^2	0,4343	0,2799	0,379	0,4534	NS	0,2709	0,5966	NS	0,8063	NS
	P-model	0,003	0,025	0,028	0,011	NS	0,027	0,006	NS	0	NS

NS = Not Significant, (*)= p< 0.1, *= p<0.05. **= p<0.025. ***p<0.01

A CCA on the abundance of individual bee species (Fig. 9) showed similar results as those obtained from the stepwise regression analysis (table 1). The area of arable land within a 400 m radius best explained the distribution of solitary bees. Arable land explained 37% of the variation (P=0.02), spring and summer active species showed contrasting responses. The assemblages of spring-emerging species, such as *Andrena* F. sp*.,* were
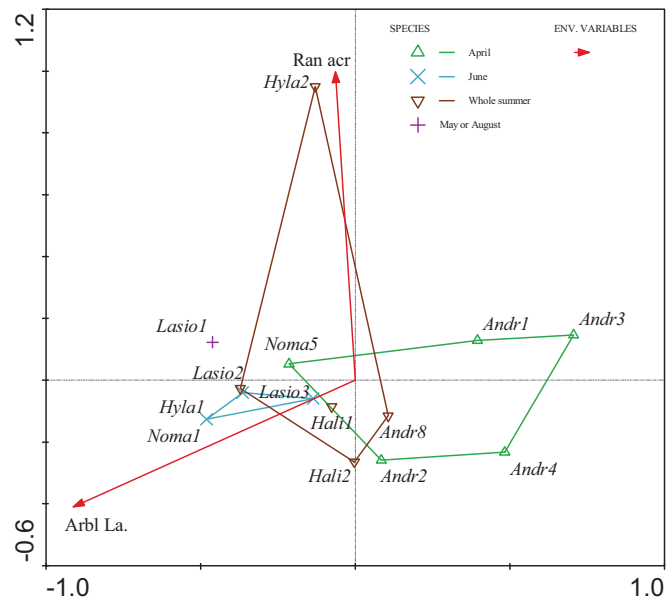
Figure 9. Canonical correspondence analysis on raw abundance of solitary bee species in Ås, 2011. Showing only species with >3 non-zero values. Arable land within 400m; 37% of the variation P=0.02. *Ranunculus acris*; 34% of the variance P=0.06. 71% of the variation was explained by the selected variables.

negatively related to arable land. Summer-active species (all groups excluding April), such as *Hylaeus* F. sp. and *Lasioglossum* C. sp., had a weak positive relationships to the area of agricultural land. The abundance of *Ranunculus acris* L. accounted for 34% of the variation (P=0.06). The majority of the species showed no clear relationships to the second axis. Of the species occurring in three field edges or more, only *Hylaeus communis* Nylander showed a strong positive relationship to *Ranunculus acris* L. However, this species only had three individuals making it hard to differ between the statistical and ecological patterns underlying its occurrence. A CCA on the presence/absence data of solitary bees (not shown) yielded similar results (arable land: 31% of the variation, P=0.07; *Ranunculus acris* L.: 41% of the variation, P=0.01; Sum of all canonical eigenvalues = 0.718), except from arable land and August plant species explaining equal amounts of variation. These variables showed a close to significant inter-correlation at 200 m and 300 m radii (Appendix 6).

5. Discussion

I found that Solitary bees were not randomly distributed across field edges in 2011, but showed an aggregative pattern. This local distribution seemed to extend over the two years that sampling was conducted. Solitary bees could be grouped according to seasonal activity patterns and the contribution of field edges to regional species richness varied during the season. The seasonally distinct groups showed specific responses to the environment.

5.1 Species turnover

The species turnover among field edges was related to their proximity to each other. Bees are able to migrate between habitat patches in the agricultural matrix (Diekotter et al. 2008), which is often necessitated by the partial nature of their habitats (Westrich 1996). The distances bees cover is related to their body size (Greenleaf et al. 2007; Guedot et al. 2009), which corresponds to the findings that smaller bees are generally more strongly negatively influenced by habitat isolation than larger bees (Bommarco et al. 2010; Williams et al. 2010). Foraging imposes a cost on bees in terms of offspring production (Zurbuchen et al. 2010a). and an increased amount of non-cropped area within 500 m radii of nest sites is related to increased fecundity of trap-nesting bees (Holzschuh et al. 2010). However, bees seem to avoid the cost of foraging by establishing nests where food plant availability is within the lower range of their foraging distance (Gathmann & Tscharntke 2002) and may be rather sedentary (Franzen et al. 2009).

These traits could lead to an aggregated distribution of bee species across the landscape, even for non-social species. This may explain why bee assemblages in field margins were not spatially independent (Fig. 3). Although the relationship was rather weak the dissimilarity in

bee assemblages between field edges increased with distance up to 1800 m for Bray-Curtis and 1900 m for the Jaccard index, which is greater than most foraging ranges (Zurbuchen et al. 2010b). The rate of species turnover declined with distance (Fig. 4), indicating that as distances increase, even within the foraging range, fewer new species are added. Such a pattern may illustrate a non-random distribution of foraging and/or nesting resources in the landscape. This implies that targeting networks of field edges for restoration within the foraging range of solitary bees may maximize field edge value in terms of both adding new species and stabilizing populations of mobile species.

5.2 Annual variation

Bee assemblages fluctuate substantially between years. Cane and Payne (1993) reported a threefold change in the annual maximum abundance of bees visiting *Vaccinium ashei* Reade flowers in South Eastern USA over a period of six years. Moreover, species composition varied up to 25% over two years in species rich habitats in Switzerland (Oertli et al. 2005). In my study 16 of 34 species occurred in only one of the two years (Appendix 4). These were typically uncommon species and their presence or absence may be more of a statistical artefact than a reflection of their affiliation to the field edge in which they were captured. It may well be that the higher capture rate in 2011 compared to 2010 (Fig. 2b-c) was due to more favourable weather conditions in 2011 (Appendix 1). It is however likely that the drivers of variation in bee assemblages between years are highly complex and include climate, changes in resource availability, mortality and human land use (Oertli et al. 2005). The variation between years may also indicate insufficient sampling intensity, supporting the notion that pan traps need to be supplemented with other techniques (Westphal et al. 2008), and may illustrate how a low density of species in the landscape increase the random occurrences of species in samples (Gotelli & Colwell 2001). These factors, together with the

low sample size for between year comparisons (n=10), may explain the weak relationships between bee species richness and abundances across years. However, removing one outlier from the analysis (n=9) made all relationships between richness and abundance significant (P<0.05), suggesting that field edges with high species richness and abundance tend to remain so across years (Fig. 5a-c). The outlier may be a result of a true variation caused by the factors described above, but may also be a result of differences in sample dates between years, especially during the spring samples. Since the spring sample in 2010 was later than in 2011 (Appendix 1) it may have missed the peak activity period of this community. My results support the findings of Oertli et al. (2005) that sampling of solitary bee assemblages must be conducted over at least two years to achieve clear results.

5.3 Monthly variation

Field edges in Ås varied in species composition throughout the season, as also found by others (Oertli et al. 2005; Richards et al. 2011). The ordination of species according to month separated the spring-emerging species from those emerging later in the season (Fig. 6). Spring-emerging solitary bees mainly consisted of the below-ground-nesting *Andrena* F. species that overwinter as adults. Although summer-emerging species did not show clearly distinct groups (Fig. 6) they could still be separated into June, and whole-summer-active groups. The two groups were dominated by small-bodied species (<9mm) from the genuses *Lasioglossum* C.*, Halictus* Latr.*, Hylaeus* F. and *Andrena* F.*,* with a variety of life histories, including sociality and solitary, above- and below-ground nesters and oligolectic and polylectic species.

My results agree with Oertli et al. (2005) and Richards et al. (2011) who partitioned bee assemblages throughout the season into three clusters (Spring, Mid-summer, late-summer).

Oertli et al. (2005) found that the clusters were related to the life-history of bees in terms of nest-site locations and that habitat requirements vary among species during the summer. This may partly explain why field edges vary in their contribution to the regional species richness through the season (Fig. 8), and suggests that resource requirements of different bee species with contrasting phenologies are fulfilled in different field edges. Moreover Russel et al. (2005) found that cavity nesting bees were more species rich in power-line sites with abundant nesting resources; similarly, ground nesting bees were more abundant in grass lands. However, although the average bee species richness in my study did not differ across months (Fig. 7a) allowing for comparisons between months, it was consistently relatively low. It is therefore also possible that the observed seasonal variation in species richness in individual field edges was partly a statistical artefact.

5.4 Effects of habitat and landscape characteristics on solitary bees

Solitary bees respond to environmental characteristics at both local and landscape levels (Table 1). A general pattern is that bee species richness and abundance increase with floral richness and abundance (Potts et al. 2006; Franzen & Nilsson 2008; Sjödin et al. 2008), which may reflect resource diversity and abundance. The availability of floral resources (i.e. pollen from the host plan *Knautia arvensis* (L.) Coult) explained 30% of the variation in population sizes of the oligolectic bee *Andrena hattorfiana* F. (Larsson & Franzen 2007). However, in the polylectic *Osmia rufa* L. an experimentally increased nest site availability increased population sizes (Steffan-Dewenter & Schiele 2008), emphasizing the importance of autecological considerations when studying the response of species to anthropogenic habitat changes.

The response to local habitat qualities can be extrapolated to a landscape scale, assuming that semi-natural landscapes harbour more suitable habitats for solitary bees than agricultural lands. Several studies have shown that both the richness and abundance of bee species is positively related to the proportion of semi-natural area in the landscape (Steffan-Dewenter et al. 2002; Morandin & Winston 2006; Franzen & Nilsson 2008; Le Feon et al. 2010). In contrast Winfree et al. (2007) found that bee species richness and abundance increased with increasing amount of cultivated lands in a landscape dominated by forested areas. However, they found that areas with extensive forest cover had more extinction prone wood nesting bee species than agricultural areas. Their findings suggest that the response of solitary bees to landscape changes depends on both the dominating habitat in the surrounding landscape and the phenology of the examined species.

I found no consistent (i.e. occurring at >1 of the four spatial scales) effect of landscape context when examining the pooled bee species richness and abundance. The area of arable land was only significant at a 100 m radius (Table 1), making it difficult to infer whether this was a statistical artefact rather than an ecological effect. This may be because the study area was relatively heterogeneous compared to those studied in Central Europe (Steffan-Dewenter et al. 2002; Carre et al. 2009). In my study area, the landscape surrounding field edges measured at a 400 m radius on average consisted of 54.5% (range: 22.4-79.2%) arable land, 33.8% (range: 15.6-67.8%) forested land and 7% (range: 1.6-17.3%) semi-natural land (Appendix 3). Compared to an average of approximately 74.6% (range: 50.8-98.3%) arable land, 9.6% (range: 0-29.3%) forests and 12% (range: 0-36.6%) semi-natural habitats within a 750 m radius of study sites in Steffan-Dewenter et al. (2002). In addition, general patterns may have been outweighed by the contrasting responses of individual species to the landscape context (Fig. 9), due to the relatively low capture rates in my study. I found a

positive relationship between bee assemblages and sun exposure (Table 1). Bees are poikilothermic and often prefer sun exposed areas for nest sites (Westrich 1996; Everaars et al. 2011). Sun exposure may positively affect bees through increasing body temperature and easing navigation. Certainly solitary bees tend to stay within nests or seek cover in cloudy weather (personal observation). In addition, by causing an increase in temperature, sun-exposure may shorten diapause in overwintering adults (Wasielewski et al. 2011).

The spring and summer bee communities showed contrasting responses to the landscape context (Fig. 9). The spring community had a decreased number of species and individuals with the area of arable lands (table 1). This relationship was strongest at a 100 m radius and accounted for most of the variation at a 200 m radius, supporting the findings of Steffan-Dewenter et al. (2002) that solitary bees respond to changes in the landscape at a local level. The spring community was dominated by the genus *Andrena* F. whose members are endogeic. Williams et al. (2010) found that endogeic bees are more adversely affect by tillage (i.e. arable land in my study system) than hypergeic bees, arguably because tillage may destroy nest sites and kill overwintering adults. However, since spring emerging bees utilize spring flowering trees as pollen and nectar resources (Richards et al. 2011), and since the proportion of forests and agricultural lands was negatively related (Appendix 4) it is also possible that the negative relationship between the spring community assemblage and agricultural land reflects a positive association of spring emerging bees with the proportion of forest in the landscape. This could be due to the affiliation of many spring emerging bees to *Salix caprea* in particular, which is common in this landscape (personal observation).

The summer community did not seem to be adversely affected by the amount of agricultural land (Table 1). Instead, an increasing proportion of arable land might even have a positive effect on at least some species (Fig. 9). The summer community consisted of species with a

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variety of nesting strategies (Fig. 6). Species of the potentially social genusses *Lasioglossum* C. and *Halictus* Latr. are endogeic, which could make them negatively influenced by tilling (Williams et al. 2010), but the presence of the abundant *Hyleaus* F. and other hypergeic species may have masked this response. In addition, even the ground nesting summer species showed a weak positive response to arable land in the CCA (Fig. 9) supporting the findings of Williams et al. (2010) that social bees (excluding the honey bee) may in fact be positively affected by tilled areas in the landscape. These findings suggest that nesting strategy may not be the underlying factor for the summer communities. Floral resources become abundant during summer and bees may collect pollen and nectar from herbs instead of trees which could make them less affected by low forest cover (i.e. high cover of arable land).

The May and June species-assemblages showed similar responses to the environment. Both groups showed more consistent responses to local factors than to the landscape context (Table 1). The species richness of both groups increased with sun exposure and factors connected to floral richness or diversity within the field edge, suggesting that the summer community may be limited by the amount of forage within field edges. Müller et al. (2006) estimated the number of flowers required for the production of a complete brood in several solitary bee species, and argued that declines in floral abundances may partly explain the reported declines in bee populations. This concern is supported by the parallel decline in bee and plant species richness in Britain and the Netherlands (Biesmeijer et al. 2006) and the findings of Hopwood (2008) that restored road verges with diverse plant communities supported more species of wild bees than non-restored.

The abundance of bees in the June assemblage also increased with sun exposure and floral richness, whereas bee abundance had a negative relationship to plant height (Table 1). Plant height may increase shade, making bare patches of ground less suitable for ground nesting

bees, such as the *Halictinae* (Westrich 1996). These results contradict Sjödin et al. (2008) who found no effect of plant height on bee abundance. However, their study was conducted on pastures where plant height ranged between 3-25 cm, whereas the range in my system was 16-72 cm. The results are therefore not directly comparable and instead they may suggest that if vegetation height within partial habitats reaches above a threshold it may have negative effects on solitary bee abundance.

6. Implications for local bee conservation

Previous studies have found that solitary bee assemblages are affected by habitat availability in the surrounding landscape (Steffan-Dewenter et al. 2002), local habitat characteristics (Hopwood 2008) or interacting effects between the two (Kleijn & van Langevelde 2006). Other studies have found that life history traits explain the susceptibility of solitary bees to environmental change (Williams et al. 2010), and that the diversity of such traits in the community may vary during the season due to the temporal activity pattern of bees (Oertli et al. 2005). The solitary bee assemblages in my study displayed seasonally dependent responses to environmental factors. These results suggest that ecological studies on solitary bee communities should aim to isolate clusters of species based on seasonal activity before analysing responses to environmental factors. In addition, my results show that successful conservation of solitary bee habitats requires a temporal perspective.

Field edges seem to be of high importance to solitary bees in the agricultural landscape as shown in my study and by others. The bee species showed an aggregative pattern, and successful habitat conservation should target clusters of proximate field edges to ensure viable populations within clusters. The distance between clusters should be at least 1500 m to maximize species turnover between them. There was a large annual species turnover, but the

species richness within field edges seems to remain stable between years, suggesting that field edges may provide a persistent value for bee conservation. Selection of field edges within clusters should be based on the temporal activity patterns of solitary bees. Field edges should be surrounded by non-arable land to increase their value to the spring community. In addition they should be sun exposed and have a diverse flora throughout the summer.

However, due to the low capture rates in my study the results presented in this thesis should be regarded as preliminary. More research is needed to disentangle the complexity of the seasonally restricted responses of solitary bees to environmental conditions. Understanding these responses will aid the understanding of the temporal dynamics of solitary bee habitats which is required for successful conservation strategies.

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8. Appendixes

Appendix 1

Climatic conditions in Ås during bee sample periods in 2010 and 2011. Months refer corresponding sample periods. Note that the sampling intensity was increased during the summer. This was due to lower capture rates as the summer progressed. Note also the differences in average temperature between years during sampling in April.

Month	Date	Ås metrological station, precipitation in mm., temperature in C.				Sarpsborg metrological station wind speeds m/s		
		rain (mm)	average temperature	minimum temperature	Maximum temperature	Average	minimum	maximum
April	05.05.2010	2.1	5.9	1.2	11.2	3.2	1.5	4.6
	06.05.2010	0	6.8	-0.1	11.7	3.9	2.6	4.6
May	29.05.2010	0.1	10.3	3.7	15.2	3.4	1	4.6
	30.05.2010	1	10.5	4.6	15.9	2.1	1.5	2.6
June	16.06.2010	0	13.6	5.7	19	2.4	1.5	3.1
	17.06.2010	0	13.4	9	17.4	3.9	2.6	4.6
August	18.07.2010	0	17	13.5	20.5	5.6	4.8	6.9
	19.07.2010	0.1	16.1	11.6	19.4	3.9	2.6	4.6
	15.08.2010	0	18.6	11.4	24	4.6	4.6	4.6
	16.08.2010	0	17.9	16.3	22	5.3	4.6	6.7
April	24.04.2011	0	11.1	2.7	17.8	2.3	1.1	4.1
	25.04.2011	0	11.1	3.2	18	2.7	1.5	3.6
May	24.05.2011	2	11.1	9.4	14.4	8.3	7.2	8.8
	25.05.2011	0	11.9	5.6	17.9	5.8	4.6	7.2
June	14.06.2011	1.1	14.9	12	19.9	5.7	3.1	8.2
	15.06.2011	0	14.2	8.5	18.8	4.6	4.6	4.6
	16.06.2011	1.9	15	7.4	19.4	2	1.4	2.6
August	27.07.2011	0	18.2	14.1	23.4	2.1	1	3.1
	28.07.2011	0	19.6	12.3	26.9	1.2	0.5	1.5
	02.08.2011	0	19.8	12.4	25.3	2.1	1	2.6
	03.08.2011	0	20.3	16.2	25.3	1.5	1.5	1.5

Appendix 2

Plant species found in field edges in Ås, Norway in 2011. Descriptive statistics refer to the number of inflorescences or flowers pr. Square meter. Nomenclature follows Pickering (1998).

Plant	average	min	max	Unit
Achillea millefolium Linnaeus.	1.0	0.0	9.8	Inflorescences
Achillea ptarmica L.	0.9	0.0	9.9	Inflorescences
Alchemilla monticola Opiz.	0.3	0.0	5.2	Inflorescences
Anemone nemorosa L.	3.0	0.0	15.4	Flowers
Angelica sylvestris L.	0.3	0.0	2.2	Inflorescences
Anthriscus sylvestris Hoffm.	4.1	0.0	17.9	Inflorescences
Campanula rotundifolia L.	0.7	0.0	8.8	Flowers
Cirsium arvense (L.) Scop.	0.0	0.0	0.2	Inflorescences
Cirsium vulgare (Savi) Ten.	0.0	0.0	0.4	Inflorescences
Convallaria majalis L.	0.5	0.0	5.2	Inflorescences
Epilobium montanum L.	0.4	0.0	1.9	Flowers
Euphorbia cyparissias L.	0.1	0.0	1.6	Inflorescences
Fragaria vesca L.	0.4	0.0	3.3	Flowers
Galeopsis bifida Boenn.	2.0	0.0	27.6	Inflorescences
Galium mollugo L.	0.4	0.0	6.8	Inflorescences
Galium sterneri Ehrend.	0.5	0.0	8.9	Inflorescences
Galium verum L.	0.1	0.0	1.4	Inflorescences
Geranium sylvaticum L.	0.1	0.0	1.0	Flowers
Geum rivale L.	0.0	0.0	0.4	Flowers
Geum urbanum L.	0.0	0.0	0.2	Flowers
Hieracium sect. *foliosa* (Fr.) Dahlst.	0.0	0.0	0.2	Inflorescences
Hieracium murorum L. agg.	0.3	0.0	3.3	Inflorescences
Hieracium umbellatum L.	0.5	0.0	3.1	Inflorescences
Hypericum maculatum Crantz	2.0	0.0	13.3	Flowers
Knautia arvensis (L.) Coult.	0.0	0.0	0.5	Inflorescences
Lapsana communis L.	0.1	0.0	0.8	Inflorescences
Lathyrus linifolius (Reichard) Bässler	0.2	0.0	1.3	Inflorescences
Lathyrus pratensis L.	0.2	0.0	2.4	Inflorescences
Leucanthemum vulgare Lam.	0.1	0.0	1.2	Inflorescences
Linaria vulgaris Mill.	0.0	0.0	0.3	Flowers
Lotus corniculatus L.	0.8	0.0	12.0	Inflorescences
Lupinus angustifolius L.	0.2	0.0	3.1	Inflorescences
Lysimachia punctata L.	0.0	0.0	0.3	Inflorescences
Maianthemum bifolium (L.) F. W. Schmidt	0.0	0.0	0.3	Inflorescences
Matricaria inodora (Merat) M. Lainz	2.3	0.0	28.3	Inflorescences
Melampyrum nemorosum (Hill) Druce	5.0	0.0	89.5	Inflorescences
Melampyrum pratense L.	4.8	0.0	64.6	Inflorescences
Melampyrum sylvaticum L.	3.5	0.0	28.4	Inflorescences

Moehringia trinervia (L.) Clairv.	0.1	0.0	0.9	Flowers
Myosotis sylvatica Ehrh, ex Hoffm.	0.6	0.0	4.5	Flowers
Potentilla erecta (L.) Raeusch.	0.5	0.0	7.3	Flowers
Prunella vulgaris L.	0.0	0.0	0.3	Inflorescences
Ranunculus acris L.	2.9	0.0	23.8	Flowers
Ranunculus auricomus L.	0.0	0.0	0.3	Flowers
Ranunculus repens L.	0.8	0.0	8.2	Flowers
Rubus saxatilis L.	0.1	0.0	1.4	Flowers
Saponaria officinalis L.	0.1	0.0	2.7	Flowers
Solidago virgaurea L.	0.0	0.0	0.8	Inflorescences
Stellaria graminea L.	1.9	0.0	28.7	Flowers
Taraxacum officinale F.H. Wigg.	0.3	0.0	4.7	Inflorescences
Trifolium hybridum L.	1.2	0.0	13.4	Inflorescences
Trifolium medium L.	0.4	0.0	4.4	Inflorescences
Trifolium pratense L.	1.6	0.0	11.1	Inflorescences
Trifolium repens L.	0.2	0.0	1.4	Inflorescences
Vaccinium myrtillus L.	0.0	0.0	0.1	Flowers
Veronica beccabunga L.	0.0	0.0	0.2	Flowers
Veronica chamaedrys L.	14.8	0.0	105.0	Flowers
Veronica officinalis L.	0.2	0.0	3.1	Flowers
Vicia cracca L.	0.4	0.0	2.2	Inflorescences
Vicia sepium L.	0.0	0.0	0.6	Inflorescences
Viola canina L.	0.2	0.0	2.1	Flowers
Viola mirabilis L.	0.1	0.0	1.3	Flowers
Viola nemoralis (Sw.) DC.	0.0	0.0	0.6	Flowers
Viola riviniana Rchb.	0.1	0.0	0.6	Flowers
Viola tricolor L.	0.1	0.0	1.7	Flowers

Appendix 3

Landscape variables measured at four spatial scales included in the study in Ås, Norway in 2011.

Radius m.	Parameter	Unit	Mean ± SD.	Abbreviation
100	Forested land	Percent	38.55±15.76	1:Frst La.
	Semi natural land	Percent	9.61±14.66	1:Semi Nt.
	Arable land	Percent	49.68±8.79	1:Arbl La.
	Road length	Meters	116.4±8.79	1:Road Le.
	Field edges	Meters	460.5±241.4	1:Fild Ed.
	Forest edges	Meters	380±238.9	1:Frst Ed.
200	Forested land	Percent	39.33±14.79	2:Frst La.
	Semi natural land	Percent	8.58±8.83	2:Semi Nt.
	Arable land	Percent	51.22±14.08	2:Arbl La.
	Road length	Meters	493.4±305.5	2:Road Le.
	Field edges	Meters	1641±765	2:Fild Ed.
	Forest edges	Meters	1247±674	2:Frst Ed.
300	Forested land	Percent	35.59±15.72	3:Frst La.
	Semi natural land	Percent	7.82±5.17	3:Semi Nt.
	Arable land	Percent	53.06±15.12	3:Arbl La.
	Road length	Meters	1025±524	3:Road Le.
	Field edges	Meters	3486±1407	3:Fild Ed.
	Forest edges	Meters	2609±1442	3:Frst Ed.
400	Forested land	Percent	33.86±15.63	4:Frst La.
	Semi natural land	Percent	7.014±3.954	4:Semi Nt.
	Arable land	Percent	54.49±15.68	4:Arbl La.
	Road length	Meters	1790±885	4:Road Le.
	Field edges	Meters	5398±1999	4:Fild Ed.
	Forest edges	Meters	4200±2104	4:Frst Ed.

Appendix 4

Species inventory on solitary bees in field edges in Ås, Norway. Showing the number of individuals of each solitary bee species captured in the ten sites samples in 2010, the 18 sites in 2011 and the in subset of the 18 sites in 2011 that were also sampled in 2010.

Species	Abreviation*	Year		
		2010 (n=10)	2011 (n=18)	2011 (n=10)**
Andrena bicolor (Fabricious, 1775)	Andr1	18	15	12
Andrena cineraria (Linnaeus, 1758)	Andr2	1	12	10
Andrena clarkella (Kirby, 1802)	-	1	0	0
Andrena haemorrhoa (Fabricious, 1781)	Andr3	5	16	7
Andrena helvola (Linnaeus, 1758)	Andr4	1	4	2
Andrena lapponica (Zetterstedt, 1838)	-	1	0	0
Andrena ruficrus (Nylander, 1848)	Andr5	0	3	3
*Andrena minutula (*Kirby, 1802)	Andr6	1	3	0
Andrena nigroaeanea (Kirby, 1802)	Andr7	0	1	1
Andrena semilaevis (Pérez, 1903)	-	1	0	0
Andrena subopaca (Nylander, 1848)	Andr8	9	16	11
Anthophora fucata (Smith, 1847)	Anth1	0	2	0
Ceratina cyanea (Kirby, 1802)	-	1	0	0
Chelostoma florisomne (Linnaeus, 1758)	Chel1	2	1	1
Eucera longicornis (Linnaeus, 1758)	Euce1	0	1	1
Halictus rubicundus (Christ, 1791)	Hali1	2	14	12
Halictus tumulorum (Linnaeus, 1758)	Hali2	4	5	3
Hoplitis claviventris (Thomson, 1872)	Hopl1	1	2	2
Hoplitis tuberculata (Nylander, 1848)	-	1	0	0
Osmia rufa (Linnaeus, 1758)	Osmi1	0	2	1
Hylaeus confusus (Nylander, 1852)	Hyla1	6	11	11
Hylaeus communis (Nylander, 1852)	Hyla2	0	3	3
Hylaeus rinki (Gorski, 1852)	Hyla3	4	3	3
Lasioglossum calceatum (Scopoli, 1763)	Lasi1	3	4	2
Lasioglossum fratellum (Pérez, 1903)	Lasi2	3	4	2
Lasioglossum leucopus (Kirby, 1802)	Lasi3	2	13	3
Megachile alpicola (Alfken, 1924)	-	2	0	0
Megachile versicolor (Smith, 1844)	Mega1	1	2	2
Nomada flavoguttata (Kirby, 1802)	Noma1	2	10	6
Nomada leucophthalma (Kirby, 1802)	Noma2	1	2	1
Nomada striata (Fabricius, 1793)	Noma3	0	1	1
Nomada ruficornis (Linnaeus, 1758)	Noma4	0	2	1
Nomada panzeri (Lepeletier, 1841)	Noma5	1	3	2
Sphecodes puncticeps (Thomson, 1870)	Sphe1	0	1	0
Sphecodes geoffrellus (Kirby, 1802)	Sphe2	0	1	1

* Abbreviations noted only for species found in 2011.
** Captures in 2011 from the subset of sites sampled also in 2010.

Pearson's correlation matrix between landscape characteristics within and between spatial scales at field edges in Ås, Norway in 2011. Only relationships with at least marginally significant correlation coefficients ($P<0.1$) are shown. See appendix 3 for list of abbreviations.

	1:Frst La.	1:Semi Nt.	1:Arbl La.	1:Road Le.	1:Fild Ed.	1:Frst Ed.	2:Frst La.	2:Semi Nt.	2:Arbl La.	2:Road Le.
1:Semi Nt.	-0.829***									
1:Road Le.	-0.551**									
1:Fild Ed.				0.821***						
1:Frst Ed.				0.6***	0.811***					
2:Frst La.	0.464(*)									
2:Semi Nt.	-0.694***	0.867***		0.432(*)						
2:Arbl La.			0.447(*)				-0.628***			
2:Road Le.	-0.403(*)	0.411(*)		0.748***	0.622***			0.508*		
2:Fild Ed.				0.503*	0.739***	0.712***				
2:Frst Ed.				0.478*	0.725***	0.789***				0.635***
3:Frst La.							0.787***		-0.802***	0.44(*)
3:Semi Nt.	-0.658***	0.701***		0.464(*)	0.406(*)			0.903***		
3:Arbl La.							-0.732***		0.9***	0.509*
3:Road Le.				0.556**	0.460(*)					
3:Fild Ed.				0.406(*)	0.643***					0.738***
3:Frst Ed.				0.411(*)	0.618***	0.618***	0.469*			0.495*
4:Frst La.							0.697***		-0.758***	0.428(*)
4:Semi Nt.	-0.506*	0.541**						0.757***		
4:Arbl La.							-0.69***		0.81***	
4:Frst Ed.					0.647***	0.655***	0.490*			

	2:Fild Ed.	2:Frst Ed.	3:Frst La.	3:Semi Nt.	3:Arbl La.	3:Road Le.	3:Fild Ed.	3:Frst Ed.	4:Frst La.
2:Frst Ed.	0.849***								
3:Arbl La.			-0.916***						
3:Road Le.	0.409(*)			0.475*					
3:Fild Ed.	0.943***	0.752***							
3:Frst Ed.	0.774***	0.941***					0.710***		
4:Frst La.			0.958***		-0.89***				
4:Semi Nt.				0.926***		0.5*			
4:Arbl La.			-0.899***		0.966***	0.744***			-0.919***
4:Frst Ed.	0.741***	0.944***					0.666***	0.971***	

(*)= $P<0.1$, *=$P<0.05$, **=$P<0.025$, ***=$P<0.01$

Appendix 6

Pearson's correlation matrix on local habitat and landscape characteristics at field edges in Ås, Norway in 2011. Only relationships with at least marginally significant correlation coefficients (P<0.1) are shown. Plant Co. is inflorescences per square meter, based on either monthly (April, May, June, August) values or values pooled throughout the entire summer. Plant Sp. is plant species richness based on either monthly occurrences or pooled throughout the entire season. For abbreviations on landscape variables see appendix 3.

	Plant Sp. (April)	Plant Co. (April)	Plant Sp. (May)	Plant Co. (May)	Plant Sp. (June)	Plant Co. (June)	Plant Sp. (August)
Plant Co. (April)	0.495*						
Plant Co. (May)			0.494*				
Plant Sp. (June)	0.458(*)						
Plant Co. (June)					0.408(*)		
Plant Sp. (August)					0.499*		
Plant Sp. (Pooled)					0.730***		0.823***
Plant Co. (Pooled)			0.42(*)	0.544**	0.429(*)	0.535**	
Plant He.				0.43(*)			
Sun Ex.	0.612***						
1:Arbl La.	-0.650***	-0.411(*)					
1:Road Le.		-0.454(*)	0.457(*)	0.453(*)			
1:Fild Ed.			0.54**				
1:Frst Ed.			0.458(*)				
2:Semi Nt.						0.543**	
2:Arbl La.	-0.451(*)						0.438(*)
2:Road Le.			0.552**	0.612***			
2:Fild Ed.			0.508*				0.503*
2:Frst Ed.			0.409(*)				
3:Semi Nt.			0.516*			0.549**	
3:Arbl La.							0.405(*)
3:Road Le.			0.537**	0.614***	-469*		
3:Fild Ed.			0.451(*)				0.534**
3:Frst Ed.			0.409(*)				
4:Semi Nt.			0.410(*)			0.481*	
4:Road Le.				0.413(*)	-0.535**		

	Plant Co. (August)	Plant Sp (pooled)	Plant Co. (Pooled)	Plant He.	Sun Ex.	Plot Ar.
Plot Ar.	0.687***				-0.552**	
1:Semi Nt.					0.505*	
1:Arbl La.					-0.475*	
1:Frst Ed.				-0.418(*)		
2:Semi Nt.			0.434(*)		0.558**	
2:Arbl La.			-0.446(*)			
2:Road Le.	-0.417(*)					-0.426(*)
2:Frst Ed.				-0.449(*)		
3:Semi Nt.					0.501*	
3:Road Le.	-0.486*				0.443(*)	
3:Fild Ed.				-0.428(*)		
3:Frst Ed.				-0.430(*)		
4:Semi Nt.					0.416(*)	
4:Road Le.		-0.449(*)				
4:Fild Ed.	-0.609***					-0.540**
4:Frst Ed.				-0.435(*)		

(*)= P<0.1, *=P<0.05, **=P<0.025, ***=P<0.01