

Fewer butterflies and a different composition of bees, wasps and hoverflies on recently burned compared to unburned clear-cuts, regardless of burn severity



Victor Johansson^{a,b,*}, Lena Gustafsson^c, Petter Andersson^b, Kristoffer Hylander^a

^a Department of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91 Stockholm, Sweden

^b Calluna AB, Linköpings slott, SE-582 28 Linköping, Sweden

^c Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, SE-75007 Uppsala, Sweden

ARTICLE INFO

Keywords:

Boreal forests
Community composition
Nectar and pollen plants
Pollinators
Prescribed burning
Wild fire

ABSTRACT

Insect pollinators are declining, which often is related to intensified agriculture. Less focus has been on the effect of forestry. In many boreal forests, clear-cutting has replaced fire as the main disturbance agent, which has been negative for many species. Therefore, prescribed burning is performed, often on clear-cuts. Knowledge on the effect of fire on pollinators is, however, scarce. We sampled pollinators and their resources in 22 burned and 15 unburned clear-cuts in and around a large wildfire area in Sweden, three years after fire. We compared potential pollinator resources as well as richness, abundance and community composition of four groups of pollinators: bees (totaling 583 individuals), wasps (1226), hoverflies (416), and butterflies (728) between burned and unburned clear-cuts. Moreover, we analyzed the effect of burn severity (depth of remaining humus). We show that the diversity and cover of potential nectar/pollen plants were clearly lower in burned clear-cuts, while potential nesting resources were higher. Butterfly richness was 67% lower and abundance 89% lower in burned clear-cuts. Differences in richness and abundance were smaller for bees, wasps, and hoverflies, but their species composition differed. We found no effect of burn severity on pollinators or their resources. We conclude that burned clear-cuts have fewer pollinators three years after fire, which is driven by a loss of butterflies. However, changes in species composition from clear-cut fires could complement the fauna of unburned sites when mixed at landscape level. Future studies should follow vegetation and pollinator communities over longer time periods following clear-cut burning.

1. Introduction

Many insect pollinators that provide important ecosystem services are declining (e.g. IPBES, 2016; Potts et al., 2010). In Europe, such patterns have been found for butterflies (e.g. Maes and Van Dyck, 2001), wild bees (including bumblebees) and hoverflies (e.g. Goulson et al., 2008; Powney et al., 2019). The decline is often related to intensified agriculture (Le Féon et al., 2010; van Swaay et al., 2006) where important habitats such as semi-natural grasslands have been lost and fragmented (e.g. Cousins et al., 2015; Wallis De Vries et al., 2002). Less focus has been on the effect of modern forestry, although many pollinators are abundant also in forest habitats (e.g. Berg et al., 2011; Hanula et al., 2016). Insect pollinators in forests are crucial e.g. for wild berry production (Fröberg, 1996), but may also affect crop production in mosaic landscapes of forest and agriculture (e.g. Monasterolo et al., 2015). Forest habitats also have the potential to

mitigate the negative effects of habitat loss caused by agricultural intensification (Bergman et al., 2018). However, the knowledge about drivers of pollinator communities in forests is still relatively limited, and likely a complex interaction between floral availability and pollinator nesting resources (Rodríguez and Kouki, 2015).

Examples of important groups of pollinators are bees and wasps (Aculeata), butterflies (Papilionoidea), and hoverflies (Syrphidae) (e.g. Corbet et al., 1991; Jauker and Wolters, 2008; Rader et al., 2016; Steffan-Dewenter et al., 2005). Species richness and abundance of these groups are often strongly linked to the availability of nectar and pollen resources (Berg et al., 2011; Lucas et al., 2017; Potts et al., 2003b; Roulston and Goodell, 2011; Rubene et al., 2015) and should therefore be positively affected by a high diversity and abundance of flowering plants. Butterflies also depend on the availability of host plants (Curtis et al., 2015) for larval development, which is another resource directly linked to plant composition. For bees and wasps, nesting substrates can

* Corresponding author at: Department of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91 Stockholm, Sweden.

E-mail address: victor.johansson@su.se (V. Johansson).

<https://doi.org/10.1016/j.foreco.2020.118033>

Received 23 January 2020; Received in revised form 26 February 2020; Accepted 26 February 2020

Available online 03 March 2020

0378-1127/ © 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

be crucial, where the availability of bare ground and dead wood constitute two particularly important resources (Potts et al., 2005; Rodríguez and Kouki, 2015; Westerfelt et al., 2018). Dead wood may also be important for larval development of hoverflies (Speight, 1989). In general, pollinators seem to benefit from forest disturbance (Rodríguez and Kouki, 2017), and are more abundant in open forests, relative to closed forests, due to a more favorable microclimate (higher temperature and more light) and more floral resources (e.g. Hanula et al., 2016). Pollinators should therefore be most abundant in the open young seral stages, which relative to old-growth forests have received little attention in biodiversity research (Swanson et al., 2011). Depending on disturbance type and forest management system, young forests may also provide plenty of nesting resources such as exposed soil (Potts et al., 2005) and large amounts of dead wood (Rodríguez and Kouki, 2015; Siitonen, 2001).

In boreal forests, fire is the most important natural driver of disturbance (Angelstam, 1998; Whelan, 1995), and fire is one of the main factors structuring plant diversity patterns globally, across many types of habitats (Pausas and Ribeiro, 2017). The fire frequency in boreal north Europe has, however, decreased considerably due to fire suppression (Zackrisson, 1977), and today less than 0.01% of the forested land in Fennoscandia burns annually (Granström, 2001). The main stand replacing disturbance is now instead clear-cutting which, although it has been suggested to mimic fire disturbance (e.g. Hunter, 1993), may differ in several fundamental ways, not the least in dead wood amounts (Siitonen, 2001). Most research on the role of forest fires for biodiversity or the effects of clear-cutting in contrast to forest fires has focused on fire-dependent species or species associated with trees and dead wood (e.g. Gibb et al., 2006; Saint-Germain et al., 2008; Suominen et al., 2018). Pollinators have received less attention (Rivers et al., 2018) even though it is known that fire can change the ground vegetation quite substantially (Abrams and Dickmann, 1984; Faivre et al., 2016) and have profound effects on e.g. the availability of floral resources (Campbell et al., 2007; Galbraith et al., 2019; Potts et al., 2003a).

Wildfires hitting production forest landscapes add qualities important to biodiversity like habitats for fire-dependent species, particular soil conditions and forest structures (Gustafsson et al. 2019). Therefore, prescribed burning has been included as a nature conservation measure in some forest certification system of boreal north Europe (Johansson et al., 2013; Lehtonen and von Stedingk, 2017). Conservation fires constitute more than half of all Swedish forest fires, and a majority of these are performed on clear-cuts (Ramberg et al., 2018). However, normally, prescribed burning on clear-cuts has low burn severity (the depth of the burn, which often is measured as the loss of organic matter in the soil, Keeley, 2009; Nilsson, 2005), which might reduce the dissimilarity between them and clear-cuts without fires (Schimmel and Granström, 1996). Burn severity regulates the subsequent vegetation succession, since it determines how much of original vegetation that remain as living vegetative tissue in the soil, for instance as vital roots of grasses (Schimmel and Granström, 1996). Thus, one could hypothesize that a deeper and more severe soil disturbance at a fire will open up the area for colonization of pioneer herbs offering large amounts of pollen and nectar, in comparison to clearcutting, usually followed by a dominance of perennial grasses with limited resources for pollinators (Uotila and Kouki, 2005). It is likely that burn severity also affects other potential pollinator nesting habitats like availability of bare ground, which may increase after fire (Rodríguez and Kouki, 2015; Williams et al., 2010). Also dead wood amounts could be affected on clear-cuts through mortality of trees retained for conservation purposes (Heikkala et al., 2014). Recent studies from regions with Mediterranean climate suggest positive or unimodal relationships between burn severity and pollinator abundance (Galbraith et al., 2019; Lazarina et al., 2019). However, we know very little about how burn severity affects pollinator resources and the composition of the pollinator community in boreal forests.

The main aim of this study was to compare the pollinator communities and their potential resources between burned and unburned clear-cuts, and to investigate putative mechanisms behind differences between these two contrasting disturbance types. Specifically, we analyzed bees, wasps, hoverflies, and butterflies. We use a large wildfire area partly burned with high severity in a production forest landscape long managed through the clearcutting system, and compare with similarly managed, unburned production forests in surroundings. We hypothesized that the pollinator communities differed between burned and unburned clear-cuts due to differences in the diversity and cover of potential nectar/pollen plants as well as the amount of potential nesting resources (for simplicity we use the term 'nesting resources' also for hoverflies, even if they do not build nests). We expected burned clear-cuts to have a more flower-rich vegetation with less grass dominance, and should therefore harbor more pollinators compared to unburned sites. Moreover, we expected fire to create more bare ground and increase dead wood amounts, and hereby favor bees, wasps and hoverflies. A second aim was to analyze how burn severity (here measured as the mean humus depth) affects the amount of pollinator resources and the pollinator community. We hypothesized that dominance of flowing herbs would increase with burn severity and hence positively affect the richness and abundance of pollinators.

2. Material and methods

2.1. Study area and selection of clear-cuts

The study was conducted in and around a large (13 100 ha) wildfire area that burned in 2014 in the county of Västmanland, Sweden (59°54'N, 16°09'E) (Gustafsson et al., 2019). Before the fire the area was dominated by low productive Scots pine (*Pinus sylvestris*, 53%), mixed conifer forests (22%) and stands dominated by spruce (*Picea abies*, 18%), while stands with a large proportion of deciduous trees were rare (Gustafsson et al., 2019). In 2017, i.e. three years after the fire, we selected 37 pine-dominated clear-cuts: 22 burned (in the fire area) and 15 unburned (in the surroundings of the fire area) spread across the landscape. The 15 unburned clear-cuts were 3–5 years old to match the time since disturbance in the fire area. The size of unburned clear-cuts was on average 12.2 ha (SE = 2.39) and the corresponding number of burned clear-cuts was 13.0 ha (SE = 1.75). The distance from one clear-cut to the closest other clear-cut was on average 1653 m (min = 332 m).

2.2. Sampling of vegetation and environmental characteristics

The field work was conducted in June and July 2017. In each clear-cut we placed three 100 m line transects spread as much as possible over the clear-cut area. The minimum distance between two transects was 30 m. For the vegetation sampling, we placed 9 circular plots with a radius of 3 m (i.e. ~28.3 m²) along each transect (i.e. 27 per clear-cut in total). The plots were evenly spaced along the transect with 12.5 m between their center points (i.e. at 0 m, 12.5 m, 25 m, 37.5 m..., 87.5 m, 100 m). In each plot we estimated the proportional cover of all vascular plant species covering more than 100 cm² (i.e. 0.035% of a plot). We used the 'aerial cover', where the total cover in a plot cannot exceed 100%. Due to uncertain species determination in the field some species where only identified to genus. These were: *Betula* spp., *Carex* spp., *Taraxacum* spp., and *Epilobium* spp. We also estimated the proportional cover of the groups: mosses, grasses, herbs, dwarf shrubs (Ericaceae), and regenerating trees. Moreover, we estimated the proportional cover of exposed soil and exposed rocks. Burn severity (Keeley, 2009) was measured as the depth of the humus layer at three representative points in each circle (the remaining humus layer has earlier been shown to correlate well with burn severity; e.g. Schimmel and Granström, 1996; Parson et al., 2010). For each plot we also estimated the basal area of standing dead and alive trees (as two separate

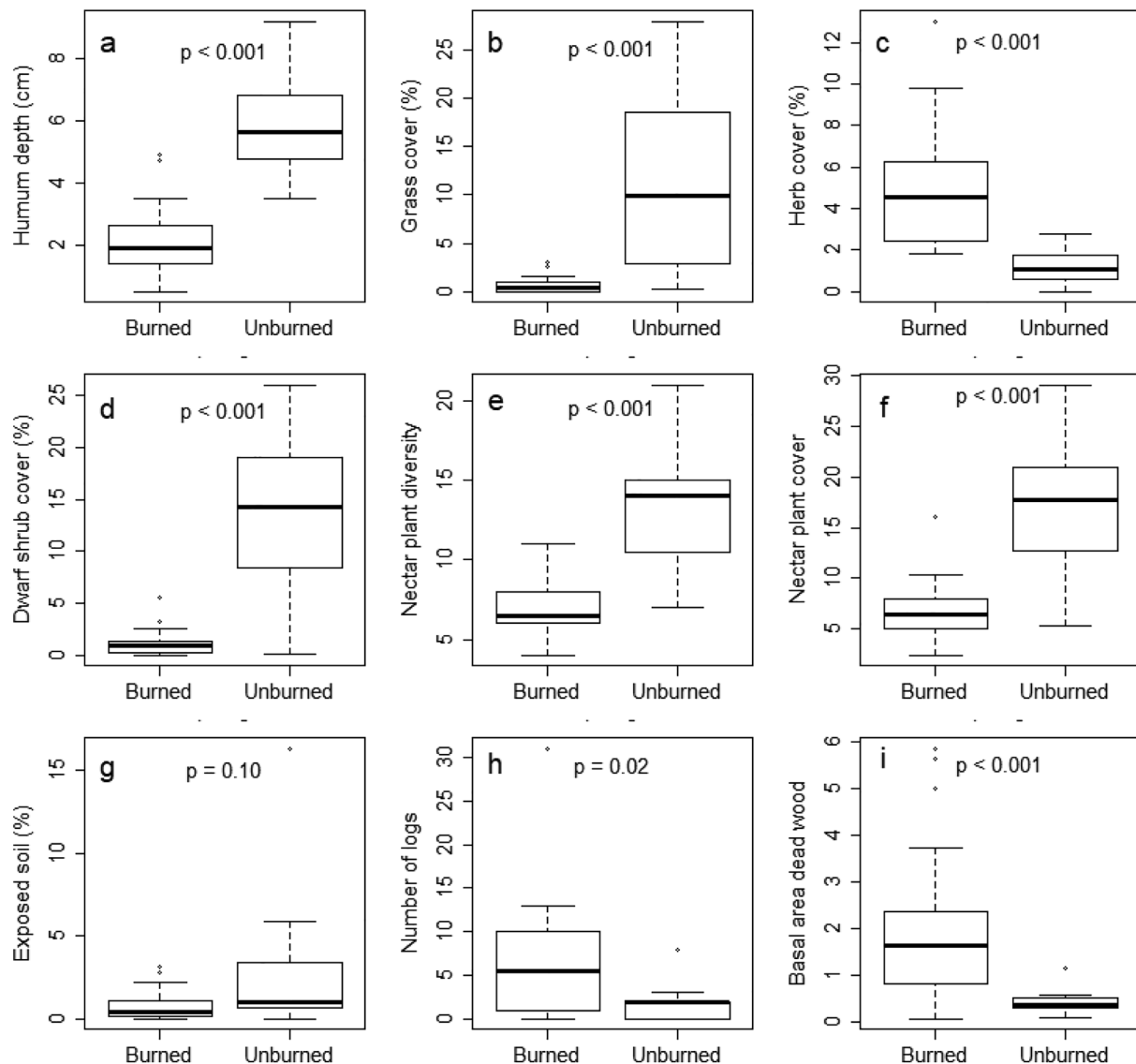


Fig. 1. The distribution of the average (a) humus depth, (b) grass cover, (c) herb cover, (d) dwarf shrub cover, (e) nectar/pollen plant diversity index, (f) nectar plant cover, (g) cover of exposed soil, (h) Number of logs > 10 cm, and (i) basal area standing dead wood in burned (n = 22) and unburned (n = 15) clear-cuts (based on 27 circular sample plots in each clear-cut). P-values from t-tests are shown for each variable in the plot. Remaining variables are shown in Appendix A, (Table A1). None of the relationships changed when excluding the four unburned clear-cuts with lost pan traps.

variables) using a relascope. Along each transect we counted the number of logs (> 10 cm in diameter) crossing the transect.

2.2.1. Moisture index

To account for differences in moisture between the clear-cuts (that may affect the vegetation) we created a community-weighted moisture index using the following formula:

$$WMI_j = \sum_{i=1}^i (EMV_i \times Ab_i) \div \sum_{i=1}^i Ab_i$$

where WMI_j = the community-weighted moisture index for clear-cut j , EMV_i = Ellenberg moisture value (Ellenberg et al., 1992) for species i , and Ab_i = mean cover in percent (among the 27 circular plots) of species i at clear-cut j . The index, hence, gives higher weight to more abundant species. However, to avoid that a few very dominant species completely drives the index, the maximum cover was delimited to 1% (i.e. cover > 1% was counted as 1%), which was the 80th percentile of the entire plant cover data (only six species covered > 1% on average).

2.2.2. Diversity and cover of potential nectar/pollen plants and butterfly host plants

Potential nectar and pollen plants were all plant species with flowers that may be visited by any of the four pollinator groups (Appendix A). We created two nectar/pollen plant indices. First, one for the diversity of nectar and pollen plants, defined as the total number of potential nectar and pollen plant species found in a clear-cut. Second, one for the total abundance of nectar/pollen plants, defined as the total cover of potential nectar and pollen plants (in the 27 circular plots) for a clear-cut. For butterflies we also created two host plant indices following the same method: one for the diversity and one for the total abundance of potential host plants. Host plants were all plants that potentially could be utilized by larvae of any species (also other than the ones we found) that occur in the study region (Eliasson and Liljeberg, 2009).

2.3. Sampling of pollinators

2.3.1. Bees, wasps and hoverflies

Bees, wasps and hoverflies were surveyed two times in 2017 (one in June and one in July) using pan traps. For each survey occasion we

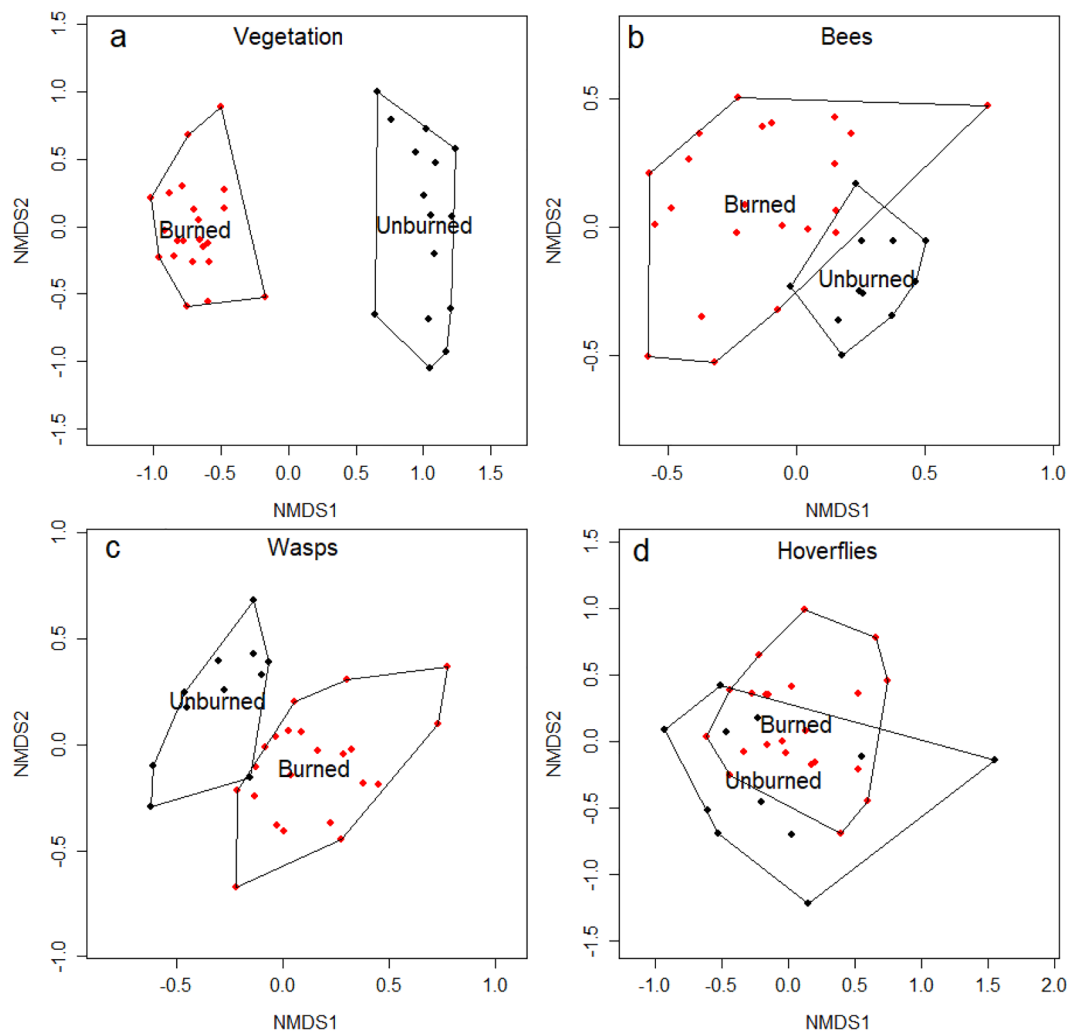


Fig. 2. The species composition of (a) vegetation, (b) bees, (c) wasps, and (d) hoverflies in burned (red dots) and unburned (black dots) clear-cuts. For plants (stress = 0.136) the ordination was 2-dimensional, while for bees (stress = 0.172), wasps (stress = 0.185), and hoverflies (stress = 0.170) needed 3-dimensional to reach convergence. However, for simplicity only the 2D-plots (of axes 1 and 2) for all groups are shown here. The black polygons show the outer limits of each group (burned or unburned). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

placed one trap at the center point of each transect (i.e. three traps per site). The pan traps consisted of round yellow plastic containers (without lid) that were 21 cm in diameter and 8 cm high (i.e. with a total volume of ~2.8 L). The traps were, thus, rather large, to increase the possibility of catching many individuals (Wilson et al., 2016). We choose yellow traps, as this color seems most efficient for capturing bees, wasps and hoverflies in Swedish clear-cuts (Berglund, 2016). The traps were filled to roughly one third with water and a drop of detergent was added in order to reduce tension of the water surface. The pan traps were placed at the clear-cut, as visible as possible (we actively avoided spots with high vegetation), during days with suitable weather conditions (sunny weather and light winds), and were emptied and removed from the sites six days later. As placing and collecting traps were time-consuming there was a few days' time-lag among stands (we did, hence, not sample exactly the same six days everywhere). However, there was no systematic difference in this time-lag between burned and unburned clear-cuts. The collected material was stored in ethanol. All bees, wasps and hoverflies were identified to species-level in the lab by species experts Lars Norén (bees and wasps) and Kristoffer Hylander (hoverflies). In the analysis, we used pooled data for each clear-cut for bees, wasps and hoverflies, respectively (i.e. both from the three traps and from the two occasions). In four of the unburned clear-cuts some of the traps either disappeared or fell over, and we therefore removed these clear-cuts from further analysis (i.e. for unburned clear-cuts $n = 11$).

2.3.2. Butterflies

Butterflies were surveyed two times in 2017 (one in June and one in July) along all transects. All individuals were determined to species in the field and counted within 10 m from the transect (i.e. 20 m width in total) when slowly walking along the transect (~10 min per transect). All butterfly inventories were performed in sunny weather with a temperature > 17 °C. Species that could not always be separated in the field were later merged and treated as one in the analysis. These were (1) *Plebejus argus* and *P. idas* (*Plebejus argus/idas* henceforth), and (2) *Leptidea sinapis* and *L. juvernica* (*Leptidea sinapis/juvernica*). In the analysis (see below) we used the pooled data for each clear-cut (i.e. both from the three transects and from the two occasions).

2.4. Statistical analysis

2.4.1. The effect of burned clear-cuts

To compare differences in the vegetation and environmental variables between burned and unburned clear-cuts we used the average values for each variable and clear-cut (from the 27 circular plots) and tested the difference between the two treatments with t-tests.

To describe the general plant species composition a nonmetric multidimensional scaling (NMDS) analysis was performed on a species-by site matrix, including plant abundance data (average cover of each species among the 27 sample plots). The NMDS was performed with the

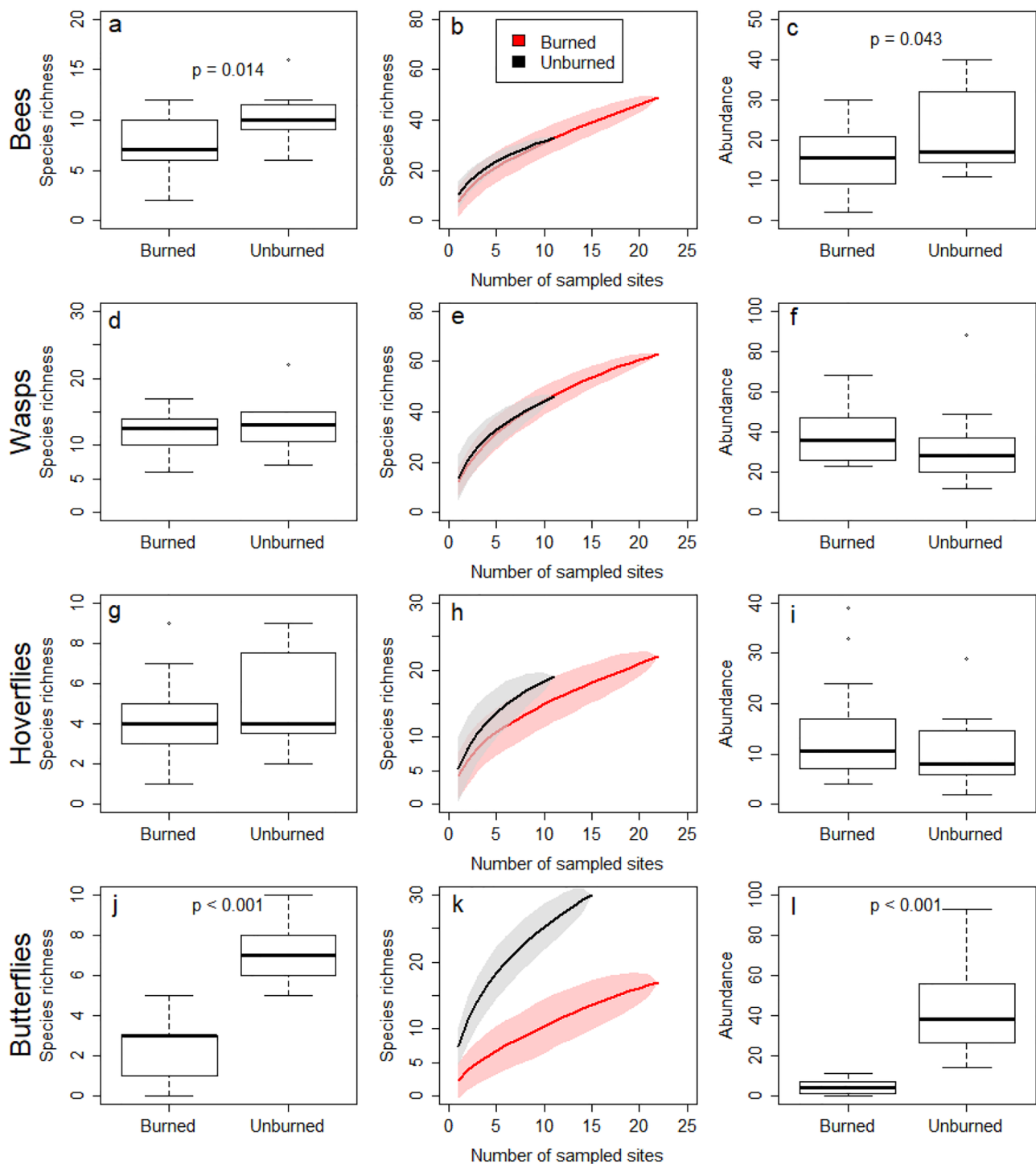


Fig. 3. The distributions of species richness (a, d, g, j) and abundance (c, f, i, l), and species accumulation curves (b, e, h, k) of bees (a, b, c), wasps (d, e, f), hoverflies (g, h, i), and butterflies (j, k, l) in burned ($n = 22$) and unburned clear-cuts ($n = 15$ for butterflies and $n = 11$ for bees, wasps, and hoverflies). Significant differences are shown with corresponding p-values. For parameter estimates and remaining p-values see Table 1. The species accumulation curves (b, e, h, k) show the mean (thick line) with 95% confidence intervals (transparent lighter color).

R package *vegan* (Oksanen et al., 2019) using the Bray–Curtis dissimilarity measure and default settings (with 2 dimensions, stress = 0.136). Significant relationships between species composition and the explanatory variables (here treatment and moisture index) were assessed with multivariate ANOVA (function *adonis2* in R package *vegan*). We investigated the marginal effect of the variables (instead of the default sequentially test of terms, which is sensitive to the order of added variables). To illustrate relationships between the species composition and the explanatory variables we used the function *envfit*.

For each pollinator group we used the pooled data from each clear-cut (i.e. from the three transects and both survey occasions) in all analyses. We tested differences in species richness and abundance at clear-cut level between the two treatments using generalized linear models (GLM), with treatment as the only explanatory variable. For species richness we used a poisson distribution (for all groups), while we used a negative binomial distributions for modeling abundance of the four groups, due to over-dispersion. To compare accumulated species richness across different clear-cuts between unburned and burned

Table 1

Parameter estimates (with standard error) and p-values for models of species richness and abundance of bees, wasps, hoverflies and butterflies in unburned compared to burned clear-cuts (i.e. statistical tests of the patterns seen in Fig. 3). Significant (< 0.05) p-values in bold.

Species group	Richness		Abundance	
	Estimate (SE)	p-value	Estimate (SE)	p-value
Bees	0.30 (0.12)	0.014	0.39 (0.19)	0.043
Wasps	0.12 (0.10)	0.23	-0.17 (0.15)	0.27
Hoverflies	0.20 (0.16)	0.24	-0.26 (0.23)	0.25
Butterflies	1.14 (0.17)	< 0.001	2.21 (0.21)	< 0.001

forest we also constructed species accumulation curves for each species group separately, with 1000 permutations and sites added in random order (function *specaccum* in R package *vegan*). Accumulated species richness can be compared at the same sample size (number of clear-cuts) for the two groups, and statistical interpretation be made by comparing the confidence bands around the curves at that point (Gotelli and Colwell, 2001).

To analyze differences in pollinator species composition between the two treatments we used the same methods as for the vegetation data (i.e. NMDS and multivariate ANOVA, see above). For the NMDS we used three dimensions to reach convergence for both bee, wasps, and hoverflies. For butterflies we could not perform any meaningful analyses of species composition as the species richness and abundances in burned clear-cuts were too low. To reveal species that contribute most to the differences in species composition between burned and unburned clear-cuts we also performed an indicator species analysis for each of the four species groups (Dufrêne and Legendre, 1997) using the *indval* function in R package *labdsv*.

2.4.2. The effect of burn severity

The effect of burn severity (i.e. mean thickness of the humus layer) on potential resources for the three groups of pollinators was assessed by Pearson correlations. The mean humus layer was correlated against: the four nectar/pollen and host plant indices, the cover of exposed soil, number of logs and the basal area of dead trees. Then we tested if

pollinator richness and abundance (for all four groups separately) could be explained by burn severity using GLM:s. For richness we used poisson distributions and for abundance we used negative binomial distributions (due to over-dispersion). To account for the fact that clear-cuts close to the border of the fire area may be situated closer to sources for recolonization (outside the fire area) compared to clear-cuts in the center we also tested if the AIC improved by adding distance to the edge (log-transformed) of the fire area in all models (i.e. having both burn severity and distance to edge in a multiple model for each response variable).

Analysis of the species composition of pollinators in burned clear-cuts could only be performed for bees, wasps and hoverflies (see above). For this analysis we used the same methods as for the whole data (i.e. NMDS and multivariate ANOVA) but included mean humus depth as the only explanatory variable.

For all statistical analyzes we used the statistical software R 3.5.1 with add-on libraries MASS, Vegan 2.5.6 (Oksanen et al., 2019) and labdsv 2.0.1 (for the indicator species analysis).

3. Results

3.1. The effect of burned clear-cuts

3.1.1. Vegetation and environmental variables

There were clear differences in most vegetation and environmental variables between burned and unburned clear-cuts (Fig. 1, Appendix A, Table A1). The mean humus layer was deeper in unburned (average = 5.9 cm) compared to burned clear-cuts (average = 2.2 cm). The unburned clear-cuts had a higher mean cover of grasses (11.6% compared to 0.7% in burned) and dwarf shrubs (13.5% compared to 1.2%), while the burned clear-cuts instead had a higher herb cover (4.9% compared to 1.2% in unburned) and moss cover (33.4% compared to 21.0%). All four indices for richness and abundance of nectar/pollen plants and host plants were clearly higher in unburned clear-cuts (Fig. 1, Table A1). Both the basal area of standing dead trees and the number of logs were larger in burned clear-cuts (Fig. 1), while the basal area of alive trees was higher in unburned clear-cuts (Table A1). The cover of exposed soil tended to be larger in unburned clear-cuts, while

Table 2

Species associated with unburned or burned clear-cuts in each species group, and the corresponding indicator species value.

Species group	Unburned		Burned	
	Species	Indicator value	Species	Indicator value
Bees	<i>Andrena fulvida</i>	0.27 (p = 0.031)	<i>Lasioglossum leucopus</i>	0.71 (p = 0.005)
	<i>Bombus lucorum</i>	0.55 (p = 0.003)		
	<i>Bombus pascorum</i>	0.89 (p = 0.001)		
	<i>Bombus pratorum</i>	0.45 (p = 0.001)		
	<i>Bombus soroeensis</i>	0.40 (p = 0.028)		
	<i>Hylaeus angustatus</i>	0.56 (p = 0.020)		
	<i>Hylaeus brevicornis</i>	0.51 (p = 0.001)		
	<i>Hylaeus confusus</i>	0.74 (p = 0.002)		
Wasps	<i>Arachnospila spissa</i>	0.55 (p = 0.003)	<i>Ammophila sabulosa</i>	0.59 (p = 0.007)
	<i>Auplopus carbonarius</i>	0.34 (p = 0.027)	<i>Nysson trimaculatus</i>	0.59 (p = 0.019)
	<i>Dipogon bifasciatus</i>	0.61 (p = 0.001)	<i>Trypoxylon medium</i>	0.72 (p = 0.002)
	<i>Dipogon variegatus</i>	0.39 (p = 0.013)		
	<i>Dolichurus corniculatus</i>	0.70 (p = 0.001)		
	<i>Priocnemis schioedtei</i>	0.43 (p = 0.013)		
Hoverflies	<i>Anasimyia interpuncta /lunulata</i>	0.50 (p = 0.013)	<i>Xylota jakutorum</i>	0.77 (p = 0.002)
	<i>Sericomyia silentis</i>	0.42 (p = 0.022)		
Butterflies	<i>Aphantopus hyperantus</i>	0.57 (p = 0.001)		
	<i>Boloria euphrosyne</i>	0.92 (p = 0.001)		
	<i>Callophrys rubi</i>	0.47 (p = 0.003)		
	<i>Coenonympha arcania</i>	0.27 (p = 0.026)		
	<i>Gonepteryx rhamni</i>	0.35 (p = 0.030)		
	<i>Melitaea athalia</i>	0.93 (p = 0.001)		
	<i>Plebejus argus/idas</i>	0.77 (p = 0.001)		

the moisture index was very similar between the two treatments (Table A1).

In total we found 81 plant taxa (that covered more than 1 dm² in any circle plot, Table A2). There were clear differences in plant species composition between unburned and burned clear-cuts based on the multivariate ANOVA ($R^2 = 0.46$, $F = 37.4$, $p = 0.001$, Fig. 2). The species composition was also weakly explained by the moisture index ($R^2 = 0.08$, $F = 6.15$, $p = 0.002$, Fig. 2). The most common species in unburned clear-cuts were *Deschampsia flexuosa*, *Vaccinium myrtillus*, *Vaccinium vitis-idea*, while the dominating species in burned sites instead were *Chamaenerion angustifolium*, *Betula* spp. and *Populus tremula*.

3.1.2. Bees

In total we recorded 583 individuals of 61 species (Appendix A, Table A3) in the 22 burned and 11 unburned clear-cuts (four burned sites were removed as trap catches were destroyed). The most abundant species were: *Hylaeus confusus* (123 individuals), *Lasioglossum leucopus* (94), and *Lasioglossum fratellum* (90). The species richness at clear-cut level was significantly higher in unburned (average = 10.2) compared to burned clear-cuts (average = 7.5, Fig. 3, Table 1). Accumulated species richness (at 11 clear-cuts) did not differ between burned and unburned clear-cuts, based on the confidence bands of the species accumulation curves (Fig. 3). The abundance was significantly higher in unburned (average = 22.5) compared to burned clear-cuts (average = 15.2, Fig. 3, Table 1). For the species composition there was a significant difference between unburned and burned clear-cuts ($R^2 = 0.13$, $F = 4.6$, $p = 0.001$, Fig. 2). Based on the indicator species analysis, eight species were significantly associated with unburned clear-cuts, while only one was associated with burned (Table 2, Table A3).

3.1.3. Wasps

In total we recorded 1226 individuals of 78 species (Appendix A, Table A3). The most abundant species were: *Anoplius nigerrimus* (248 individuals), *Trypoxylon medium* (245), *Nysson trimaculatus* (140), and *Trypoxylon minus* (93). Species richness and abundance at clear-cut level did not differ significantly between unburned and burned clear-cuts (Fig. 3, Table 1), which was also true for the accumulated richness (at 11 clear-cuts) according to the species accumulation curves (Fig. 3). For the species composition there was a significant difference between unburned and burned clear-cuts ($R^2 = 0.12$, $F = 4.3$, $p = 0.001$, Fig. 2). Based on the indicator species analysis, six species were significantly associated with unburned clear-cuts, while three were associated with burned (Table 2, Table A4).

3.1.4. Hoverflies

In total we recorded 416 individuals of 29 species (Appendix A, Table A5). The most abundant species (together comprising 73% of all individuals) were *Xylota jakutorum* (219), *Anasimyia interpuncta/lunulata* (38), *Orthonevra intermedia/stackelbergi* (24) and *Xylota florum* (24). Species richness and abundance at clear-cut level did not differ significantly between unburned and burned clear-cuts (Fig. 3, Table 1). However, the accumulated richness (at 11 clear-cuts) suggested a slighter higher total species richness in unburned clear-cuts. (Fig. 3). For the species composition there was a significant difference between unburned and burned clear-cuts ($R^2 = 0.11$, $F = 3.8$, $p = 0.003$, Fig. 2). The indicator species analysis showed that two species were significantly associated with unburned clear-cuts, and one with burned clear-cuts (Table 2, Table A5).

3.1.5. Butterflies

In total we recorded 728 individuals of 33 species (Appendix A, Table A5). The three most common species overall (comprising almost 80% of all individuals) were *Plebejus argus/idas* (378), *Boloria euphrosyne* (131), and *Melitaea athalia* (65). Both species richness and abundance was clearly higher in unburned clear-cuts compared to

burned clear-cuts (Fig. 3, Table A6), which was also true for the accumulated richness (Fig. 3). Unburned clear-cuts had on average 7.4 species and 41.8 individuals, while the corresponding numbers for burned sites were 2.4 and 4.6, respectively. The indicator species analysis showed that seven species were associated with unburned clear-cuts, while no species were associated with burned (Table 2).

3.2. Effects of burn severity on pollinators and their resources

The mean humus depth (i.e. our proxy for burn severity) did not show any significant relationship with species richness, abundance, or species composition of the four pollinator groups, and none of these response variables were explained by the distance to the edge of the fire area. None of the potential resources for pollinators (i.e. the diversity of nectar/pollen plants and host plants, abundance of nectar/pollen plants and host plants, cover of exposed soil, basal area standing dead wood and number of logs) were significantly correlated with the mean humus depth (Appendix B, Table B1).

4. Discussion

We show that fire had large effects on the resources for pollinators on clear-cuts. The diversity and cover of potential nectar/pollen plants decreased, while potential nesting resources to some extent instead increased on burned compared to unburned clear-cuts. The additional effect of fire had strong negative effects on butterfly richness and abundance, while this effect was smaller for bees, wasps and hoverflies. However, for the latter three groups the community composition differed. Burn severity seems to have relatively small effects on pollinators and their resources.

4.1. The effects of fire on potential resources for forest pollinators

We show that fire on clear-cuts has profound effects on the vegetation, in accordance with earlier studies in boreal forests (e.g. Faivre et al., 2016; Schimmel and Granström, 1996; Turner et al., 1997) and from other forested ecosystems (e.g. Foster et al., 2017). There was not only a clear difference in the vegetation composition between unburned and burned clear-cuts, but also a clear reduction of vegetation cover in general in the latter (Table A1). The grass cover was significantly lower in burned sites, while the cover of flowering herbs instead was higher, in accordance with our hypothesis. However, as the cover of dwarf shrubs, which also constitute important floral resources for pollinators in forests (Rodríguez and Kouki, 2015), also decreased the overall effect of fire on the nectar/pollen plant cover and host plant cover was very negative. This is in contrast to several other studies from temperate managed conifer forests and Mediterranean forests instead showing clear positive effects on floral resources for forest pollinators shortly after fire (e.g. Campbell et al., 2007; Galbraith et al., 2019; Potts et al., 2003a). The most likely reason for this is that these studies investigate the effect of fire opening up the canopy of mature forests, which should benefit flowering plants in general, while we compare the burned clear-cuts with already harvested forests. However, also compared to a study of prescribed burning of clear-cuts (Rubene et al. 2015), we show more negative effects on the amounts of potential nectar and pollen plants, even if one herb *Chamaenerion angustifolium* increased very much. One reason could be differences in burn severity. The small average humus depth in the present study, and the fact that the rhizomatous taxa *Deschampsia flexuosa* and dwarf shrubs *Vaccinium* spp. still had a low recovery after three years, suggest a generally high burn severity in the present study (Schimmel and Granström, 1996), while prescribed clear-cut burnings most often are less intense (Nilsson, 2005).

Our results also suggest that fire may affect the amount of potential nesting resources for pollinators, which agrees with e.g. Potts et al. (2005). Both standing and downed coarse dead wood was more abundant in burned, compared to unburned clear-cuts. The reason is most

likely that fire kills retained trees (Heikkala et al., 2014; Hyvärinen et al., 2009), which both could create standing and downed dead wood, and also explains the smaller basal area of alive trees in burned clear-cuts (Table A1). Surprisingly, the cover of exposed soil was not higher in burned compared to unburned clear-cuts, even though the vegetation cover was lower. One reason could be that the generally high burn severity completely removes the soil layer and instead expose underlying rocks (the cover of rocks was 6.4 times higher in burned sites, Table A1), or that exposed soil blows away.

4.2. The effects of clear-cut burning on forest pollinators

Our results show that fire has strong effects on pollinator communities, in accordance with earlier research from other regions (e.g. Bogusch et al., 2015; Campbell et al., 2007; Galbraith et al., 2019; Potts et al., 2003a). However, earlier studies have shown that after an initial decrease in abundance, due to fire mortality (even if ground nesting species may survive fire, Cane and Neff, 2011), the pollinator community usually peaks during the two to three post-fire years (Bogusch et al., 2015; Potts et al., 2003b). In contrast to this and our hypothesis, we mainly show negative effects on the pollinator community three years after fire on clear-cuts. The main reason is likely the clear reduction in the cover of potential nectar/pollen plants, driven by the reduction of dwarf shrubs *Vaccinium* spp. in burned clear-cuts (see above), which is an obvious factor of importance for pollinators in general (e.g. Berg et al., 2011; Lucas et al., 2017; Potts et al., 2003b; Roulston and Goodell, 2011; Rubene et al., 2015). It is also possible that the change in vegetation composition due to fire has led to differences in the flower phenology. Burned clear-cuts are mainly dominated by one relatively late-flowering species (*Chamaenerion angustifolium*), while unburned clear-cuts may provide a longer season of plants important to pollinators (Ebeling et al., 2008). Another potential reason for fewer pollinators in the fire area could be slow recolonization after fire, as many pollinators may have a rather poor dispersal ability (e.g. Steffan-Dewenter et al., 2002). However, if dispersal was limiting we would expect significant relationships between richness/abundance and how far into the fire area a clear-cut was situated (distance to edge), which we did not find for any of the three groups.

The effect of fire differed among the three taxonomic groups. Butterflies showed the strongest negative effect, with a 67% lower richness and an almost 90% lower abundance in burned compared to unburned sites. Our results suggest that this reduction of butterflies may not only be an effect of fewer nectar resources, but could also be a loss of host plants that should decrease larval development (Curtis et al., 2015). The effect of fire was less pronounced for the remaining three groups, even if the richness and abundance of bees was slightly lower in burned sites. All these three groups, however, showed a rather clear difference in community composition between burned and unburned clear-cuts. One reason could be that bees, wasps and hoverflies also depend on nesting resources (larval substrates for hoverflies), and it is increasingly acknowledged that such resources are important for forming the pollinator community (e.g. Murray et al., 2012; Potts et al., 2005; Rodríguez and Kouki, 2015). It is possible that the larger amounts of coarse dead wood in burned clear cuts benefit these groups (Speight, 1989; Westerfelt et al., 2018). This may to some extent buffer the negative effects of decreased cover of potential nectar/pollen plants.

The indicator species analyzes point out species that are the strongest drivers of differences in species composition between burned and unburned clear-cuts. Most of these are rather common generalist species, and none of them is of special conservation concern. As the indicator species are relatively few (especially in the burned clear-cuts) it is difficult to see any general patterns when it comes to e.g. nesting preferences for species associated with burned and unburned sites. Above and below ground nesters (for bees and wasps) are not clearly overrepresented in any of the two treatments, and the same goes for species depending on dead wood. However, at the individual species

level there are probably some differences in nesting conditions or resources between the two treatments. For example, four bumblebee species (*Bombus*) were associated with unburned clear-cuts, perhaps because they require early floral resources, such as *Vaccinium myrtillus*. More detailed knowledge of individual species are, thus, required to understand the observed patterns, and perhaps also more detailed data on the distribution of specific substrates and resources.

4.3. The effect of burn severity on pollinators and their resources

Burn severity can have large effects on available floral resources and nesting availability (both above and below ground) for pollinators (e.g. Galbraith et al., 2019; Lazarina et al., 2019). However, we show no significant relationships between burn severity (humus depth) and pollinator richness, abundance or composition, and no correlation to their potential resources. One reason could be that the burn severity in general was rather high (see above), and the lack of lightly burned sites could decrease the variability in pollinator resources along the burn severity gradient. Another possible reason for the limited explanatory power of the humus depth is that this proxy does not completely capture 'burn severity' due to e.g. pre-fire variation in humus depth across the fire area (Parson et al., 2010).

4.4. Potential caveats of the sampling method

Some methodological issues associated with the pan traps need to be considered when interpreting our results. As our main aim was to compare drivers of differences between burned and unburned clear-cuts, we prioritized to sample many clear-cuts rather than having many replicates at each site (which could include using more pan traps with additional colors and more visits over the season). The mega-fire (the largest fire for at least 100 years in Sweden; Gustafsson et al., 2019) also offered a unique opportunity to sample over a large burned landscape. Nevertheless, by using this approach, we clearly miss many species (based on the accumulation curves, Fig. 3). Even though yellow traps seem to be most efficient for capturing many insect pollinators in Swedish clear-cuts (Berghlund, 2016), it is likely that we miss species that are more often trapped using other colors (e.g. Heneberg and Bogusch, 2014). Moreover, by focusing on the period when pollinators in our study region generally should be most active (and flowers most abundant) we probably also miss species with activity peaks before or after June and July, for example species that depend much on early-flowering *Salix* spp. (Pekkarinen, 1997). There are also two possible caveats when it comes to the comparison between treatments; both potentially underestimating densities of bees, wasps and hoverflies in unburned clear-cuts. First, even if we tried to place the traps as visible as possible in all clear-cuts, the generally higher cover of surrounding vegetation in unburned sites may to some extent reduce their visibility. Second, colored pan traps may generally underestimate population sizes in more flower-rich environments, such as the unburned clear-cuts, as they prefer real flowers (e.g. Berghlund, 2016; Roulston et al., 2007), leading to a reduced visitation rate to pan traps. All these caveats will have strongest effects on species richness, as we miss many rare species, while composition and total abundance are less affected, as they depend more on the common species.

5. Conclusions and conservation implications

Early successional forests can harbor a relatively diverse pollinator community that should contribute to the maintenance of biodiversity and ecosystem services in forests (Hanula et al., 2016). Even though it is unclear whether these forests contribute with unique species, it is possible that they also have positive effects on crop production in mosaic landscapes of forest and agriculture (Monasterolo et al., 2015). Clear-cuts often provide flower-rich vegetation and nesting substrate that should benefit pollinators (e.g. Romey et al., 2007; Rubene et al.,

2015). We show that fire on clear-cuts mainly seem to have negative effects on the pollinator richness and abundance, at least in the short term, which most likely mainly is driven by a reduction of flowering plants such as dwarf shrubs *Vaccinium* spp., despite a higher herb cover. The negative effect is evident for butterflies, while differences are smaller for bees, wasps and hoverflies. For the latter three, fire nevertheless leads to changes in the community composition, and it is possible that increased nesting resources in burned clear-cuts to some extent buffer the negative effect of reduced cover of potential nectar and pollen plants. Ponisio et al. (2016) recommend heterogeneity in burn severity over landscapes to promote pollinators, since they found community differences between severities. Although we did not detect such differences, a large-scale mix of unburned and burned forests would due to the complementarity in species composition between them, result in an overall more diverse pollinator community. It should also be remembered that our study only considers a relatively short time-frame (three years), and it is therefore possible that burned clear-cuts will provide better habitat for pollinators in the future. It is, thus, important to follow the development of vegetation and changes in the pollinator community over longer time-periods. Future studies would also benefit from more intensive sampling at site level, to get better data on species richness, including rare species. Based on our current results, however, we conclude that fire on clear-cuts does not seem to benefit pollinators in general, which agrees with Rubene et al. (2015). As we see no clear reduction in negative effects with decreasing burn severity, it is likely that also low-severity prescribed fires could disfavor

pollinators. However, it is possible that the severity of prescribed clear-cut fires is lower than the entire burn severity gradient of the wildfire we study, and this hence needs further investigation.

CRediT authorship contribution statement

Victor Johansson: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Visualization, Funding acquisition. **Lena Gustafsson:** Conceptualization, Methodology, Writing - review & editing. **Petter Andersson:** Conceptualization, Methodology, Writing - review & editing. **Kristoffer Hylander:** Conceptualization, Methodology, Formal analysis, Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

We have no conflicts of interest.

Acknowledgements

We thank Oskar Kindvall, Andreas Press, and Claes Vernerback for conducting the field inventories and Lars Norén for identifying all Aculeata species, and Jan Edelsjö for confirming the identification of some hoverflies. The work was funded by Skogssällskapet grant no 2017-231.

Appendix A. Environmental characteristics, vegetation and pollinators in burned and unburned clear-cuts

Table A1

Environmental characteristics (mean and range) in burned (n = 22) and unburned clear-cuts (N = 15). The p-values are from t-tests between the two groups (p < 0.05 in bold).

Variable	Burned	Unburned	p-value
Clear-cuts size (ha)	13.0 (3.3–34.9)	12.2 (3.7–33.2)	p = 0.79
Humus depth (cm)	2.2 (0.5–4.9)	5.9 (3.5–9.2)	p < 0.001
Exposed rocks (%)	31.4 (5.4–51.1)	4.9 (1.2–16.6)	p < 0.001
Exposed soil (%)	0.8 (0–3.2)	2.8 (0–16.3)	p = 0.10
Total vegetation cover (%)	13.3 (8.5–19.2)	34.8 (20.8–52.7)	p < 0.001
Moss cover (%)	33.4 (11.8–57.8)	21.0 (3.7–53.4)	p < 0.001
Grass cover (%)	0.7 (0–3.0)	11.6 (0.33–27.9)	p < 0.001
Herb cover (%)	4.9 (1.8–13.0)	1.2 (0–2.8)	p < 0.001
Dwarf shrub cover (%)	1.2 (0.01–5.6)	13.5 (0.1–26.0)	p < 0.001
Regeneration of deciduous trees (%)	5.4 (1.2–13.1)	2.5 (0–11.0)	p = 0.010
Regeneration of conifer trees (%)	0.02 (0–0.4)	1.0 (0.1–4.9)	p = 0.005
Basal area alive trees	0.3 (0–3.2)	1.9 (0–6.1)	p = 0.012
Basal area dead trees	2.0 (0.1–5.9)	0.4 (0.1–1.1)	p < 0.001
Number of logs (> 10 cm in diameter)	6.2 (0–31)	2.1 (0–8)	p = 0.02
Moisture index	5.1 (4.8–5.8)	4.9 (4.1–6.0)	p = 0.16
Host plant diversity	8.5 (5–11)	11.5 (6–17)	p = 0.002
Host plant cover (%)	7.4 (2.4–16.7)	27.8 (19.5–37.6)	p < 0.001
Nectar/pollen plant diversity	6.8 (4–11)	13.1 (7–21)	p < 0.001
Nectar/pollen plant cover (%)	6.7 (2.4–16.0)	17.6 (5.4–29.0)	p < 0.001

Table A2

The mean cover (%) among sites for all vascular plants included in the study (i.e. covering > 1 dm² in any plot) in unburned (n = 15) and burned (n = 23) clear-cuts. The table also shows the Ellenberg moisture value and if the plant was classified as potential host plant (for butterflies) and potential nectar/pollen plant for any of the three pollinator groups.

Species	Ellenberg moisture	Host plant	Nectar/pollen plant	Mean cover (%) unburned	Mean cover (%) burned
<i>Agrostis canina</i>	9	1	0	0.0173	0.0000
<i>Agrostis capillaris</i>	NA	1	0	0.0151	0.0144
<i>Agrostis gigantea</i>	8	1	0	0.1239	0.0363
<i>Alnus glutinosa</i>	9	0	0	0.0000	0.0002
<i>Anemone nemorosa</i>	5	0	1	0.0105	0.0000
<i>Arctostaphylos uva-ursi</i>	3	1	1	0.0074	0.0269

(continued on next page)

Table A2 (continued)

Species	Ellenberg moisture	Host plant	Nectar/pollen plant	Mean cover (%) unburned	Mean cover (%) burned
<i>Betula</i> spp.	NA	1	0	2.2623	3.9567
<i>Calamagrostis arundinacea</i>	5	1	0	0.7045	0.2898
<i>Calamagrostis canescens</i>	9	1	0	0.0580	0.0000
<i>Calamagrostis epigeios</i>	NA	1	0	0.0099	0.0000
<i>Calluna vulgaris</i>	NA	1	1	0.6795	0.7372
<i>Carex</i> spp.	NA	0	0	0.7645	0.4227
<i>Cerastium fontanum</i>	5	0	1	0.0002	0.0008
<i>Chamaenerion angustifolium</i>	5	0	1	0.2924	4.7814
<i>Cirsium helenioides</i>	8	1	1	0.0025	0.0000
<i>Cirsium palustre</i>	8	1	1	0.0012	0.0000
<i>Cirsium vulgare</i>	5	1	1	0.0003	0.0000
<i>Deschampsia cespitosa</i>	7	1	0	0.0938	0.0018
<i>Deschampsia flexuosa</i>	NA	1	0	10.5447	0.3224
<i>Dryopteris carthusiana</i>	NA	0	0	0.0139	0.0008
<i>Dryopteris filix-mas</i>	5	0	0	0.0025	0.0000
<i>Empetrum nigrum</i>	6	0	1	0.0247	0.0000
<i>Epilobium</i> spp.	NA	0	1	0.0000	0.0041
<i>Equisetum sylvaticum</i>	7	0	0	0.0097	0.0025
<i>Eriophorum angustifolium</i>	9	0	0	0.0000	0.0034
<i>Eriophorum vaginatum</i>	9	0	0	0.0347	0.0320
<i>Festuca ovina</i>	NA	1	0	0.0074	0.0000
<i>Fragaria vesca</i>	5	0	1	0.0025	0.0000
<i>Frangula alnus</i>	8	1	1	0.0030	0.0000
<i>Galeopsis speciosa</i>	5	0	1	0.0496	0.0000
<i>Gymnocarpium dryopteris</i>	6	0	0	0.0014	0.0021
<i>Hieracium</i> L. sect. <i>Hieracium</i>	NA	0	1	0.0039	0.0000
<i>Juncus conglomeratus</i>	7	0	0	0.0259	0.0004
<i>Juncus effusus</i>	7	0	0	0.1411	0.0156
<i>Juncus filiformis</i>	9	0	0	0.0235	0.0011
<i>Juniperus communis</i>	4	0	0	0.1069	0.0000
<i>Lathyrus linifolius</i>	4	1	1	0.0003	0.0003
<i>Lathyrus pratensis</i>	6	1	1	0.0000	0.0008
<i>Linnea borealis</i>	5	0	1	0.0587	0.0000
<i>Logfia arvensis</i>	3	0	0	0.0000	0.0001
<i>Lotus corniculatus</i>	4	1	1	0.0000	0.0439
<i>Lupinus polyphyllus</i>	5	1	1	0.0000	0.0152
<i>Luzula multiflora</i>	5	0	0	0.0012	0.0000
<i>Luzula pilosa</i>	5	0	0	0.7673	0.1443
<i>Lycopodium annotinum</i>	6	0	0	0.0086	0.0000
<i>Maianthemum bifolium</i>	5	0	1	0.0321	0.0000
<i>Melampyrum pratense</i>	NA	1	1	0.0589	0.0086
<i>Melampyrum sylvaticum</i>	5	1	1	0.1797	0.0000
<i>Milium effusum</i>	5	1	0	0.0025	0.0000
<i>Mycelis muralis</i>	5	0	1	0.0029	0.0001
<i>Oxalis acetosella</i>	5	0	1	0.0012	0.0000
<i>Picea abies</i>	NA	0	0	0.7449	0.0000
<i>Pilosella dubia</i>	NA	0	1	0.0000	0.0017
<i>Pinus sylvestris</i>	NA	0	0	0.1763	0.0212
<i>Populus tremula</i>	5	1	0	0.0330	1.2453
<i>Potentilla erecta</i>	NA	0	1	0.1638	0.0036
<i>Pteridium aquilinum</i>	5	0	0	0.4346	0.1094
<i>Quercus robur</i>	NA	0	0	0.0012	0.0000
<i>Rubus idaeus</i>	NA	0	1	2.6066	0.3751
<i>Rubus saxatilis</i>	6	0	1	0.0099	0.0000
<i>Rumex acetosa</i>	NA	1	0	0.0088	0.0000
<i>Rumex acetosella</i>	3	1	0	0.0049	0.0109
<i>Rumex crispus</i>	7	0	0	0.0062	0.0000
<i>Salix aurita</i>	8	1	1	0.0235	0.0042
<i>Salix caprea</i>	6	1	1	0.0470	0.2300
<i>Salix cinerea</i>	9	1	1	0.0000	0.0025
<i>Salix repens</i>	7	1	1	0.0000	0.0025
<i>Sambucus racemosa</i>	5	0	1	0.0469	0.0000
<i>Senecio sylvaticus</i>	5	0	1	0.0358	0.0049
<i>Solidago canadensis</i>	NA	0	1	0.0000	0.0002
<i>Sorbus aucuparia</i>	NA	0	1	0.1777	0.0008
<i>Stellaria graminea</i>	5	0	1	0.0099	0.0000
<i>Taraxacum</i> spp.	NA	0	1	0.0025	0.0000
<i>Trientalis europaea</i>	NA	0	1	0.2537	0.0000
<i>Trifolium hybridum</i>	6	1	1	0.0000	0.0017
<i>Typha latifolia</i>	10	0	0	0.0000	0.0042
<i>Vaccinium myrtillus</i>	NA	1	1	5.6429	0.3458
<i>Vaccinium uliginosum</i>	NA	1	1	0.2706	0.0165
<i>Vaccinium vitis-idea</i>	4	1	1	6.8717	0.0584
<i>Veronica officinalis</i>	5	0	1	0.0522	0.0035
<i>Viola riviniana</i>	4	1	1	0.0025	0.0000

Table A3

The mean number of individuals of bees among sites in burned (n = 22) and unburned (n = 11) clear-cuts for all species found in the study. Bold values shows the species with a significant indicator species value (based on incidence and abundance) compared to the other treatment (see Table 2).

Species	Mean in burned	Mean in unburned
<i>Andrena fucata</i>	0.00	0.09
<i>Andrena fulvida</i>	0.00	0.27
<i>Andrena fuscipes</i>	0.14	0.00
<i>Andrena intermedia</i>	0.50	0.00
<i>Andrena lapponica</i>	0.00	0.09
<i>Andrena minutula</i>	0.05	0.00
<i>Andrena nigroaena</i>	0.05	0.00
<i>Andrena subopaca</i>	0.00	0.09
<i>Andrena tarsata</i>	0.00	0.09
<i>Andrena wilkella</i>	0.00	0.09
<i>Anthidium manicatum</i>	0.14	0.00
<i>Anthidium punctatum</i>	0.05	0.00
<i>Anthophora quadrimaculata</i>	0.05	0.00
<i>Apis mellifera</i>	0.05	0.00
<i>Bombus campestris</i>	0.05	0.09
<i>Bombus distinguendus</i>	0.05	0.00
<i>Bombus lapidarius</i>	0.09	0.00
<i>Bombus lucorum</i>	0.14	0.91
<i>Bombus pascuorum</i>	0.27	2.18
<i>Bombus pratorum</i>	0.00	0.55
<i>Bombus ruderals</i>	0.05	0.09
<i>Bombus soroeensis</i>	0.09	0.64
<i>Bombus sylvarum</i>	0.32	0.00
<i>Chelostoma campanularum</i>	0.05	0.18
<i>Coelioxys elongata</i>	0.09	0.00
<i>Colletes daviesanus</i>	0.05	0.00
<i>Colletes floralis</i>	0.05	0.00
<i>Eucera longicornis</i>	0.05	0.00
<i>Halictus rubicundus</i>	0.09	0.09
<i>Halictus tumulorum</i>	0.05	0.00
<i>Hoplitis claviventris</i>	0.14	0.09
<i>Hylaeus angustatus</i>	0.73	1.55
<i>Hylaeus annulatus</i>	0.45	0.36
<i>Hylaeus brevicornis</i>	0.05	0.73
<i>Hylaeus communis</i>	0.23	0.18
<i>Hylaeus confusus</i>	2.27	6.64
<i>Hylaeus hyalinatus</i>	0.27	0.27
<i>Hylaeus incongruus</i>	0.95	0.64
<i>Hylaeus rinki</i>	0.00	0.09
<i>Lasioglossum albipes</i>	0.41	0.18
<i>Lasioglossum calceatum</i>	0.00	0.09
<i>Lasioglossum fratellum</i>	2.14	3.91
<i>Lasioglossum leucopus</i>	3.86	0.82
<i>Lasioglossum morio</i>	0.09	0.00
<i>Lasioglossum rufitarse</i>	0.55	0.82
<i>Lasioglossum semilucens</i>	0.05	0.00
<i>Lasioglossum villosulum</i>	0.05	0.00
<i>Lasioglossum zonulum</i>	0.05	0.00
<i>Megachile alpicola</i>	0.05	0.00
<i>Megachile centuncularis</i>	0.05	0.00
<i>Megachile circumcincta</i>	0.09	0.00
<i>Megachile lapponica</i>	0.05	0.00
<i>Megachile ligniseca</i>	0.05	0.00
<i>Megachile versicolor</i>	0.05	0.00
<i>Nomada flavoguttata</i>	0.05	0.09
<i>Nomada goodeniana</i>	0.00	0.09
<i>Nomada panzeri</i>	0.05	0.00
<i>Osmia parietina</i>	0.00	0.18
<i>Sphecodes geofrellus</i>	0.05	0.18
<i>Sphecodes hyalinatus</i>	0.00	0.18
<i>Trachusa byssina</i>	0.05	0.00

Table A4

The mean number of individuals of wasps among sites in burned (n = 22) and unburned (n = 11) clear-cuts for all species found in the study. Bold values shows the species with a significant indicator species value (based on incidence and abundance) compared to the other treatment (Table 2).

Species	Mean in burned	Mean in unburned
<i>Agenoideus cinctellus</i>	0.64	1.27
<i>Allodynerus delphinalis</i>	0.00	0.18
<i>Alysson ratzeburgi</i>	0.05	0.00
<i>Ammophila sabulosa</i>	1.23	0.09
<i>Anoplius nigerrimus</i>	8.27	6.00
<i>Anoplius viaticus</i>	0.14	0.09
<i>Arachnospila anceps</i>	1.73	1.45
<i>Arachnospila hedicki</i>	0.09	0.45
<i>Arachnospila spissa</i>	0.18	1.09
<i>Arachnospila trivialis</i>	0.05	0.00
<i>Astata boops</i>	0.14	0.36
<i>Auplopus carbonarius</i>	0.09	1.45
<i>Bethylus fuscicornis</i>	0.05	0.00
<i>Caliadurgus fasciatellus</i>	0.36	0.27
<i>Cerceris arenaria</i>	0.09	0.00
<i>Cerceris ruficornis</i>	0.09	0.00
<i>Ceropales maculata</i>	0.14	0.00
<i>Chrysis fulgida</i>	0.05	0.00
<i>Chrysis illigeri</i>	0.09	0.18
<i>Chrysis rutilans</i>	0.00	0.09
<i>Chrysura hirsuta</i>	0.14	0.00
<i>Crossocerus leucostoma</i>	0.00	0.09
<i>Crossocerus vagabundus</i>	0.09	0.00
<i>Diodontus medius</i>	0.00	0.09
<i>Dipogon bifasciatus</i>	0.05	1.00
<i>Dipogon variegatus</i>	0.09	0.55
<i>Discoelius zonalis</i>	0.05	0.00
<i>Dolichovespula norvegica</i>	0.68	0.00
<i>Dolichovespula saxonica</i>	0.23	0.00
<i>Dolichurus corniculatus</i>	0.05	1.00
<i>Ectemnius borealis</i>	0.05	0.00
<i>Ectemnius continuus</i>	0.32	0.73
<i>Ectemnius dives</i>	0.45	0.00
<i>Ectemnius ruficornis</i>	0.32	0.09
<i>Episyron albonotatum</i>	0.05	0.00
<i>Eumenes coronatus</i>	0.14	0.09
<i>Eumenes pedunculatus</i>	0.05	0.00
<i>Euodynerus quadrfasciatus</i>	0.05	0.09
<i>Evagetus alamannicus</i>	0.27	0.00
<i>Evagetus crassicornis</i>	0.00	0.09
<i>Evagetus sahlbergi</i>	0.05	0.18
<i>Gorytes laticinctus</i>	0.09	0.00
<i>Harpactus lunatus</i>	0.05	0.00
<i>Hedychrum nobile</i>	0.09	0.00
<i>Homonotus sanguinolentus</i>	0.00	0.09
<i>Lindeni albilabris</i>	0.05	0.09
<i>Mimumesa dahlbomi</i>	1.36	1.55
<i>Myrmica atra</i>	0.00	0.09
<i>Nitela borealis</i>	0.00	0.18
<i>Nysson distinguendus</i>	0.05	0.00
<i>Nysson spinosus</i>	0.00	0.09
<i>Nysson trimaculatus</i>	5.68	1.36
<i>Odynerus spinipes</i>	0.05	0.00
<i>Passaloecus borealis</i>	0.00	0.09
<i>Passaloecus gracilis</i>	0.05	0.00
<i>Passaloecus singularis</i>	0.09	0.27
<i>Pemphredon inornata</i>	0.41	0.18
<i>Pemphredon littoralis</i>	0.05	0.00
<i>Pemphredon wesmaeli</i>	0.45	0.09
<i>Podalonia hirsuta</i>	0.14	0.00
<i>Priocnemis hyalinata</i>	0.05	0.00
<i>Priocnemis pusilla</i>	0.09	0.00
<i>Priocnemis schioedtei</i>	0.09	1.64
<i>Priocnemis cordivalvata</i>	0.00	0.09
<i>Priocnemis exaltata</i>	0.55	1.09
<i>Pseudomalus auratus</i>	0.00	0.18
<i>Stenodynerus dentisquama</i>	0.05	0.00
<i>Symmorphus bifasciatus</i>	0.05	0.00
<i>Symmorphus crassicornis</i>	0.05	0.00
<i>Tachysphex obscuripennis</i>	0.00	0.09
<i>Tachysphex pompiliiformis</i>	0.14	0.18
<i>Trichrysis cyanea</i>	0.00	0.18

(continued on next page)

Table A4 (continued)

Species	Mean in burned	Mean in unburned
<i>Trypoxylon attenuatum</i>	0.41	0.00
<i>Trypoxylon clavicernum</i>	0.00	0.27
<i>Trypoxylon figulus</i>	0.86	0.64
<i>Trypoxylon medium</i>	9.32	3.64
<i>Trypoxylon minus</i>	2.18	4.09
<i>Vespula rufa</i>	0.18	0.00

Table A5

The mean number of individuals of hoverflies among sites in burned (n = 22) and unburned (n = 11) clear-cuts for all species found in the study. Bold values shows the species with a significant indicator species value (based on incidence and abundance) compared to the other treatment (Table 2).

Species	Mean in burned	Mean in unburned
<i>Anasimyia lineata</i>	0.36	0.27
<i>Anasimyia interpuncta/lunulata</i>	0.23	3.00
<i>Brachypaloides lentus</i>	0.05	0.00
<i>Chalcosyrphus nemorum</i>	0.77	0.27
<i>Chalcosyrphus valgius</i>	0.05	0.00
<i>Chrysotoxum arcuatum</i>	0.05	0.00
<i>Chrysotoxum binctum</i>	0.05	0.18
<i>Episyrphus balteatus</i>	0.05	0.00
<i>Eristalinus sepulchralis</i>	0.09	0.00
<i>Eristalis interrupta</i>	0.05	0.00
<i>Eristalis pseudorupium</i>	0.05	0.18
<i>Eumerus flavitarsis</i>	0.00	0.09
<i>Helophilus groenlandicus</i>	0.05	0.00
<i>Helophilus pendulus</i>	0.00	0.09
<i>Microdon miki</i>	0.00	0.09
<i>Orthonevra intermedia stackelbergi</i>	0.77	0.64
<i>Parhelophilus consimilis</i>	0.00	0.18
<i>Pipiza quadrimaculata</i>	0.05	0.00
<i>Pipizella viduata</i>	0.00	0.09
<i>Platycheirus granditarsis</i>	0.00	0.09
<i>Sericomyia lappona</i>	0.09	0.27
<i>Sericomyia silentis</i>	0.23	0.73
<i>Sphaerophoria sp</i>	0.05	0.18
<i>Syrphus torvus</i>	0.00	0.09
<i>Xylota florum</i>	0.86	0.45
<i>Xylota ignava</i>	0.09	0.00
<i>Xylota jakutorum</i>	8.64	2.64
<i>Xylota segnis</i>	0.86	0.91
<i>Xylota tarda</i>	0.23	0.00

Table A6

The mean number of individuals of butterflies among sites in burned (n = 22) and unburned (n = 15) clear-cuts for all species found in the study. Bold values shows the species with a significant indicator species value (based on incidence and abundance) compared to the other treatment (Table 2).

Species	Mean in burned	Mean in unburned
<i>Aglais urticae</i>	0.05	0.07
<i>Aphantopus hyperantus</i>	0.09	1.60
<i>Argynnis adippe</i>	0.00	0.07
<i>Argynnis aglaja</i>	0.00	0.07
<i>Argynnis paphia</i>	0.05	0.07
<i>Boloria euphrosyne</i>	0.09	8.60
<i>Boloria selene</i>	0.05	0.20
<i>Brenthis ino</i>	0.00	0.27
<i>Callophrys rubi</i>	0.00	1.20
<i>Carterocephalus silvicola</i>	0.00	0.07
<i>Celastrina argiolus</i>	0.00	0.07
<i>Coenonympha arcania</i>	0.00	0.40
<i>Coenonympha pamphilus</i>	0.00	0.13
<i>Colias palaeno</i>	0.55	0.60
<i>Erebia ligea</i>	0.05	0.27
<i>Erynnis tages</i>	0.00	0.07
<i>Gonepteryx rhamni</i>	0.09	0.67
<i>Lasiommata maera</i>	0.36	0.40
<i>Leptidea juvernica/sinapis</i>	0.00	0.13
<i>Lycaena phlaeas</i>	0.05	0.13
<i>Lycaena virgaureae</i>	0.00	0.07

(continued on next page)

Table A6 (continued)

Species	Mean in burned	Mean in unburned
<i>Melitaea athalia</i>	0.00	4.33
<i>Nymphalis antiopa</i>	0.00	0.07
<i>Ochlodes sylvanus</i>	0.05	0.47
<i>Papilio machaon</i>	0.09	0.00
<i>Pieris napi</i>	0.05	0.07
<i>Plebejus argus/idas</i>	2.77	21.13
<i>Plebejus optilete</i>	0.05	0.27
<i>Polygonia c-album</i>	0.00	0.13
<i>Polyommatus amandus</i>	0.00	0.07
<i>Polyommatus icarus</i>	0.14	0.00
<i>Thymelicus lineola</i>	0.00	0.13
<i>Vanessa cardui</i>	0.05	0.00

Appendix B. Environmental characteristics in relation to burn severity

Table B1

The correlation between mean humus layer thickness (a proxy for burn severity) and potential pollinator resources in burned clear-cuts (n = 22). Burn severity increases with decreasing depth of the humus layer.

Potential resource for bees (be), wasps (w), butterflies (bu), and hoverflies (h)	Pearson's r, and p-value
Nectar plant diversity (be, w, bu, h)	r = 0.09, p = 0.67
Nectar plant cover (be, w, bu, h)	r = 0.14, p = 0.55
Host plant diversity (bu)	r = 0.05, p = 0.80
Host plant cover (bu)	r = 0.02, p = 0.92
Exposed soil (be, w)	r = -0.10, p = 0.66
Number of logs (be, w, h)	r = -0.03, p = 0.89
Basal area dead wood (be, w, h)	r = -0.16, p = 0.47

References

- Abrams, M.D., Dickmann, D.I., 1984. Floristic composition before and after prescribed fire on a jack pine clear-cut site in northern lower Michigan. *Can. J. For. Res.* 14, 746–749. <https://doi.org/10.1139/x84-133>.
- Angelstam, P.K., 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *J. Veg. Sci.* 9, 593–602. <https://doi.org/10.2307/3237275>.
- Berg, Å., Åhrné, K., Öckinger, E., Svensson, R., Söderström, B., 2011. Butterfly distribution and abundance is affected by variation in the Swedish forest-farmland landscape. *Biol. Conserv.* 144, 2819–2831. <https://doi.org/10.1016/j.biocon.2011.07.035>.
- Berglund, H.-L., 2016. Effects of Flower Abundance and Colour on Pan-Trap Catches. Master thesis. Linköping University, Linköping, Sweden.
- Bergman, K.-O., Daniel-Ferreira, J., Milberg, P., Öckinger, E., Westerberg, L., 2018. Butterflies in Swedish grasslands benefit from forest and respond to landscape composition at different spatial scales. *Landsc. Ecol.* <https://doi.org/10.1007/s10980-018-0732-y>.
- Bogusch, P., Blažej, L., Trýzna, M., Heneberg, P., 2015. Forgotten role of fires in Central European forests: critical importance of early post-fire successional stages for bees and wasps (Hymenoptera: Aculeata). *Eur. J. For. Res.* 134, 153–166. <https://doi.org/10.1007/s10342-014-0840-4>.
- 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.
- Cane, J.H., Neff, J.L., 2011. Predicted fates of ground-nesting bees in soil heated by wildfire: thermal tolerances of life stages and a survey of nesting depths. *Biol. Conserv.* 144, 2631–2636. <https://doi.org/10.1016/j.biocon.2011.07.019>.
- Corbet, S.A., Williams, I.H., Osborne, J.L., 1991. Bees and the pollination of crops and wild flowers in the European community. *Bee World* 72, 47–59. <https://doi.org/10.1080/0005772X.1991.11099079>.
- Cousins, S.A.O., Auffret, A.G., Lindgren, J., Tränk, L., 2015. Regional-scale land-cover change during the 20th century and its consequences for biodiversity. *AMBIO* 44, 17–27. <https://doi.org/10.1007/s13280-014-0585-9>.
- Curtis, R.J., Brereton, T.M., Dennis, R.L.H., Carbone, C., Isaac, N.J.B., 2015. Butterfly abundance is determined by food availability and is mediated by species traits. *J. Appl. Ecol.* 52, 1676–1684. <https://doi.org/10.1111/1365-2664.12523>.
- Dufrène, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366. [https://doi.org/10.1890/0012-9615\(1997\)067\[0345:SAIST\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0345:SAIST]2.0.CO;2).
- Ebeling, A., Klein, A.-M., Schumacher, J., Weisser, W.W., Tschamntke, T., 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos* 117, 1808–1815. <https://doi.org/10.1111/j.1600-0706.2008.16819.x>.
- Eliasson, C.U., Liljeberg, G., 2009. Dagfjärilar i Örebro och Västmanlands län: en fälthandbok. Länsstyrelsen i Örebro län, Örebro.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scr. Geobot.* 18, 1–258.
- Faivre, N., Boudreault, C., Renard, S., Fenton, N.J., Gauthier, S., Bergeron, Y., 2016. Prescribed burning of harvested boreal black spruce forests in eastern Canada: effect on understory vegetation. *Can. J. For. Res.* 46, 876–884. <https://doi.org/10.1139/cjfr-2015-0439>.
- Foster, C.N., Barton, P.S., Robinson, N.M., MacGregor, C.I., Lindenmayer, D.B., 2017. Effects of a large wildfire on vegetation structure in a variable fire mosaic. *Ecol. Appl.* 27, 2369–2381. <https://doi.org/10.1002/eap.1614>.
- Fröberg, H., 1996. Pollination and seed production in five boreal species of Vaccinium and Andromeda (Ericaceae). *Can. J. Bot.* 74, 1363–1368. <https://doi.org/10.1139/b96-165>.
- Galbraith, S.M., Cane, J.H., Moldenke, A.R., Rivers, J.W., 2019. Wild bee diversity increases with local fire severity in a fire-prone landscape. *Ecosphere* 10, e02668. <https://doi.org/10.1002/ecs2.2668>.
- Gibb, H., Pettersson, R.B., Hjältén, J., Hilszczański, J., Ball, J.P., Johansson, T., Atlegrim, O., Danell, K., 2006. Conservation-oriented forestry and early successional saproxylic beetles: responses of functional groups to manipulated dead wood substrates. *Biol. Conserv.* 129, 437–450. <https://doi.org/10.1016/j.biocon.2005.11.010>.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>.
- Goulson, D., Lye, G.C., Darvill, B., 2008. Decline and conservation of bumble bees. *Annu. Rev. Entomol.* 53, 191–208. <https://doi.org/10.1146/annurev.ento.53.103106.093454>.
- Granström, A., 2001. Fire management for biodiversity in the European boreal forest. *Scand. J. For. Res.* 16, 62–69. <https://doi.org/10.1080/028275801300090627>.
- Gustafsson, L., Berglund, M., Granström, A., Grelle, A., Isacson, G., Kjellander, P., Larsson, S., Lindh, M., Pettersson, L.B., Strengbom, J., Stridh, B., Sävström, T., Thor, G., Wikars, L.-O., Mikusiński, G., 2019. Rapid ecological response and intensified knowledge accumulation following a north European mega-fire. *Scand. J. For. Res.* 34, 234–253. <https://doi.org/10.1080/02827581.2019.1603323>.
- Hanula, J.L., Ulyshen, M.D., Horn, S., 2016. Conserving pollinators in North American forests: a review. *Nat. Areas J.* 36, 427–439. <https://doi.org/10.3375/043.036.0409>.
- Heikkala, O., Suominen, M., Junninen, K., Hämäläinen, A., Kouki, J., 2014. Effects of

- retention level and fire on retention tree dynamics in boreal forests. *For. Ecol. Manag.* 328, 193–201. <https://doi.org/10.1016/j.foreco.2014.05.022>.
- Heneberg, P., Bogusch, P., 2014. To enrich or not to enrich? Are there any benefits of using multiple colors of pan traps when sampling aculeate Hymenoptera? *J. Insect Conserv.* 18, 1123–1136. <https://doi.org/10.1007/s10841-014-9723-8>.
- Hunter, M.L., 1993. Natural fire regimes as spatial models for managing boreal forests. *Biol. Conserv.* 65, 115–120. [https://doi.org/10.1016/0006-3207\(93\)90440-C](https://doi.org/10.1016/0006-3207(93)90440-C).
- Hyvärinen, E., Kouki, J., Martikainen, P., 2009. Prescribed fires and retention trees help to conserve beetle diversity in managed boreal forests despite their transient negative effects on some beetle groups. *Insect Conserv. Divers.* 2, 93–105. <https://doi.org/10.1111/j.1752-4598.2009.00048.x>.
- IPBES, 2016. *The Assessment Report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on Pollinators, Pollination and Food Production*. IPBES, Bonn, Germany.
- Jauker, F., Wolters, V., 2008. Hover flies are efficient pollinators of oilseed rape. *Oecologia* 156, 819–823. <https://doi.org/10.1007/s00442-008-1034-x>.
- Johansson, T., Hjaltn, J., de Jong, J., von Stedingk, H., 2013. Environmental considerations from legislation and certification in managed forest stands: a review of their importance for biodiversity. *For. Ecol. Manag.* 303, 98–112. <https://doi.org/10.1016/j.foreco.2013.04.012>.
- Keeley, J.E., 2009. Fire intensity, fire severity and burn severity: A brief review and suggested usage. *Int. J. Wildland Fire* 18, 11. <https://doi.org/10.1071/WF07049>.
- Lazarina, M., Devallez, J., Neokosmidis, L., Sgardelis, S.P., Kallimanis, A.S., Tschulin, T., Tsakatis, P., Kourtidou, M., Mizerakis, V., Nakas, G., Palaiologou, P., Kalabokidis, K., Vujic, A., Petanidou, T., 2019. Moderate burn severity is best for the diversity of most of the pollinator guilds in Mediterranean pine forests. *Ecology* 100, e02615. <https://doi.org/10.1002/ecy.2615>.
- Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Bugter, R., Hendrickx, F., Burel, F., 2010. Intensification of agriculture, landscape composition and wild bee communities: a large scale study in four European countries. *Agric. Ecosyst. Environ.* Special section Harvested perennial grasslands: Ecological models for farming's perennial future 137, 143–150. <https://doi.org/10.1016/j.agee.2010.01.015>.
- Lehtonen, E., von Stedingk, H., 2017. The contribution of FSC certification to biodiversity in Finnish forests. *FSC Sweden Report 2017*. Forest Stewardship Council.
- Lucas, A., Bull, J.C., de Vere, N., Neyland, P.J., Forman, D.W., 2017. Flower resource and land management drives hoverfly communities and bee abundance in seminatural and agricultural grasslands. *Ecol. Evol.* 7, 8073–8086. <https://doi.org/10.1002/ece3.3303>.
- Maes, D., Van Dyck, H., 2001. Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? *Biol. Conserv.* 99, 263–276. [https://doi.org/10.1016/S0006-3207\(00\)00182-8](https://doi.org/10.1016/S0006-3207(00)00182-8).
- Monasterolo, M., Muscatelli, M.L., Valladares, G.R., Salvo, A., 2015. Soybean crops may benefit from forest pollinators. *Agric. Ecosyst. Environ.* 202, 217–222. <https://doi.org/10.1016/j.agee.2015.01.012>.
- Murray, T.E., Fitzpatrick, U., Byrne, A., Fealy, R., Brown, M.J.F., Paxton, R.J., 2012. Local-scale factors structure wild bee communities in protected areas. *J. Appl. Ecol.* 49, 998–1008. <https://doi.org/10.1111/j.1365-2664.2012.02175.x>.
- Nilsson, M., 2005. *Naturvårdsbränning - Vägledning för brand och bränning i skyddad skog* (No. 5438). Naturvårdsverket, Stockholm, Sweden.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. *vegan: Community Ecology Package*.
- Parson, A., Robichaud, P.R., Lewis, S.A., Napper, C., Clark, J.T., 2010. Field guide for mapping post-fire soil burn severity. *Gen Tech Rep RMRS-GTR-243* Fort Collins CO US Dep. Agric. For. Serv. Rocky Mt. Res. Stn. 49 P, 243. <https://doi.org/10.2737/RMRS-GTR-243>.
- Pausas, J.G., Ribeiro, E., 2017. Fire and plant diversity at the global scale. *Glob. Ecol. Biogeogr.* 26, 889–897. <https://doi.org/10.1111/geb.12596>.
- Pekkarinen, A., 1997. *Oligolectic bee species in Northern Europe (Hymenoptera, Apoidea)*. *Entomologica Fennica* 8, 205–214.
- Ponisio, L.C., Wilkin, K., McGonigle, L.K., Kulhanek, K., Cook, L., Thorp, R., Griswold, T., Kremen, C., 2016. Pyrodiversity begets plant–pollinator community diversity. *Glob. Change Biol.* 22, 1794–1808. <https://doi.org/10.1111/gcb.13236>.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>.
- Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., O'Toole, C., Roberts, S., Willmer, P., 2003a. Response of plant–pollinator communities to fire: changes in diversity, abundance and floral reward structure. *Oikos* 101, 103–112. <https://doi.org/10.1034/j.1600-0706.2003.12186.x>.
- Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., Willmer, P., 2003b. *Linking bees and flowers: how do floral communities structure pollinator communities?* *Ecology* 84, 2628–2642.
- Potts, S.G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'eman, G., Willmer, P., 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecol. Entomol.* 30, 78–85. <https://doi.org/10.1111/j.0307-6946.2005.00662.x>.
- Powney, G.D., Carvell, C., Edwards, M., Morris, R.K.A., Roy, H.E., Woodcock, B.A., Isaac, N.J.B., 2019. Widespread losses of pollinating insects in Britain. *Nat. Commun.* 10, 1–6. <https://doi.org/10.1038/s41467-019-08974-9>.
- Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., Cunningham, S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R., Brittain, C., Carvalho, L.G., Chacoff, N.P., Entling, M.H., Foully, B., Freitas, B.M., Gemmill-Herren, B., Ghazoul, J., Griffin, S.R., Gross, C.L., Herberstein, L., Herzog, F., Hipólito, J., Jaggard, S., Jauker, F., Klein, A.-M., Kleijn, D., Krishnan, S., Lemos, C.Q., Lindström, S.A.M., Mandelik, Y., Monteiro, V.M., Nelson, W., Nilsson, L., Pattemore, D.E., Pereira, N.de.O., Pisanty, G., Potts, S.G., Reemer, M., Rundlöf, M., Sheffield, C.S., Scheper, J., Schüepp, C., Smith, H.G., Stanley, D.A., Stout, J.C., Szentgyörgyi, H., Taki, H., Vergara, C.H., Viana, B.F., Woyciechowski, M., 2016. Non-bee insects are important contributors to global crop pollination. *Proc. Natl. Acad. Sci.* 113, 146–151. <https://doi.org/10.1073/pnas.1517092112>.
- Ramborg, E., Strengbom, J., Granath, G., 2018. Coordination through databases can improve prescribed burning as a conservation tool to promote forest biodiversity. *Ambio* 47, 298–306. <https://doi.org/10.1007/s13280-017-0987-6>.
- Rivers, J.W., Galbraith, S.M., Cane, J.H., Schultz, C.B., Ulyshen, M.D., Kormann, U.G., 2018. A review of research needs for pollinators in managed conifer forests. *J. For.* 116, 563–572. <https://doi.org/10.1093/jofore/fvy052>.
- Rodríguez, A., Kouki, J., 2017. Disturbance-mediated heterogeneity drives pollinator diversity in boreal managed forest ecosystems. *Ecol. Appl. Publ. Ecol. Soc. Am.* 27, 589–602. <https://doi.org/10.1002/eap.1468>.
- Rodríguez, A., Kouki, J., 2015. Emulating natural disturbance in forest management enhances pollination services for dominant *Vaccinium* shrubs in boreal pine-dominated forests. *For. Ecol. Manag.* 350, 1–12. <https://doi.org/10.1016/j.foreco.2015.04.029>.
- Romey, W.L., Ascher, J.S., Powell, D.A., Yanek, M., 2007. Impacts of logging on mid-summer diversity of native bees (Apoidea) in a northern hardwood forest. *J. Kans. Entomol. Soc.* 80, 327–338.
- Roulston, T.H., Goodell, K., 2011. The role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol.* 56, 293–312. <https://doi.org/10.1146/annurev-ento-120709-144802>.
- Roulston, T.H., Smith, S.A., Brewster, A.L., 2007. A comparison of pan trap and intensive net sampling techniques for documenting a bee (Hymenoptera: Apiformes) fauna. *J. Kans. Entomol. Soc.* 80, 179–181. [https://doi.org/10.2317/0022-8567\(2007\)80\[179:ACOPTA\]2.0.CO;2](https://doi.org/10.2317/0022-8567(2007)80[179:ACOPTA]2.0.CO;2).
- Rubene, D., Schroeder, M., Ranius, T., 2015. Diversity patterns of wild bees and wasps in managed boreal forests: effects of spatial structure, local habitat and surrounding landscape. *Biol. Conserv.* 184, 201–208. <https://doi.org/10.1016/j.biocon.2015.01.029>.
- Saint-Germain, M., Drapeau, P., Buddle, C.M., 2008. Persistence of pyrophilous insects in fire-driven boreal forests: population dynamics in burned and unburned habitats. *Divers. Distrib.* 14, 713–720. <https://doi.org/10.1111/j.1472-4642.2007.00452.x>.
- Schimmel, J., Granström, A., 1996. Fire severity and vegetation response in the boreal Swedish forest. *Ecology* 77, 1436–1450. <https://doi.org/10.2307/2265541>.
- Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol. Bull.* 11–41. <https://doi.org/10.2307/20113262>.
- Speight, M., 1989. *Saproxylic invertebrates and their conservation*. Council of Europe, Strasbourg.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tscharnke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83, 1421–1432. [https://doi.org/10.1890/0012-9658\(2002\)083\[1421:SDEOLC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2).
- Steffan-Dewenter, I., Potts, S.G., Packer, L., 2005. Pollinator diversity and crop pollination services are at risk. *Trends Ecol. Evol.* 20, 651–652. <https://doi.org/10.1016/j.tree.2005.09.004>.
- Suominen, M., Junninen, K., Heikkala, O., Kouki, J., 2018. Burning harvested sites enhances pollinator diversity on stumps and slash. *For. Ecol. Manag.* 414, 47–53. <https://doi.org/10.1016/j.foreco.2018.02.007>.
- van Swaay, C., Warren, M., Lois, G., 2006. *Biotope use and trends of European butterflies*. *J. Insect Conserv.* 10, 189–209. <https://doi.org/10.1007/s10841-006-6293-4>.
- Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B., Swanson, F.J., 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Front. Ecol. Environ.* 9, 117–125. <https://doi.org/10.1890/090157>.
- Turner, M.G., Romme, W.H., Gardner, R.H., Hargrove, W.W., 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecol. Monogr.* 67, 411–433. [https://doi.org/10.1890/0012-9615\(1997\)067\[0411:EOFSAP\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0411:EOFSAP]2.0.CO;2).
- Uotila, A., Kouki, J., 2005. Understorey vegetation in spruce-dominated forests in eastern Finland and Russian Karelia: successional patterns after anthropogenic and natural disturbances. *For. Ecol. Manag.* 215, 113–137. <https://doi.org/10.1016/j.foreco.2005.05.008>.
- Wallis De Vries, M.F., Poschlod, P., Willems, J.H., 2002. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biol. Conserv.* 104, 265–273. [https://doi.org/10.1016/S0006-3207\(01\)00191-4](https://doi.org/10.1016/S0006-3207(01)00191-4).
- Westerfelt, P., Weslien, J., Widenfalk, O., 2018. Population patterns in relation to food and nesting resource for two cavity-nesting bee species in young boreal forest stands. *For. Ecol. Manag.* 430, 629–638. <https://doi.org/10.1016/j.foreco.2018.08.053>.
- Whelan, R.J., 1995. *The Ecology of Fire*, first ed. Cambridge University Press, Cambridge, New York.
- 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. <https://doi.org/10.1016/j.biocon.2010.03.024>.
- Wilson, J.S., Jahner, J.P., Starley, L., Calvin, C.L., Ikerd, H., Griswold, T., 2016. Sampling bee communities using pan traps: alternative methods increase sample size. *J. Insect Conserv.* 20, 919–922. <https://doi.org/10.1007/s10841-016-9914-6>.
- Zackrisson, O., 1977. Influence of forest fires on the north Swedish boreal forest. *Oikos* 29, 22–32. <https://doi.org/10.2307/3543289>.