Diversity patterns of wild bees and wasps in managed boreal forests: Effects of spatial structure, local habitat and surrounding landscape

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ABSTRACT

Understanding patterns of species diversity at different spatial scales is important for adapting management and conservation efforts. We have therefore studied wild bee and wasp (Hymenoptera: Aculeata) diversity structure in forest landscapes and evaluated the importance of conservation management at the local and landscape levels. Surveys were conducted at 32 clearcuts in eight landscapes in a managed boreal forest region. We assessed the influence of local habitat and landscape composition on species richness patterns and the effect of prescribed burning and landscape affinity on species composition for all bees and wasps as well as ecological and functional groups. The relative contribution of alpha and beta diversity on the regional level was assessed by diversity partitioning and the beta diversity between landscapes further partitioned into components of species turnover and nestedness. Bee and wasp species richness increased with high flower richness and clearcut size, and species composition differed between burned and unburned sites. Thus, flower-rich early-successional sites in boreal forest landscapes are important habitats for wild bees and wasps. To support this fauna, openness should be maintained for extended periods by delaying or avoiding tree plantation at flower-rich spots on clearcuts. Beta diversity between landscapes accounted for the greatest proportion of the total regional gamma diversity, and over 70% of this diversity was due to species turnover. This implies that in order to maintain regional diversity, conservation efforts should be spatially dispersed, i.e. applied to every landscape of a few hundred square kilometers and adapted to the local species assemblages.

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1. Introduction

Biodiversity conservation on managed land is a necessary complement to protected areas (Kouki et al. 2001; Bengtsson et al. 2003) because existing reserve networks usually cover small areas and are therefore insufficient to ensure the long term viability of all species (Franklin and Lindenmayer 2009). Furthermore, biodiversity may be important for the provision of ecosystem services on managed land (Tscharntke et al. 2005; Gamfeldt et al., 2013). In order to develop successful conservation strategies that counteract declines in biodiversity, we must understand the factors that affect patterns of species diversity in managed landscapes.

Species diversity patterns are shaped by ecological processes operating on different scales (Willis and Wittaker, 2002; Tscharntke et al. 2012). Resource availability and species interactions operate on a local scale (Azeria et al. 2012), while species-specific dispersal (Baguette et al. 2000), habitat amount and

configuration are important on a landscape scale (Holzschuh et al. 2010; Fahrig 2013). At the regional level, species pools shaped by current and historical environmental conditions may affect the diversity patterns (Kouki et al. 2012; Lindborg and Eriksson 2004). Consequently, to understand local and regional species diversity patterns, it is necessary to study habitat factors across different spatial scales.

In large parts of Europe and North America, boreal forest landscapes have been heavily affected by the conversion of old-growth forests into even-aged stands harvested by clearcutting (Berg et al. 1994; Kouki et al. 2001; Siitonen 2001). Intensive forestry and fire suppression lead to losses of natural disturbance dynamics (Kuuluvainen 2009) and structural diversity (Siitonen 2001; Andersson and Östlund, 2004), which may cause the simplification of entire forest landscapes. Concerns about losses of forest biodiversity due to large scale intensive management have prompted the integration of conservation procedures into forestry operations, such as the retention of living and dead trees during final harvests (Franklin et al. 1997; Gustafsson et al. 2012). Prescribed fires are also sometimes used to emulate natural disturbances (Toivanen and Kotiaho 2007). The effects of forest

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management and tree retention on diversity have been evaluated for a number of taxa, including birds, rodents and certain insect groups – mainly beetles that are dead wood dependent or ground living (Rosenvald and Lõhmus, 2008; Gustafsson et al. 2010). However, little is known about the impact of forest management on other functionally important insect groups such as bees and wasps.

Due to their important roles in ecosystem functioning as pollinators, predators and parasites (natural enemies of pest insects), bees and wasps have been extensively studied in agricultural systems (Tscharntke et al. 2005). Species diversity in agricultural sites has been shown to increase with proximity to forests (Schuepp et al. 2011; Taki et al. 2007). Conversely, in forest sites, high forest cover in the surrounding landscape has negative effects on bee and wasp diversity, indicating that most species are associated with open habitats (Winfree et al. 2007). Consequently, the abundance and species richness of bees in early-successional (natural or managed) forest habitats is higher than in later successional stages (Romey et al. 2007; Pengelly and Cartar 2010; Taki et al. 2013).

Forest fires can create suitable conditions for bees and wasps on a local scale. Diversity tends to be particularly high in freshly burned areas due to their high floral richness, low tree cover and abundant dead wood (Williams et al. 2010; Potts et al. 2003; Moretti et al. 2009; Mateos et al. 2011). However, negative effects of fire on ground-nesting species (Winfree et al. 2009) and aboveground nesters in fresh burns (Williams et al. 2010) have also been reported. It appears that bees and wasps are generally positively associated with recently disturbed forest habitats, but very little is known about landscape -scale patterns, so current knowledge is of limited use in conservation.

We have studied wild bees and wasps (Hymenoptera: Aculeata) on clearcuts in a managed boreal forest region to assess patterns of species diversity across spatial scales and to determine the effects of local habitat and landscape properties on species richness and composition. The responses of species with different nesting preferences (ground nesters and dead wood nesters) and ecological functions (pollinators, predators and parasites) were analysed separately because it was expected that these preferences and functions would affect the species' habitat requirements (Holzschuh et al. 2010; Neame et al. 2013). Local scale factors were chosen to reflect the abundance of potentially important foraging and nesting resources such as flowering plants and dead wood. We specifically focused on prescribed fires, which should be initiated on at least 5% of all harvested forest land according to Sweden's forest certification (FSC) standards (Swedish FSC, 2010). We hypothesized that prescribed fires would have positive effects on at least some species because they change the flora and may increase the abundance of nesting substrates such as exposed soils and charred wood. On the landscape level, we assessed the importance of early-successional habitats and forest heterogeneity. This work was intended to answer the following questions: (i) What are the main local and landscape factors determining species richness at a given site? (ii) Does the species composition of bees and wasps differ between landscapes and between sites that have or have not undergone prescribed burning? (iii) What is the relative contribution of alpha and beta diversity across spatial scales to the regional gamma diversity, and is the beta diversity between landscapes mainly created by species turnover or nestedness?

2. Methods

2.1. Site selection

The study region was situated in south-central Sweden, in the southern boreal zone, and dominated by managed forests of mainly *Pinus sylvestris* and *Picea abies*, with negligible amounts of

agricultural habitats. The forests are dominated by even-aged stands which are harvested by clearcutting with green tree retention (10 live trees per hectare, according to the certification standards); preexisting dead wood must be retained and new dead wood is created during harvesting in the form of artificial snags, felled logs, tree-tops and branches. The average amount of dead wood in managed Swedish forests is around 6 m³ ha⁻¹ (Fridman and Walheim 2000), which is up to ten times lower than the volumes in unmanaged forests (Siitonen 2001).

Eight landscapes (approximately 10 km × 10 km) were selected within the region, all of which were separated by at least 20 km (Fig. 1). Within each landscape, we chose 3–5 clearcuts separated by at least 500 m. Clearcut data were obtained from the Swedish Forest Agency and data on prescribed fires from the two main forest-owning companies in the region, Bergvik Skog AB and Sveaskog AB. Where possible, two burned and two unburned clearcuts were selected within each landscape; in cases where only one burned clearcut was available, an additional burned site was added in another landscape to ensure that the numbers of burned and unburned clearcuts were balanced on the regional level. All of the burned sites were in cut managed forests; some of them were salvage-logged after wildfires and some were clearcut first and then subjected to prescribed burning.

Sites that had been cut/burned 3–5 years ago were selected to capture the post-disturbance stage with the highest biodiversity, which peaks after up to 5 years (Moretti et al. 2009; Mateos et al. 2011). During this stage, flowering herbs have become established but the tree cover has not yet regenerated. An advantage of studying slightly older clearcuts is that it increases the likelihood of collecting species that have actually reproduced on the sites whereas studies on sites that were disturbed more recently may predominantly collect those individuals that were initially attracted to the disturbance (Saint-Germain et al. 2004).

Within each clearcut, a trapping area was chosen with sufficient snags (⩾7) to enable all the traps to be set up. Where possible, the trapping areas were at least 50 m from any forest or water edge. The site area (hereafter site) was defined by the trapping area plus a 50 m buffer measured from the outermost trap locations (mean size ± SD = 2.3 ± 0.5 ha).

2.2. Sampling methods

Bees and wasps (Hymenoptera: Aculeata, except ants) were collected during summer 2011 (June 1 to August 22), using a combination of trapping methods: pan traps, window traps and trap-nests. We used multiple collection methods, since different functional groups are caught in different traps (Rubene et al. 2014).

The pan traps were spray-painted with UV-bright white, yellow and blue paint (Spraycolor Leuchtfarbe, Germany) and a cluster of three such traps (one of each color) was attached to a wooden pole approximately 0.5 m above ground to avoid obscuring by vegetation. Two such clusters were set up at each site. The window traps consisted of a Plexiglas plate (20 cm × 20 cm) with a plastic tray (3 l) attached beneath. Three traps per site were set up on the south-facing sides of snags 1.5 m high. The pan traps and window traps were filled with a mix of propylene glycol and water. Trap-nests were made from bamboo sticks that were cut to a length of 30 cm with a node in the middle to allow colonization from both ends. Four bundles of 10 were set up at each site, on the south-facing sides of snags. Each bundle had a roughly equal number of traps with diameter 3–6 mm, 7–10 mm and 11–14 mm.

The pan and window traps were emptied four and three times over the sampling season, respectively. The trap-nests were collected in August and reared indoors over winter in order to collect hatching bees and wasps. Aculeate bees and wasps were identified to the species level (with the exception of the genera
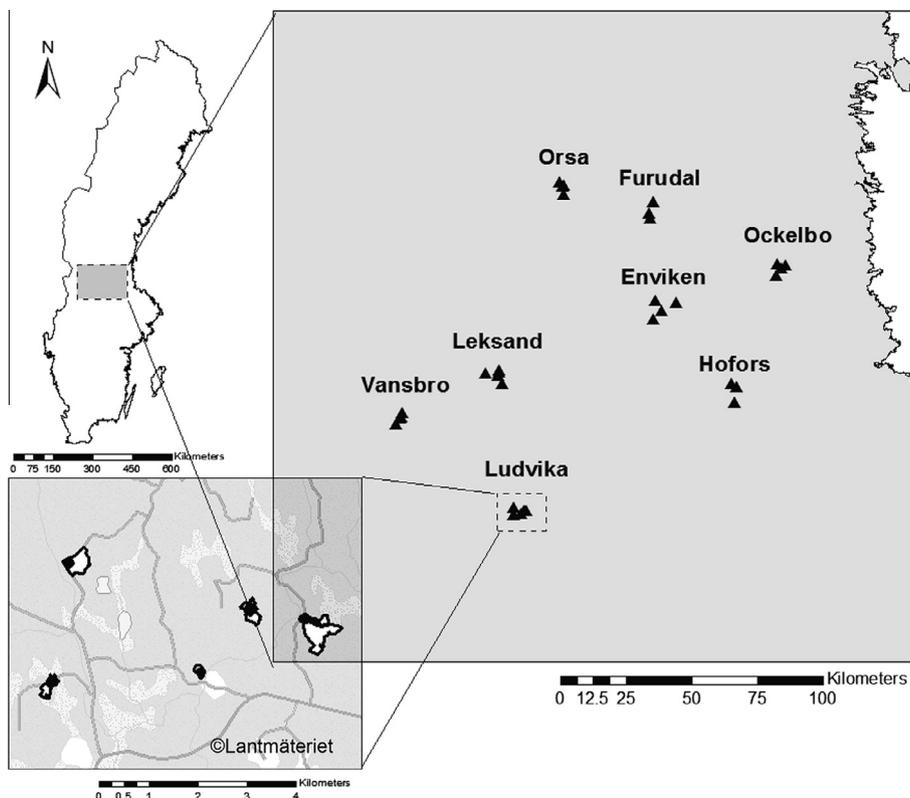
Fig. 1. The location of the study region in Sweden (top left), with marked site locations (triangles) and landscape identities (top right). Bottom left: location of sites within a single landscape, white polygons mark clearcut borders and black polygons mark the surveyed site areas. Map published with permission from Lantmäteriet, Sweden.

Laelius, Plastanoxus, Anteon, and the species group Chrysis ignita, for which species identification is difficult) by taxonomy experts (see acknowledgements). Species data from all traps and collection events were pooled for each site prior to analysis.

We assigned species to ecological groups using available literature and expert knowledge (see acknowledgements), based on their nesting biology (ground nesters or dead wood nesters) and ecological function (pollinators, predators or parasites) (Supplementary material Appendix A, Table A.1). We did not assign nesting preferences for parasitic species because their nesting behavior is only indirectly dependent on habitat properties. The assignment to functional groups was based on larval provisioning, i.e. the food type collected by the adult females for their offspring. We thus defined all non-parasitic bee species (Apoidea) as pollinators because bees that collect pollen for their larvae are efficient pollinators of flowering plants (Linkowski et al. 2004, Gómez et al., 2010). All species that collect arthropod prey were assigned as predators and all cleptoparasitic and parasitoid species as parasites.

2.3. Local habitat properties

For each site, we estimated the amount of downed and standing dead wood, the number of flowering plant species, and recorded the site's burned or unburned status (Table 1). The volume of downed dead wood was calculated by measuring all logs >15 cm in diameter within the site. The volume of standing dead wood was calculated by measuring all snags with a diameter of >5 cm at base. To account for flower species richness, we recorded all flowering and nectar producing plant species encountered while systematically walking through the site area in line transects separated by intervals of around 5 meters. All sites were surveyed by the same person.

The clearcuts were mapped and their size was calculated using ArcMap 10.1 (ArcGIS, ESRI, Redland, CA, USA), by defining each clearcut as the total contiguous area of cut forest at each location. Cuts were identified based on the appearance of the vegetation in satellite images (Google Earth): each clearcut was defined as a contiguous region of approximately uniform vegetation height with no sharp changes in vegetation height between adjoining stands.

2.4. Landscape composition

We assessed two landscape components of potential importance for bee and wasp diversity: the proportion of early-successional habitats and forest heterogeneity (Table 1). The landscape components were measured on three scales, i.e. over radii of 500 m, 1000 m and 2000 m centered on each site, based on the fact that most bees' documented foraging ranges are somewhere between a few hundred meters and a few kilometers (Greenleaf et al. 2007) and the surrounding landscape has been found to affect bees in agricultural habitats at this range of scales (Steffan-Dewenter et al. 2002).

Early-successional habitats were assumed to be important for diversity because most bees and wasps are associated with open habitats (New 2012). In forest landscapes, open habitats are created by natural disturbances or by clearcutting. We combined the area of all clearcuts and burned forest land between three and ten years prior to the start of the study; the burned land was identified using data on forest wildfires, prescribed fires and woodland key habitats classified as "burned forest". This group thus includes forests disturbed at the same time as the studied sites and less recently disturbed sites that could potentially function as dispersal sources.

We approximated forest heterogeneity by measuring the proportion of habitats with high conservation value: (i) nature

Table 1
Local and landscape factors included as explanatory variables in the analyses.

Factor	Scale	Units	Range (fire; no fire)	Median (fire; no fire)
Flower richness	Local	# of species	4–14 (4–14; 5–14)	9 (9; 9)
Dead wood amount	Local	$m^3 \ ha^{-1}$	1.82–25.58 (2.68–25.58; 1.82–9.65)	5.2 (5.82; 4.33)
Fire	Local	Burned/unburned	–	–
Clearcut size	Local/Landscape	ha	3.19–115 (4.1–115; 3.19–39.5)	13.68 (21.5; 8.83)
Early-successional habitats	Landscape 500 m	Proportion area	0.04–0.69 (0.2–0.69; 0.04–0.55)	0.29(0.39; 0.15)
	1000 m		0.03–0.53 (0.09–0.53; 0.03–0.3)	0.16 (0.29; 0.15)
	2000 m		0.02–0.31 (0.06–0.31; 0.02–0.18)	0.11 (0.16; 0.09)
Forest heterogeneity	Landscape 500 m	Proportion area	0–0.206 (0.001–0.039; 0–0.206)	0.008 (0.006; 0.12)
	1000 m		0.0002–0.242 (0.0005–0.048; 0.0002–0.24)	0.017 (0.018; 0.015)
	2000 m		0.001–0.098 (0.0002–0.048; 0.0001–0.098)	0.017 (0.013; 0.019)

reserves and woodland key habitats (WKH), excluding WKH described as "burned", which were treated as early-successional habitats; and (ii) forests with high volumes ($\geqslant 50 \ m^3 \ ha^{-1}$) of deciduous trees. These habitats were chosen because they are uncommon in managed forest landscapes. Reserves and WKH are characterized by natural-like forests with large volumes of dead wood (Ekbom et al. 2006; Jönsson and Jonsson 2007). Deciduous trees in boreal forests are important for biodiversity (Berg et al. 1994) because their relative abundance has declined as a result of the preference for planted conifers in forestry.

The landscape components were calculated with ArcMap 10.1 (ArcGIS, ESRI, Redland, CA, USA). Forests with high volumes of deciduous trees was identified using kNN maps of Swedish forest land, which have a resolution of 25 m × 25 m and are based on data from ground surveys (Swedish National Forest Inventory) together with satellite images (Landsat ETM) (Reese et al. 2003).

2.5. Analyses

In order to explore bee and wasp diversity patterns, we used a combination of analyses. First, we performed a mixed model analysis to evaluate the effects of local and landscape factors on total species richness and the species richness of ecological groups. Second, we used multivariate methods to examine differences in community composition associated with prescribed fires and the landscape (sub-region) in which the site was situated. Finally, we assessed the relative contribution of diversity components across spatial scales and habitat types (burned or not) by diversity partitioning (Lande 1996; Jost et al. 2010). As beta diversity can reflect different patterns (species turnover or nestedness), which have different implications for conservation, we also estimated the relative contribution of turnover and nestedness to beta diversity between landscapes (Baselga 2010).

Effects of local and landscape factors on species richness were analysed with linear mixed models (Bunnefeld and Phillimore 2012) in R (R Core Team, 2013) using the *nlme* package (Pinheiro et al. 2013). As response variables we used the estimated species richness per site, for all species and each ecological group. To address sampling efficiency and estimate species richness we used rarefaction in EstimateS 9.1.0 (Colwell 2013). The species rarefaction showed that the sampling was insufficient for direct comparison of observed species richness; therefore we calculated non-parametric species richness estimators (ACE, ICE, Chao1 and 2, Jacknife 1 and 2). We used small sample grain size (single collection from each trap), as Hortal et al. (2006) have shown that this approach provides more accurate estimates. We then chose the estimator that appeared most stable at the sample size used in this work, produced no or few extreme (outlier) values, and had low variation (SD). The estimator chosen for all species, ground and deadwood nesters, pollinators and predators was ICE (Chao et al.

2000; Chazdon et al. 1998) whereas for parasites it was Chao1 (Chao 1984).

Continuous variables (dead wood volume and clearcut size) were log10-transformed and all landscape proportion variables square-root transformed to improve skew distributions. The variables were also centered to a mean of zero to simplify the interpretation of interaction effects and reduce collinearity between factors included in the interaction and the interaction term (Schielzeth 2010). Normality was assessed using histograms and QQ-plots of residuals (Zuur et al. 2010); parasite species richness was log10-transformed to achieve normality.

For landscape factors, we determined the scale at which the diversity response was highest using correlations (Spearman coefficient) of species richness to landscape components. The scale of highest correlation was used for each factor in all subsequent analyses (Steffan-Dewenter 2002; Martin and Fahrig 2012). All analysed variables are described in Table 1.

Landscape identity was included in the models as a random factor to account for the spatial clustering of sites within landscapes. We tested the interactions between prescribed burning and all other local and landscape variables, as the response to fire may be modified by other habitat factors (Toivanen and Kotiaho 2007). Because the models involved many explanatory variables and interactions, they were built by forward selection based on Akaike's Information Criterion (AIC, Akaike 1974), corrected for small sample sizes (AICc). First, we built a main effects model by adding explanatory variables one at a time, in each step adding the variable that lowered AICc the most. Interactions were then added to the main effects model one at a time and only retained if they lowered the AICc.

To study differences in bee and wasp community composition between sites, we performed non-metric multi-dimensional scaling (NMDS) using the R package *vegan* (Oksanen et al. 2013). We fitted two environmental variables to the NMDS – fire (burned/unburned) and landscape identity, and their significance was assessed with a permutation test using the *env* function in *vegan* (Oksanen et al. 2013).

Diversity partitioning was performed in PARTITION 3.0 (Veech and Crist 2009). We used an additive richness approach without sample weighting (i.e. common and rare species were given equal weights) and 1000 randomisations. PARTITION produces a null distribution (expected if individuals were randomly distributed) and performs a Monte Carlo randomization to assess the relationship between the observed values for alpha and beta and the null values (Crist et al. 2003, Partition 3.0 User's Manual, unpublished document). We calculated the alpha (number of species per site) diversity for each site and two levels of beta diversity (between sites within landscapes and between landscapes). We performed a separate partitioning in order to estimate a beta value between sites that had and had not undergone prescribed burning. Additive partitioning of beta diversity between landscapes was done using a

method derived by Baselga (2010), which is based on calculating the total multiple-site dissimilarity (derived from the pairwise Sørensen dissimilarity), which is then decomposed into components of species turnover and nestedness.

3. Results

We collected a total of 9553 Aculeata individuals belonging to 208 species (excluding the honeybee *Apis mellifera*, whose occurrence is determined by bee-keeping) (Supplementary material Appendix A, Table A.1). The number of ground-nesting species (79) was greater than that of dead wood nesters (59 species), and there were more predator species (101) than pollinators (53) or parasites (49). Only two species were unique and abundant ($\geqslant 10$ individuals) in each habitat type: *Heriades truncorum* (Mehachilidae) and *Cerceris ruficornis* (Crabronidae) on burned sites, and *Crossocerus varus* (Crabronidae) and *Rhopalum clavipes* (Crabronidae) on unburned sites.

3.1. Species richness

The total species richness per site increased with flower richness and clearcut size (Table 2). These factors were also included in the final species richness models for ground nesters, pollinators and predators. In addition, there was a positive relationship between ground nesting species richness and the proportion of early-successional habitats in the surrounding landscape. Predator richness was negatively affected by prescribed burning.

3.2. Species composition

Community composition appears to vary considerably among sites, as indicated by the dispersed points in the NMDS (Fig. 2). Fire was the main factor affecting site dissimilarity for all species combined (Fig. 2; $k = 3$, stress $= 0.13$, $r^2_{fire} = 0.32$, $p = 0.001$, $r^2_{landscape} = 0.21$, $p = ns$), and similar results were obtained for pollinators ($k = 2$, stress $= 0.14$, $r^2_{fire} = 0.25$, $p = 0.002$, $r^2_{landscape} = 0.33$, $p = ns$) and parasites ($k = 3$, stress $= 0.14$, $r^2_{fire} = 0.16$, $p = 0.004$, $r^2_{landscape} = 0.28$, $p = ns$). Predator species composition differed between burned and unburned sites, as well as between landscapes ($k = 3$, stress $= 0.14$, $r^2_{fire} = 0.15$, $p = 0.008$, $r^2_{landscape} = 0.4$, $p = 0.015$). Ground nesting species were the only group for which species composition was not affected by fire; instead, sites within the same landscape were more similar to each other ($k = 3$, stress $= 0.15$, $r^2_{fire} = 0.04$, $p = ns$, $r^2_{landscape} = 0.55$, $p = 0.002$). Finally, none of the tested factors affected the composition of dead wood nesters ($k = 3$, stress $= 0.15$, $r^2_{fire} = 0.07$, $p = ns$, $r^2_{landscape} = 0.25$, $p = ns$).

3.3. Diversity partitioning

Most of the bee and wasp diversity in the region was contained in the beta component, with beta diversity between landscapes accounting for the majority of the total (gamma) diversity (Fig. 3). The beta diversity between sites within each landscape contributed somewhat less, and the beta diversity between habitat
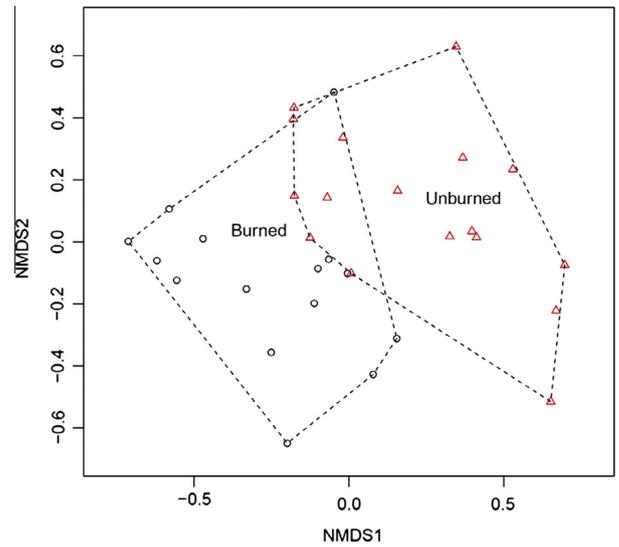

Fig. 2. NMDS plot illustrating compositional dissimilarity of all species between sites; each point represents one site, circles = burned sites, triangles = unburned sites. Group boundaries for burned and unburned sites are drawn using *ordihull* function in vegan (Oksanen et al. 2013). The labels mark the centroids of each group.
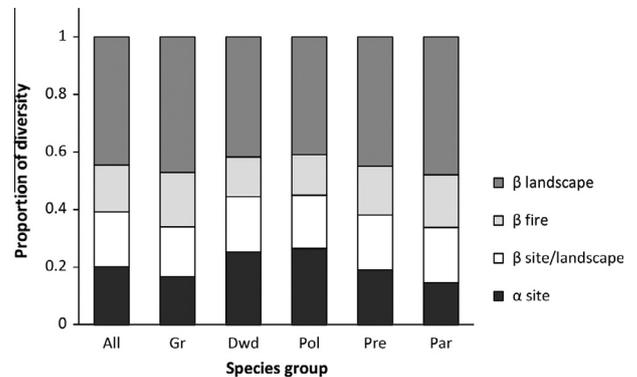

Fig. 3. Proportion of diversity explained by the different alpha and beta components. Species groups: All – all species combined, Gr – ground nesters, Dwd – dead wood nesters, Pol – pollinators, Pre – predators, Par – parasites.

types (i.e. between habitats with and without prescribed burning) contributed less still. These patterns were similar between species groups. For most species groups, the observed alpha and beta diversity between sites within landscapes were significantly lower than expected from the null distribution (MC randomization test), whereas the observed values for the other beta diversity components were greater than expected (Supplementary material Appendix B, Table B.1). Partitioning of beta diversity between landscapes showed that the bulk of the beta diversity (72–90%) for all groups could be attributed to species turnover, while the

Table 2
Fixed effects of final mixed models for species richness. Estimate values (standard errors) and ΔAICc values relative to intercept and random factor-only models are shown.

Response (species richness)	Flower richness	Clearcut size (log10)	Fire	Early succ. habitats 2000 m (sqrt)	Fire × Flower richness	ΔAICc
All species	3.34 (1.03)	23.36 (8.03)				10.1
Ground nesters	2.03 (0.7)	13.28 (5.93)		34.6 (21.24)		8.47
Dead wood nesters[a]	−1.41 (1.71)		−0.05 (0.44)		1.45 (0.65)	0.22
Pollinators	1.02 (0.35)	8.42 (2.86)				8.62
Predators	1.82 (0.6)	14.6 (5.23)	−6.57 (3.49)			7.39
Parasites (log10)[a]		0.25 (0.13)				1.07

[a] The models for dead wood nesters and parasites were not significantly different from random factor and intercept-only models (ΔAICc ⩽ 2).

nestedness component was small (10–28%) (Supplementary material Appendix C, Table C.1).

4. Discussion

We show that diversity of wild bees and wasps in managed forests is structured by factors on several spatial scales. Locally, flowering plants are important resources for bees and wasps. Prescribed fire has some effect; burned and unburned sites have similar species richness but the species composition differs for most groups. The species richness per site increased with the area of the local open habitat and the proportion of early-successional habitats in the surrounding landscape. We observed high species turnover between landscapes, suggesting that spatially clustered species assemblages exist within regions.

4.1. Local resources

High local flower species richness increased the species richness of bees and wasps, as has been shown previously (Potts et al. 2003). Even though pollen-collecting species ("pollinators" in this study) are the only group that depends on flowers through all their life stages, adults of most other species also forage on nectar and pollen, which explains why flower richness is an important predictor of species richness also for other ecological groups. Thus, promoting high flower diversity will have positive effects on bees and wasps. Forest landscapes in southern Sweden used to be rich in pastures and hay meadows, and the forests were shaped by mowing and grazing until about 100 years ago. Since then, the meadows have been replaced by forests, and forests have become denser due to plantation and the cessation of livestock grazing (Dahlström, 2006). However, remnant plant populations can persist for a long time (Lindborg and Eriksson 2004) and may support associated insect species. For example, the species richness of butterflies on clearcuts that had been meadows one tree generation previously was greater than that on clearcuts that had been forested at the same point in time (Ibbe et al. 2011). Such sites may be particularly important for bee and wasp diversity. Managing them to prolong the open habitat stage, e.g. by delaying or avoiding tree plantation and removing shrubs on the whole clearcut or just on flower-rich patches, is likely to promote high diversity of flowering plants and thus also a high diversity of bees and wasps. Many other early-successional forest species may also benefit from a slower, more natural regeneration on clearcuts (Swanson et al. 2010), e.g. species associated with sun-exposed dead wood (Kouki et al. 2001). Species that require a canopy cover may be disfavored, but they survive poorly on clearcuts and young managed forests in any event and thus require different conservation approaches (Rudolphi et al. 2014; Johnson et al. 2014).

We did not observe any relationship between the volume of dead wood and species richness even though such a relationship was expected because many species of forest bees and wasps nest in cavities in dead wood (Morato and Martins 2006; New 2012). The apparent absence of a relationship may have been because most of the dead wood in the studied sites was rather fresh (3–5 years) and contained few cavities. Most cavity nesting wasps and bees use preexisting tunnels bored by other insects (especially beetles) rather than excavating their own nests (Morato and Martins 2006). Therefore, the volume of dead wood within the sites may have been only loosely related to the availability of cavities suitable for nesting.

4.2. Prescribed fire

In studies that report higher bee richness in burnt sites, recent fire is usually associated with greater habitat openness and flowering plant diversity, and larger volumes of dead wood (e.g. Campbell et al. 2007; Mateos et al. 2011). This makes it difficult to assess the effect of fire itself. Fire might affect species by modifying other habitat features such as vegetation structure (Nimmo et al. 2014), plant diversity (Potts et al. 2003; Moretti et al. 2009) or the availability of warmer microhabitats on blackened soil and wood surfaces (DeBano et al. 1998). To our knowledge, however, no evidence for any strict dependence of bee and wasp species on fire has ever been reported, and our sampling revealed only two species that were both reasonably abundant and found exclusively on burned sites. Although we examined potential interactions between burning and other habitat factors, we found no effect of fire on most species groups. Burnt and unburnt sites did not differ in flower richness (Table 1) or bee and wasp species richness, whereas flower richness had strong effects on bee and wasp species richness (Table 2). Prescribed burning did affect the species composition of most groups of bees and wasps, and negatively affected predator species richness. Negative effects of fire have previously been attributed to increased mortality and destruction of nesting sites during fires (Winfree et al. 2009; Williams et al. 2010). Thus, fire does not appear to increase overall diversity and is probably not necessary for the conservation of wild bees and wasps in managed forest landscapes.

4.3. Landscape composition

The proportion of early-successional habitats within 2 km increased the species richness of ground nesters (Table 2). Early-successional habitats may favor ground nesting species because they need open ground for constructing nests. Moreover, flowering plants are more abundant in open areas than in forests. Therefore, open habitats in forest landscapes can positively contribute to regional Hymenoptera diversity (Schuepp et al. 2012; Tylianakis et al. 2005). Our results indicate that at least some wild bees and wasps benefit from an abundance of early-successional habitats in forest dominated landscapes.

Species richness was positively associated with clearcut size for the complete set of studied species and for most of the ecological groups. In studies where the sampling effort is adjusted to habitat patch size, the effect of patch size on species richness may reflect the effect of sample size (Fahrig 2013). To avoid this problem, we used the same level of sampling effort at all sites. Consequently, the relationship between clearcut size and species richness determined in this work probably reflects the tendency for larger habitat patches to harbor viable local populations of more species, which has also been observed in a few other insect studies (Steffan-Dewenter and Tscharntke 2000; Ranius 2002; Sahlin and Schroeder, 2010). The strong species-area associations observed suggest that clearcuts constitute habitat patches for the studied groups, situated in a matrix. This is consistent with the assumptions of the theory of island biogeography (MacArthur and Wilson, 1967), although these assumptions have been questioned in terrestrial patch networks (Fahrig 2013). Larger patches also contain more resources, which can sustain more individuals (Connor et al., 2000), decreasing extinction risks. Furthermore, larger patches may be more heterogeneous, which means that there may be habitat available for a larger number of species.

Forest heterogeneity (i.e. the proportion of protected forests and forests with a high volume of deciduous trees) did not affect species richness (Table 2). Other studies have shown that the heterogeneity of the surrounding landscape has a positive effect on local bee and wasp diversity (Watson et al. 2011; Taki et al. 2007; Schuepp et al. 2011). Heterogeneity was measured in habitat types that tend to have higher within-stand variation in tree characteristics (especially species and age) than typical managed forests and which are rare in managed landscapes. The lack of relationship may indicate that these types of forest habitats are

not important for most bee and wasp species found in clearcuts. However, some species may still depend on late-successional forests; for example Winfree et al. (2007) found that despite an overall negative association of species richness with forest cover, 18 out of 130 species were associated with forests. Species associated with mature forest may be underrepresented in this study since we only examined clearcuts. Therefore, additional forest habitat types should be investigated to support the development of conservation strategies that will protect the full range of bee and wasp fauna found in forest landscapes.

4.4. Spatial diversity patterns

We found that most of the observed regional diversity was due to beta diversity on the largest spatial scale, i.e. species turnover between landscapes. The geographic structuring of communities was also apparent in the species composition of ground nesters. These results suggest that different species communities exist on a scale of 10–100 km^2. Other arthropod studies have also revealed rather high levels of beta diversity on a large spatial scale, which can be explained by differences in habitat characteristics or species pools between regions (Clough et al. 2007; Murray et al. 2011). Our result is somewhat unexpected, because all of the studied sites have the same habitat types and the whole region is dominated by the same type of forest. Still, it is possible that the differences between the studied landscapes were due to variation in habitat factors that were not measured in this study. Alternatively, they could be due to historical patterns of forest dynamics and management or differences in the historical extent of grassland habitats (Lindborg and Eriksson 2004; Kouki et al. 2012). It is often suggested that conservation efforts should be spatially concentrated (Hanski 2011), but our results do not support this. The fact that species composition varies over relatively small scales means that it may be beneficial to spatially disperse conservation or restoration efforts across regions and ensure that these efforts are adapted to the habitat requirements of each species pool where possible in order to maintain the entire fauna of a region.

4.5. Conclusions

Early successional sites in boreal forest landscapes are important habitats for wild bees and wasps, especially if they have high flower species richness. Species diversity benefits from large clearcuts. Even though boreal forest landscapes are apparently homogeneous, species composition and richness is spatially structured in landscapes of a few hundred square kilometers. To maintain regional diversity, biodiversity-oriented management and conservation efforts should be applied to every landscape of this scale and tailored to the local species assemblages. By maintaining the openness of flower-rich sites for extended periods of time, it may be possible to increase the amount of high quality habitats for bees and wasps at a landscape scale.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.01.029.

References

Akaike, H., 1974. A new look at the statistical model identification. IEEE T. Automat. Contr. 19, 716–723.

Andersson, R., Östlund, L., 2004. Spatial patterns, density changes and implications on biodiversity for old trees in the boreal landscape of northern Sweden. Biol. Conserv. 118, 443–453.

Azeria, E., Ibarzabal, J., Hébert, C., 2012. Effects of habitat characteristics and interspecific interactions on co-occurrence patterns of saproxylic beetles breeding in tree boles after forest fire: null model analyses. Oecologia 168, 1123–1135.

Baguette, M., Petit, S., Quéva, F., 2000. Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. J. Appl. Ecol. 37, 100–108.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecol. Biogeogr. 19, 134–143.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., Nyström, M., 2003. Reserves, resilience and dynamic landscapes. AMBIO 32, 389–396.

Berg, Å., Ehnström, B., Gustavsson, L., Hallingbäck, T., Jonsell, M., Weslien, J., 1994. Threatened plant, animal and fungus species in Swedish forests: distribution and habitat associations. Conserv. Biol. 8, 718–731.

Bunnefeld, N., Phillimore, A.B., 2012. Island, archipelago and taxon effects: mixed models as a means of dealing with the imperfect design of nature's experiments. Ecography 35, 15–22.

Campbell, J.W., Hanula, J.L., Waldrop, T.A., 2007. Effects of prescribed fire and fire surrogates on floral visiting insects of the Blue Ridge province in North Carolina. Biol. Conserv. 134, 393–404.

Chao, A., 1984. Non-parametric estimation of the number of classes in a population. Scand. J. Stat. 11, 265–270.

Chao, A., Hwang, W.-H., Chen, Y.-C., Kuo, C.-Y., 2000. Estimating the number of shared species in two communities. Stat. Sinica 10, 22–246.

Chazdon, R.L., Colwell, R.K., Denslow, J.S., Guariguata, M.R., 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. In: Dallmeier, F., Comiskey, J.A. (Eds.), Forest Biodiversity Research, Monitoring and Modeling: Conceptual background and Old World case studies. Parthenon Publ, Carnforth, UK.

Clough, Y., Holzschuh, A., Gabriel, D., Purtau, T., Kleijn, D., Kruess, A., Steffan-Dewenter, I., Tscharntke, T., 2007. Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. J. Appl. Ecol. 44, 804–812.

Crist, T.O., Veech, J.A., Summerville, K.S., Gering, J.C., 2003. Partitioning species diversity across landscapes and regions: a hierarchical analysis of α, β, and γ diversity. Am. Nat. 162, 734–743.

Colwell, R.K., 2013. EstimateS: statistical estimation of species richness and shared species from samples, version 9.1.0. <http://viceroy.eeb.uconn.edu/estimates/index.html>, (accessed 03.05.14).

Connor, E.F., Courtney, A.C., Yoder, J.M., 2000. Individuals–area relationships: the relationship between animal population density and area. Ecology 81, 734–748.

Dahlström, A., 2006. The history (1620–2003) of land use, people and livestock, and the relationship to present plant species diversiy in a rural landscape in Sweden. Environ. Hist. 12, 191–212.

DeBano, L.F., Neary, D.G., Folliott, P.F., 1998. Fire's Effects on Ecosystems. John Wiley and Sons, USA.

Ekbom, B., Schroeder, L.M., Larsson, S., 2006. Stand specific occurrence of coarse woody debris in a managed boreal forest landscape in central Sweden. For. Ecol. Manage. 221, 2–12.

Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. J. Biogeogr. 40, 1649–1663.

Franklin, J.F., Berg, D.R., Thornburgh, D.A., Tappeiner, J.C., 1997. Alternative Silvicultural Approaches to Timber Harvesting: Variable retention Systems. Creating a Forestry for the 21st Century. In: Kohm, K.A., Franklin, J.F. (Eds.), The Science of Forest Management. Island Press, Washington, USA.

Franklin, J., Lindenmayer, D., 2009. Importance of matrix habitats in maintaining biological diversity. PNAS 106, 349–350.

Fridman, J., Walheim, M., 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. For. Ecol. Manage. 131, 23–36.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nat. Commun. 4, 1340. http://dx.doi.org/10.1038/ncomms2328.

Gómez, G.M., Abdelaziz, M., Lorite, J., Munos-Pajares, A.E., Perfectti, F., 2010. Changes in pollinator fauna cause spatial variation in pollen limitation. J. Ecol. 98, 1243–1252.

Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. Oecologia 153, 589–596.

Gustafsson, L., Kouki, J., Sverdrup-Thygeson, A., 2010. Tree retention as a conservation measure in clearcut forests of northern Europe: a review of ecological consequences. Scand. J. For. Res. 25, 295–308.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lõhmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A., Franklin, J.F., 2012. Retention forestry to maintain multifunctional forests: a world perspective. BioScience 62, 633–645.

Hanski, I., 2011. Habitat loss, the dynamics of biodiversity, and a perspective on conservation. AMBIO 40, 248–255.

Holzschuh, A., Steffan-Dewenter, I., Tscharntke, T., 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? J. Anim. Ecol. 79, 491–500.

Hortal, J., Borges, P.A.V., Gaspar, C., 2006. Evaluating the performance of species richness estimators: sensitivity to sample grain size. J. Anim. Ecol. 75, 274–287.

Ibbe, M., Milberg, P., Tunér, A., Bergman, K.-O., 2011. History matters: impact of historical land use on butterfly diversity in clear-cuts in a boreal landscape. For. Ecol. Manage. 261, 1885–1891.

Johnson, S., Strengbom, J., Kouki, J., 2014. Low levels of tree retention do not mitigate the effects of clearcutting on ground vegetation dynamics. For. Ecol. Manage. 330, 67–74.

Jost, L., DeVries, P., Walla, T., Greeney, H., Chao, A., Ricotta, C., 2010. Partitioning diversity for conservation analyses. Divers. Distrib. 16, 65–76.

Jönsson, M., Jonsson, B.G., 2007. Assessing coarse woody debris in Swedish woodland key habitats: implications for conservation and management. For. Ecol. Manage. 242, 363–373.

Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S., Uotila, A., 2001. Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. Scand. J. For. Res. Suppl. 3, 27–37.

Kouki, J., Hyvärinen, E., Lappalainen, H., Martikainen, P., Similä, M., 2012. Landscape context affects the success of habitat restoration: large-scale colonisation patterns of saproxylic and fire-associated species in boreal forests. Divers. Distrib. 18, 348–355.

Kuuluvainen, T., 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe. The complexity challenge. The complexity challenge. AMBIO 38, 309–315.

Lande, R., 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 109, 203–207.

Lindborg, R., Eriksson, O., 2004. Historical landscape connectivity affects present plant species diversity. Ecology 85, 1840–1845.

Linkowski, V.I., Cederberg, B., Nilsson, L.A., 2004. Vildbin och fragmentering. Kunskapssammanställning om situationen för de viktigaste pollinatörerna i det svenska jordbrukslandskapet. ArtDatabanken, SLU, Avd. för växtekologi. Uppsala universitet, Uppsala, Sweden.

Martin, A.E., Fahrig, L., 2012. Measuring and selecting scales of effect for landscape predictors in species–habitat models. Ecol. Appl. 22, 2277–2292.

Mateos, E., Santos, X., Pujade-Villar, J., 2011. Taxonomic and functional responses to fire and post-fire management of a mediterranean Hymenoptera community. Environ. Manage. 48, 1000–1012.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Morato, E.F., Martins, R.P., 2006. An overview of proximate factors affecting the nesting behaviour of solitary wasps and bees (Hymenoptera: Aculeata) in preexisting cavities in wood. Neotrop. Entomol. 35, 285–298.

Moretti, M., de Bello, F., Roberts, S.M.P., Potts, S.G., 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. J. Anim. Ecol. 78, 98–108.

Murray, T.E., Fitzpatrick, U., Byrne, A., Fealy, R., Mark, J.F., Brown, M.J.F., Paxton, R.J., 2011. Local-scale factors structure wild bee communities in protected areas. J. Appl. Ecol. 49, 998–1008.

Neame, L.A., Griswold, T., Elle, E., 2013. Pollinator nesting guilds respond differently to urban habitat fragmentation in oak-savannah ecosystems. Insect Conserv. Divers. 6, 57–66.

New, T.R., 2012. Hymenoptera and Conservation. John Wiley & Sons, Chichester, UK.

Nimmo, D.G., Kelly, L.T., Farnsworth, L.M., Watson, S.J., Bennett, A.F., 2014. Why do some species have geographically varying responses to fire history? Ecography 37, 805–813.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.S., Solymos, P., Henry, M., Stevens, H., Wagner, H., 2013. Vegan: community ecology package, R package version 2.0-7, <http://CRAN.R-project.org/package=vegan>, (accessed 08.12.14).

Pengelly, C.J., Cartar, R.V., 2010. Effects of variable retention logging in the boreal forest on the bumble bee-influenced pollination community, evaluated 8–9 years post-logging. For. Ecol. Manage. 260, 994–1002.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team. 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-110, <http://CRAN.R-project.org/package=nlme>, (accessed 29.08.14).

Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., O'Toole, C., Roberts, S., Willmer, P., 2003. Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure. Oikos 101, 103–112.

R Core Team, 2013. R: ZA language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ranius, T., 2002. Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biol. Conserv. 103, 85–91.

Reese, H., Nilsson, M., Pahlén, T., Hagner, O., Joyce, S., Tingelöf, U., Egberth, M., Olsson, H., 2003. Countrywide estimates of forest variables using satellite data and field data from the national forest inventory. AMBIO 32, 542–548.

Romey, W.L., Ascher, J.S., Powell, D.A., Yanek, M., 2007. Impacts of logging on midsummer diversity of native bees (Apoidea) in a northern hardwood forest. J. Kansas Entomol. Soc. 80, 327–338.

Rosenvald, R., Lõhmus, A., 2008. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. Biol. Conserv. 255, 1–15.

Rudolphi, J., Jönsson, M.T., Gustafsson, L., 2014. Biological legacies buffer species extinction after logging. J. Appl. Ecol. 51, 53–62.

Rubene, D., Schroeder, M., Ranius, T., 2014. Estimating bee and wasp (Hymenoptera: Aculeata) diversity on clear-cuts in forest landscapes – an evaluation of sampling methods. Insect Conserv. Diver. http://dx.doi.org/10.1111/icad.12105.

Sahlin, E., Schroeder, L.M., 2010. Importance of habitat patch size for occupancy and density of aspen-associated saproxylic beetles. Biodiv. Conserv. 19, 1325–1339.

Saint-Germain, M., Drapeau, P., Hébert, C., 2004. Habitat use of pyrophilous Coleoptera in recently burned black spruce forest of Central Québec. Biol. Conserv. 118, 583–592.

Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. MEE 1, 103–113.

Schuepp, C., Herrman, J.D., Herzog, F., Schmidt-Entling, M.H., 2011. Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies. Oecologia 165, 713–721.

Schuepp, C., Rittiner, S, Martin H., Entling, M.H., 2012. High bee and wasp diversity in a heterogeneous tropical farming system compared to protected forest. PLoS ONE, 7.

Siitonen, J., 2001. Forest management coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. Ecol. Bull. 49, 11–41.

Steffan-Dewenter, I., 2002. Landscape context affects trap-nesting bees, wasps and their natural enemies. Ecol. Entomol. 27, 631–637.

Steffan-Dewenter, I., Tscharntke, T., 2000. Butterfly community structure in fragmented habitats. Ecol. Lett. 3, 449–456.

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tscharntke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83, 142–1432.

Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B., Swanson, F.J., 2010. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Front. Ecol. Environ. 9, 117–125.

Swedish FSC, 2010. Svensk skogsbruksstandard enligt FSC med SLIMF-indikatorer V2–1 050510. F. S. C.

Taki, H., Kevan, P.G., Ascher, J.S., 2007. Landscape effects of forest loss in a pollination system. Landsc. Ecol. 22, 1575–1587.

Taki, H., Okochi, I., Okabe, K., Inoue, T., Goto, H., Matsumura, T., Makino, S., 2013. Succession influences wild bees in a temperate forest landscape: the value of early successional stages in naturally regenerated and planted forests. PLoS ONE 8, e56678.

Toivanen, T., Kotiaho, J.S., 2007. Burning of logged sites to protect beetles in managed boreal forests. Conserv. Biol. 21, 1562–1572.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenterm, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecol. Lett. 8, 857–874.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Ljeijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Schreber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes – eight hypotheses. Biol. Rev. 87, 661–685.

Tylianakis, J.M., Klein, A.M., Tscharntke, T., 2005. Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. Ecology 86, 3296–3302.

Veech, J.A., Crist, T.O., 2009. PARTITION: software for hierarchical partitioning of species diversity, version 3.0. <http://www.users.muohio.edu/cristto/partition.htm>, (accessed 03.05.14).

Watson, J.C., Wolf, A.T., Ascher, J.S., 2011. Forested landscapes promote richness and abundance of native bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin apple orchards. Environ. Entomol. 40, 621–632.

Williams, N.M., Crone, E.E., Roulston, T.H., Minckley, R.L., Packer, L., Potts, S.G., 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biol. Conserv. 143, 2280–2291.

Willis, K.J., Wittaker, R.J., 2002. Species diversity – scale matters. Science 295, 1245–1248.

Winfree, R., Griswold, T., Kremen, C., 2007. Effect of human disturbance on bee communities in a forested ecosystem. Conserv. Biol. 21, 213–223.

Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G., Aizen, M.A., 2009. A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90, 2068–2076.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. MEE 1, 3–14.