Norwegian University of Life Sciences
Faculty of Environmental Sciences
and Natural Resource Management

Philosophiae Doctor (PhD)
Thesis 2020:31

The conservation value of power-line clearings for native insect-pollinated plants and wild bees in boreal forest landscapes

Verdien av kraftgater for bevaring av stedegne insektpollinerte planter og villbier i boreale skoger

Mari Steinert

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Contents

List of papers

Paper I

Steinert, M., S. R. Moe, M.A.K. Sydenham, and K. Eldegard. 2018. Different cutting regimes improve species and functional diversity of insect-pollinated plants in power-line clearings. *Ecosphere* 9:e02509.

Paper II

Steinert, M., M. A. K. Sydenham, K. Eldegard, and S. R. Moe. 2020. Conservation of solitary bees in power line clearings: Sustained increase in habitat quality through woody debris removal. *Global Ecology and Conservation* 21:e00823.

Paper III

Steinert, M., K. Eldegard, M.A.K. Sydenham, and S. R. Moe. Bumble bee communities in power-line clearings: Effects of experimental management practices. *Submitted manuscript*

Paper IV

Steinert, M., K. Eldegard, M.A.K. Sydenham, and S. R. Moe. Power-line clearings provide important late-season foraging resources for bumble bees in boreal production forests. *Manuscript*

Summary

Worldwide declines in wild pollinators are threatening the provision of vital pollination functions and services to both native plant communities and crops. Habitat loss due to human land use changes is identified as one of the main drivers of wild bee decline. Particularly, farmland abandonment and conversion of natural forests into even-aged managed stands have greatly reduced the availability of essential early successional habitats in the landscape. In recent decades, to mitigate the loss of native biodiversity, there has been a growing interest in the conservation management of human modified landscapes. Modified landscape features, such as power-line clearings, can provide valuable alternative habitats for early successional plant species, which in turn offer important flower resources for wild bees.

The main objectives for the four studies in this thesis were to study the conservation value of power-line clearings as habitat for insect-pollinated plant and wild bee communities in forest landscapes and to identify effects of different maintenance clearing practices.

We carried out a large-scale field experiment and an observational study in power-lines clearings. In the first three papers, we studied the experimental treatment effects on insect-pollinated plant (forbs, shrubs, and dwarf shrubs) (**Paper I**), solitary bee (**Paper II**) and bumble bee (**Paper III**) communities in response to different vegetation clearing practices (treatments), where woody vegetation was: (i) cut, with woody debris left to decay; (ii) cut-remove, with woody debris removed; and (iii) uncut. To study the effects of management practices we used different combinations of taxonomic and functional trait diversity indices or traits groups. We assessed the modifying influence of environmental conditions, and whether the treatment effects were maintained three years post-treatment (**Paper I, II, III**). In **Paper II** and **III**, we used the floral resources from **Paper I** as important explanatory factors for the wild bee communities. To identify the value of power-line clearings as a pollinator habitat in boreal production forests, we carried out an observational study on bumble bees (**Paper IV**). We studied the spatiotemporal variation in bumble bee richness and abundance between open habitats in power-line clearings and adjacent forest habitats throughout one foraging season, related to environmental conditions.

Overall, the studies presented in this thesis show that power-line clearings can be important habitats for communities of both insect-pollinated plants and wild bees, and that habitat quality can be enhanced with proper management. We found that cutting the vegetation had a positive effect on plants and wild bees compared to the uncut plots, regardless of woody debris removal (**Paper I, II, III**). However, the effect of management practices was context dependent. Under certain environmental conditions the removal of woody debris led to a higher richness and functional diversity of plants (**Paper I**) which promoted a higher functional diversity of wild bees (**Paper II, III**). For solitary bees, woody debris removal promoted a strong positive effect which was sustained three years after cutting. Bumble bees seemed to thrive in both cut treatments. We found that the power-line clearings are valuable open canopy habitats for bumble bees in managed forests and that the power-line clearings provide essential late-season foraging resources, particularly heather (*Calluna vulgaris*) (**Paper IV**).

In forest landscapes, power-line clearings can function as alternative habitats for wild bees in boreal forests and species associated with semi-natural habitats, providing potential nesting substrates and enhanced native flower resources. To improve habitat conditions for the solitary bees, removing the woody debris is highly recommended, whereas to improve habitat conditions for bumble bees, woody debris removal is beneficial, but not as important. Implementation of management efforts should be carefully located to areas of certain environmental conditions to achieve the best possible effect. Additionally, targeted enhancement of flower species with high nectar content or flowers with late phenology (i.e. heather), would further enhance the conservation value. Our results also highlight the importance of open habitats in managed forests and that less dense forest stands are important for wild bee conservation. To conserve native plants and wild bees species, the populations need to be maintained at a landscape level. Hence, management practices should be implemented in areas enabling connectivity between open semi-natural habitats in the landscape.

Recommendations for overall wild bee conservation would thus be to implement a mosaic of woody debris retention and removal in power-line clearings, to support diverse wild bee communities. Together, the findings of this thesis represent a foundation for developing pollinator-friendly management strategies in power-line clearings in forest landscapes and suggest how power-line clearings should be included in integrated conservation plans.

Synopsis

1 Introduction

Pollinators play a key role in many terrestrial ecosystems, providing vital ecosystem functions and services to both native plant communities and cultivated crops (Potts et al. 2010, Winfree et al 2011, Klein et al. 2007). About 87.5 % of the world's plants are dependent on biotic pollination for sexual reproduction (Ollerton et al. 2011). Among the pollinators, wild bees are considered the most effective at performing this ecosystem function. In recent decades, a worldwide decline in both pollinators and the plants that rely upon them has been documented (Biesmejer et al. 2006, Cameron et al. 2011, Potts et al. 2010, 2016), which has led to a growing concern about the prospects of human food security and conservation of biodiversity. It is now widely accepted that wild bee declines are mainly driven by habitat loss, degradation and fragmentation caused by human land-use changes, in addition to other, possibly interacting factors of climate change, pesticides, pests and pathogens (Potts et al. 2010; Winfree et al. 2009, Sánchez-Bayo and Wyckhys 2019). However, human land-use modifications are not uniformly negative (Wojcik and Buchmann 2012), and modified landscape features, such as power-line clearings, may serve as valuable early successional habitats for a wide range of native plants and pollinators (Hanula et al. 2016, Villemey et al. 2018). With proper management, early successional vegetation in human-modified habitats may play an important role in the conservation of pollination functions and services (Villemey et al. 2018).

1.1 Land use changes

Changes in natural and anthropogenic disturbance regimes have reduced the amount of early successional habitats in boreal forest landscapes (King and Schlossberg 2014). The landscape in Europe has been formed by centuries of natural disturbance regimes together with diverse farming and forestry practices, shaping the continent's biodiversity. Forest stands used to vary in size, age, composition, and structure, and thereby offered habitats with a niche space for a diverse range of native species (Kuuluvainen 2002). Over the last centuries, modern forestry has considerably changed the Scandinavian boreal forest systems (Östlund et al. 1997). Managed forests have become heavily homogenized due to intensive timber production and fire suppression (Kuuluvainenn 2009). Homogenous and dense forests with reduced understory diversity threaten the provision of flower resources for wild bees throughout their foraging season.

At the same time, agricultural intensification and abandonment of previous small-scale agricultural farmland has resulted in major declines in semi-natural grasslands (Aune et al. 2018, Norderhaug and Johansen 2011). Currently, semi-natural grasslands are categorized as vulnerable and hay meadows as critically endangered in the Norwegian Red list for nature types (Hovstad et al. 2018), which is critical for a number of endangered native plants and pollinators (Henriksen and Hilmo 2015). Semi-natural grasslands are essential habitats for many native plant species associated with the cultural landscape, including species of special conservation concern (Hamre et al. 2010). And semi-natural grasslands provide essential habitat for many wild bees through provision of a high diversity of flower and nesting resources (Potts et al. 2016). However, in the absence of natural and semi-natural habitats, human disturbance regimes may provide alternative early successional habitats for species that initially have evolved under natural disturbance regimes.

1.2 Human modified habitats

Modified habitats like road-verges (Hopwood 2008; Noordijk et al. 2009), railway lines (Moroń et al. 2014), hedgerows (Hanley and Wilkins 2015), field margins (Carvell et al. 2004) and power-line clearings (Russel et al. 2005, 2019, Wagner et al. 2019) may provide important pollinator habitats. Power-line clearings have traditionally been thought to have a negative impact on biodiversity (Nekola 2012, Wojcik and Buchmann 2012), but over the past decades several studies have highlighted the potential value of power-line clearings as habitats for plants (Luken et al. 1992, Wagner et al. 2014b, Lampinen et al. 2015, Eldegard et al. 2017), vertebrates (Clarke and White 2008, Askins et al. 2012) and invertebrates, such as butterflies (Smallidge et al. 1996, Forrester et al. 2005, Berg et al. 2013; 2016) and bees (Hill and Bartomeus 2016, Russel et al. 2005; 2018, Sydenham et al. 2016, Wagner et al. 2014a, 2019). Previous studies on plant communities in power-line clearings have typically focused on facilitation of self-maintaining vegetation to minimize regeneration of trees (Bramble et al. 1990, Clarke and White 2008, Luken et al 1992, Nowak et al. 1992). Other studies have compared habitat quality in power-line corridors with other habitats, such as grasslands (Hill & Bartomeus 2016), or adjacent forests (Clarke & White 2008, Wagner et al. 2019). Several studies have suggested that proper vegetation management in power-line clearings can increase the ecosystem service pollination (Hill & Bartomeus 2016, Dupras et al 2016, Russel et al. 2005; 2018, Sydenham et al. 2016). However, studies assessing the immediate and longer term effects of experimentally removing the woody debris after maintenance clearing on insect-pollinated plants or wild bee communities, are lacking.

1.3 Vegetation in power-line clearings

Power-line clearings constitute extensive networks of modified habitats and disturbance regimes throughout the northern hemisphere. In Norway, the area below the main power-line grid covers a substantial area of the landscape, with 10-80 m wide corridors, with a total length of approximately 11 000 km throughout the country, covering around 200 km^2 in forested areas (Statnett 2019). Current practice in Norway is to clear the woody vegetation every 5 – 12 years depending on site productivity. However, within and among other countries, there are large variations in management practices. It ranges from more severe disturbances of herbicide application and frequent mechanical mowing of all vegetation (Russel et al. 2018) to less intensive manual clearing every 8-12 years (Berg et al. 2016, Eldegard et al. 2017). Such management practices represent repeated disturbances that transform and maintain the plant communities in early successional phases. Compared to the adjacent forest, the habitats are often dominated by native early successional graminoids, forbs, shrubs and dwarf shrubs, with numerous plant species associated with semi-natural grasslands (Eldegard et al. 2017, Wagner et al. 2014b). But the power-line clearings may also attract invasive species (Lampinen et al. 2015, Russel et al. 2018, Wagner et al. 2014b). Within forests, disturbance dynamics have been important drivers of regeneration and dispersal of many vascular plant species. For instance, gap formation is important for plant dispersal, germination, survival of seedlings, growth and reproduction (Pickett and White 1985, Muscolo et al. 2014). Consequently, open canopy habitats create herbaceous rich plant communities which provide nectar and pollen resources in addition to nesting possibilities for wild bees. Accordingly, wild bee species in forested landscapes are generally associated with patches of land in early succession forest openings (New 2012, Roberts et al. 2017). Similarly, management practices in power-line clearings, which leaves the field layer intact, likely maintain a more stable habitat for plant communities and pollinating insects.

1.4 Wild bees

Globally, there are likely more than 20 000 species of wild bees (Michener 2007). In Europe there are nearly 2 000 species, and 9% of these are recognized as threatened on the IUCN Red list (Nieto et al. 2014). In Norway there are 207 wild bee species, of which 172 are solitary bees and 35 are bumble bees (Artsdatabanken 2020). Wild bees display a wide range of life-history strategies, with large variation among species when it comes to e.g. phenology, dietary preferences (pollen and nectar specializations), body size, sociality and nesting substrate (Westrich 1990, Michener 2007).

Solitary bees at northern latitudes generally have a short activity span, with marked seasonal patterns (Oertli et al. 2005) and generally low population growth rates (each female has few offspring) (Danforth et al. 2019, Minckley and Danforth 2019). Many solitary bees are flower generalists, but due to short adult activity periods, quite a few are specialists on particular flowers (Michener 2007). Among the solitary bees, facultatively social species are typically solitary at northern latitudes (Soro et al. 2010). Solitary bees are also central-place foragers with generally short dispersal distances (Franzén et al. 2009, Greenleaf et al. 2007) and respond to land use intensification at relatively small spatial scales (Steffan-Dewenter et al. 2002).

Bumble bee species have widespread geographic distributions. Most species are eusocial and nest below ground in abandoned rodent holes, under rocks, or above ground in tree cavities or in twig or litter piles (Hatfield et al 2012). Some species are parasites on other social species (Ødegaard et al. 2015). In general, bumble bees are large-bodied and thus able to fly long distances to forage (Greenleaf et al. 2007), and this makes them efficient at collecting food resources in the landscape. Eusocial bumble bees need continuous flower resources throughout their colony lifespan (Pywell et al. 2005), from early snow melt in spring to early autumn. Most bumble bees are floral generalists and forage on several different plants over a season (Michener 2007). Thus, the spatiotemporal variation in bumble bees are often related to spatiotemporal availability in flower resources. In boreal forested landscapes, bumble bees provide essential pollination functions to ericaceous dwarf shrubs, because most ericaceous species are dependent on buzz-pollination (Buchmann 1983).

Understanding how the different guilds of bees respond to management practices – and how they interact with the environment – is of critical importance for developing efficient management programs. The effects of habitat management efforts are found to be dependent on the environmental context, and particularly floral resources (Carvell et al. 2011; Sydenham et al. 2016). Thus, management practices should be assessed under different abiotic and biotic environmental conditions to ensure pollinator friendly conservation plans.

1.5 Biological diversity

There are many ways to quantify biodiversity. The most widely used diversity measures are species richness and abundance in addition to associated taxonomic indices (Magurran and McGill 2012). However, management practices that promote species-based diversity, may not necessarily maintain ecosystem functions and services (Forrest et al. 2015). Consequently, functional traits, rather than species identities, are increasingly being used in ecological studies (Cadotte et al. 2011, Gagic et al. 2015). Functional traits are characteristics of an organism which is linked to the organism's function. Traits may be categorized according to whether the trait is influenced by responses to the environment (response traits) or whether the trait has an effect on ecosystem processes (effect traits) (de Bello et al. 2010, Keddy 1992, Suding et al. 2008). In plants, functional traits may for example include morphological, ecophysiological or regeneration traits, whereas in invertebrates, these traits are also combined with life-history and behavioral characteristics (de Bello et al. 2010, Moretti et al 2017). Effect traits are particularly relevant for studies of ecosystem services, like pollination (Díaz et al. 2007, de Bello et al. 2010). For instance, an increased diversity of floral forms (effect traits) in plants represent an increased variety of niches for pollinators to occupy. Whereas response traits of the pollinators, such as food specialization or body size, are relevant for studying the invertebrate communities (Moretti et al 2017).

Functional diversity is important in assessment of ecosystem management and conservation (Hooper et al. 2005, Cadotte et al. 2011). The use of functional traits allows us to identify groups of special conservation concern, or to maximize the preservation of ecosystem functions. In contrast to species-based approaches, functional trait approaches enable generalizations across communities and ecosystems. Functional diversity of pollinators has been found to be complementary to the functional diversity of flowering plants (Fontaine et al. 2005). Accordingly, management practices that promote a high functional diversity of plants may increase the stability of higher trophic levels (Wagner et al. 2014b). And management practices that promote a high functional trait diversity in bee communities increases pollination through provision of complementary pollination services (Hoehn et al. 2008; Albrecht et al. 2012). Mechanisms that are important to sustain mutualistic plant-pollinator interactions. Furthermore, diverse communities of both species and functional traits provide us with future ecological insurance if certain key species decline or go extinct (Yachi & Loreau 1999). Consequently, to assess the effects of habitat management, several measures of bee community responses should be considered, since they may reflect contrasting responses to habitat modifications or the environmental context (Forrest et al. 2015).

1.6 Objectives

The overarching objective of my thesis was to identify the conservation value of power-line clearings as habitat for insect-pollinated plants and wild bee communities in forest landscapes (Figure 1). To do this we conducted an experiment in power-line clearings where woody vegetation was (i) cut and left to decay; (ii) cut and removed from the plot; or (iii) uncut (4-9 years of regrowth). First, we assessed effects of management practices (i.e. cut, cut-remove, uncut) on insect-pollinated plants (i.e. forbs, dwarf shrubs and shrubs), and the modifying effects of the environmental context or time since clearing (**Paper I**). Then, we identified whether a change in the current management regime in power-line clearings (i.e. removing the woody vegetation instead of leaving it to decay on the ground) would enhance the habitat quality for solitary bees and bumble bees, and whether the effect was modified by abiotic or biotic environmental conditions and time after maintenance clearing (**Paper II, III**). Vegetation clearing is costly and time consuming, and a better understanding of the spatio-temporal effects of clearing on plants and wild bee communities will aid in optimizing the timing and frequency of vegetation clearing in different areas (Hanula et al. 2016). Studies in forest clear-cuts have found that in order to promote flowering species and flower-visiting insects, the logging residue should be removed (Korpela et al. 2015, Rivers et al. 2018). Removing woody debris may increase plant diversity, through reduced competition for light and space, and alter ground-level microclimatic conditions of solar irradiation, temperature and moisture (Weng et al. 2007). Conditions which in turn would benefit wild bees associated with semi-natural grasslands and forest dwelling species. Finally, we assessed the importance of power-line clearings compared to forest habitats for bumble bees, throughout the foraging season, in landscapes dominated by production forests. We also studied whether the habitat use was influenced by flower resources, light availability and tree cover density. We evaluated the conservation value of power-line clearings for plants and wild bees – and by consequence – their associated ecosystem functions and services, by specifically addressing following questions:

1) How do the management practices (i.e. cut, cut-remove, uncut) in power-line clearings affect species-based and functional trait diversity of insect-pollinated plants? (**Paper I**)
2) How do the management practices in power-line clearings affect the species-based diversity, functional trait diversity, and species composition of solitary bees? (**Paper II)**
3) How do the management practices in power-line clearings affect the species-based diversity and functional trait groups of bumble bees? (**Paper III**)
4) Is there a spatial and temporal variation in bumble bees in power-line clearings and forest habitats during the foraging season? (**Paper IV**)

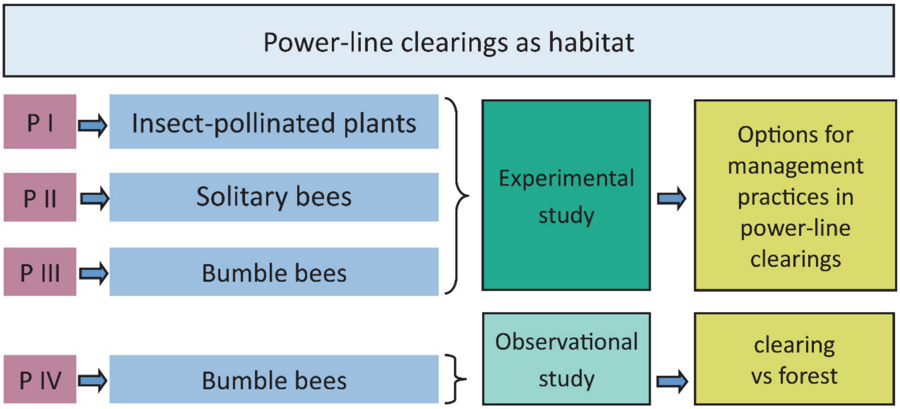

***Figure 1:** Schematic overview of the four studies (Paper I - Paper IV) included in the thesis. All four studies were done within power-line clearings. In the first tree studies (P I - P III) we conducted a large-scale field experiment mimicking different maintenance clearing practices, in which the woody vegetation was: (1) cut and left to decay in the clearing; (2) cut and removed from the plot; and (3) uncut. We explored the effects on insect-pollinated plants and solitary bees and bumble bees. In the fourth study (P IV) we investigated the spatio-temporal variation of bumble bees in power-line clearings and adjacent forest habitats.*

2 Methods

2.1 Study system – Boreal forest

The studies in this thesis have taken place in power-lines transecting boreal forest landscapes in South-Eastern Norway (Figure 2). The boreal forest is widely distributed across the northern hemisphere, mainly covering Canada, Alaska, Russia and Scandinavia (Brandt et al. 2013), and comprise one-third of the world's forests (Gauthier et al. 2015). The boreal forest in our study area is dominated by the coniferous tree species, Norway spruce *Picea abies* and Scots pine *Pinus Sylvestris.* The most common deciduous trees are birch, *Betula spp.,* rowan *Sorbus aucuparia*, *Salix spp.* and European aspen *Populus tremula*, but the deciduous component is usually scarce. Understory vegetation typically include herbaceous species, grasses and dwarf shrubs in the field layer, and bryophytes and lichens in the bottom layer (Nilsson and Wardle 2005). Large proportions of the Scandinavian forests are managed production forest (Gauthier et al. 2015). In Norway, 37% (121 000 km^2) of the total land area is covered by forest and around 68 % of these forested areas are managed forest (Landsskogtakseringen 2019, Tomter and Dalen 2018).

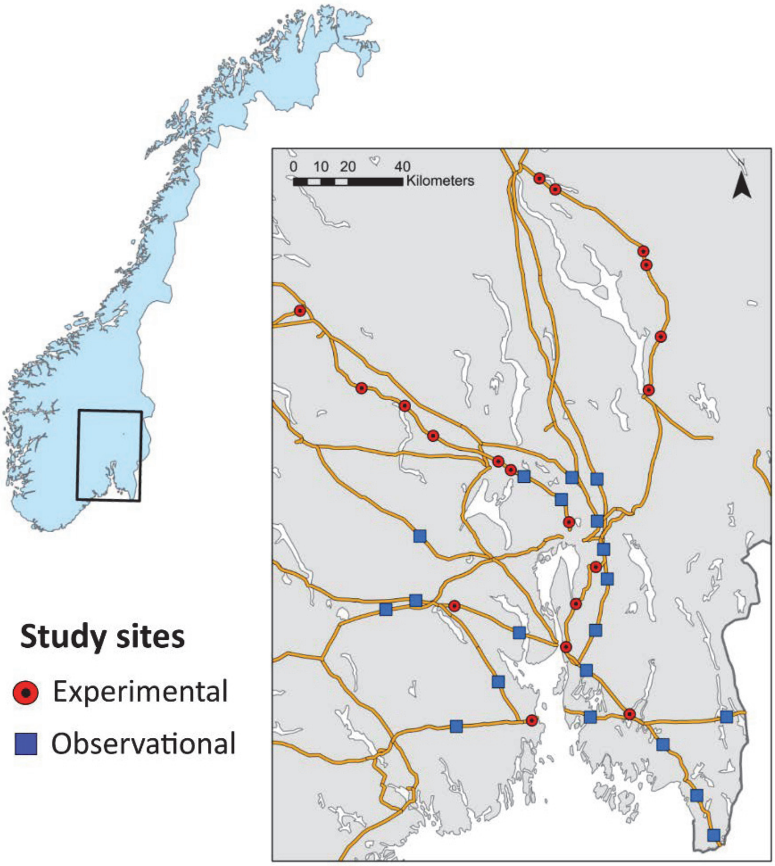

Figure 2: *Geographic distribution of the study sites located along the main power-line grid in South East Norway. There were 19 study sites in the experimental study (red circles), and 20 sites in the observational study (blue squares).*

2.2 Study sites – Power-line clearings

All study sites in this thesis were located along the main power-line grid transecting boreal forest systems, mainly consisting of mixed stands of Norway spruce, Scots pine, and birch, in South-Eastern Norway. Each site had been subjected to the same management regime with manual cutting of all woody vegetation every 5 to 12 years. The frequency of cutting is dependent on the site productivity and is targeted towards preventing trees from reaching the aerial lines. In Norway, the management practices are also conducted without any use of chemicals and with little disturbance of the ground layer. After cutting, the biomass (fine woody debris <10 cm in diameter) is left to decay on the ground. The cut vegetation in the clearings comprises trees in an early successional phase. Productive sites are dominated by a substantial regrowth of deciduous trees, together with shrubs and forbs, whereas low-productive sites are often dominated by ericaceous dwarf shrubs (Eldegard et al. 2017) (Figure 3).

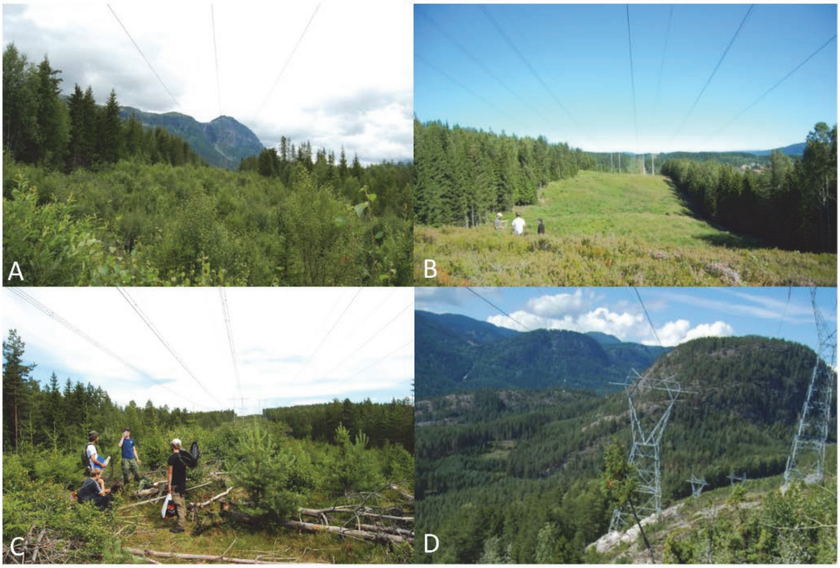

Figure 3: *Illustration of differences in environmental conditions in the power-line clearings. Productive sites are dominated by regrowth of deciduous trees (A), low-productive sites are dominated by ericaceous dwarf shrubs (B). Other sites are dominated by coniferous trees and have larger dimensions of dead wood in the clearings (C). Sites are located at different elevations with variation in topography, in which the different slopes and directions define the light availability of the plot (D). Photo: Lisbeth Nordtiller.*

2.3 Study design (Paper I, II, III)

2.3.1 Experimental study (Paper I, II, III)

We conducted a large-scale field experiment within the main power-line grid in South East Norway (Figure 4). We identified 19 sites below power-lines located between latitudes 59.33°–61.12°N and longitudes 08.95°–11.36°E at 45–535 masl, where there was a stretch of at least 200 m with substantial regrowth of trees. At each site, we established three treatment plots of approx. 30 m × 60 m [corridor width], with an average distance of 120m apart (min=50, max= 345) (established autumn 2012 [n = 16] or early spring 2013 [n = 3]). The relatively short distances between treatment plots ensured low site-specific variation between treatments. Within each site, we randomly assigned one of three treatments to each plot: (i) uncut (4-9 years of regrowth); (ii) cut: woody vegetation cut and left to decay in the clearing; (iii) cut-remove: woody vegetation cut and removed from the plot (Figure 3). The woody debris in the cut-remove treatment was moved and assembled into a pile at one of the edges of the treatment plot.

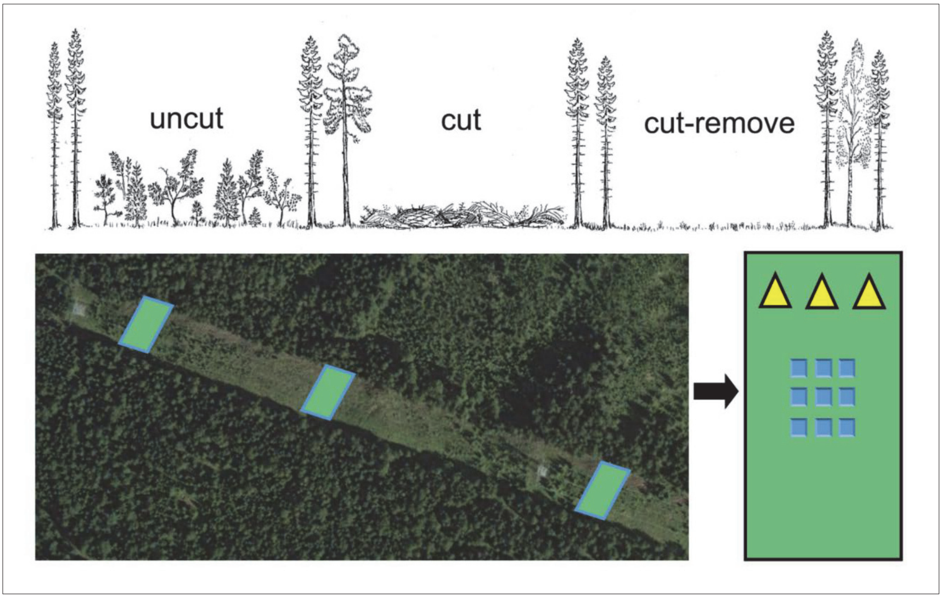

Figure 4: *Illustration of the study design in the experimental study: 19 sites located along the main power-line grid. Illustration of the three experimental treatments at each site (top), (i) woody vegetation below aerial lines uncut; (ii) trees cut and woody debris left to decay in the clearing; and (iii) trees cut and woody debris removed. Aerial photo of one site with three treatment plots (bottom right). Mean distance between plots was 120 m. Arrangement within one treatment plot (bottom left): three flight-interception traps (triangles) placed along the northern side of each treatment plot; nine 1 m^2 subplots (squares) placed in the center of each treatment plot.*

Plant surveys

In each treatment plot, we surveyed the plant community (floral resources). Plant surveys were carried out in late June and early July in 2013, 2014 and 2015. We spaced nine quadratic subplots of 1 m^2 regularly within a 10 × 10 m quadrat in the center of each treatment plot (Figure 4, 5). We identified all vascular plant species and the cover of each species were visually estimated to the nearest 1% from the nine subplots. From these data we calculated the different variables of plant groups, such as insect-pollinated plants (forbs, dwarf shrubs and shrubs) (**Paper I**), forbs (**Paper II, III**), ericaceous dwarf shrubs and Salix species (**Paper III**).

Wild bee sampling

We installed three flight interception traps (window traps) within each treatment plot (19 sites, 3 treatments), placed along the northernmost end of the treatment plot, to maximize sun exposure (Figure 4). Bees were sampled continuously throughout their main foraging-activity season. Traps were installed immediately after snowmelt (April/May) and removed in early autumn (September). We emptied traps four times in 2013 and 2014 and five times in 2015, due to an earlier onset of snowmelt. The sampling procedure enabled a continuous and consistent sampling intensity throughout the main foraging activity season of wild bees. Responses to management practices is initially occurring at a behavior level (Wong and Candolin 2015). The differences in species and number of individuals among the treatments likely reflect habitat preferences by bees from the local species pool. And we assume that differences in habitat preferences is a good proxy for habitat quality (i.e. food and nesting locations), which may in turn influence local abundances.

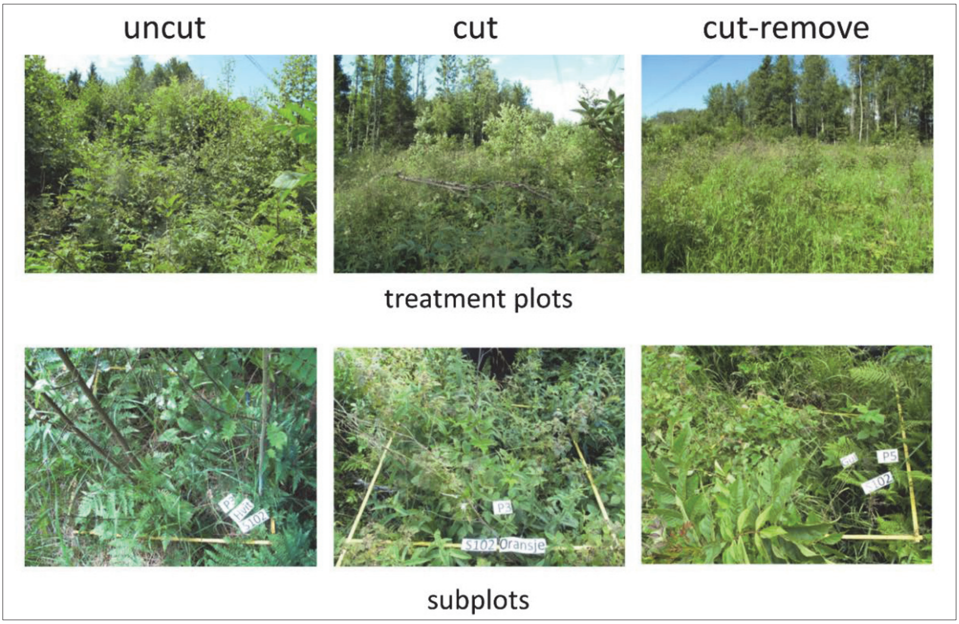

Figure 5: *Photos of one site in the experimental study. On top, the three treatment plots which were subjected to three different treatments: (1) uncut, woody vegetation not cut, (2) cut, woody vegetation cut and left to decay, and (3) cut-remove, woody vegetation cut and removed. Below, photos of one of the 1m^2 subplots within each treatment, for conducting plant surveys. In total there were 9 subplots located in the center of each treatment plot.*

The collected material was stored in 80% ethanol until identification in the lab. All bees were identified using regional identification keys; i.e. Schmid-Egger and Scheuchl 1997, Amiet 1999, 2001, Scheuchl 2000, 2006, Amiet 2004 for the solitary bees (**Paper II**) and Bollingmo 2012, Løken 1985, Ødegaard et al. 2015 for the bumble bees (**paper III, IV**). All individuals from the *B. lucorum s.str.* group (i.e. *B. cryptarum*, *B. lucorum*, *B. magnus*, and *B. terrestris*), were pooled into one operational taxonomic unit in the analyses (**Paper III, IV**). In **Paper II**, the cleptoparasites were removed from the analyses of solitary bees, due to their host dependence.

2.3.2 Observational study (Paper IV)

We carried out a large-scale observational field study distributed across the main power-line grid in South East Norway (58°–61°N, 8–11°E), at 25–1055 m.a.s.l. (Figure 2). We selected 20 sites with 200 m of forest perpendicular to the power-line clearing on both sides and placed four plots (4 m × 5 m) in the clearing center, 50 m apart, and a parallel set of plots into the adjacent forest interior, 100 m from the forest edge in the power-line clearing. Within each plot we placed five 1-m^2 subplots along the center line of each plot to assess the flowers resources, and one flight-interception trap to collect bumble bees (Figure 6). The traps were installed in spring in late April or early May and removed in early autumn in September. Each container was emptied four times in spring/early summer (May/June); early/mid-summer (June/July); late summer (July/August); and late summer/autumn (August/September), i.e. once a month, during the main activity period of bumble bees. We collected data on understory vegetation and habitat characteristics at 12 sites in 2009 (July 6th–Aug 5th) and 8 sites in 2010 (June 29th–Aug 5th). We visually estimated total cover and richness of all vascular plant species in the five 1-m^2 subplots within each of the 8 plots at every site (Figure 6).

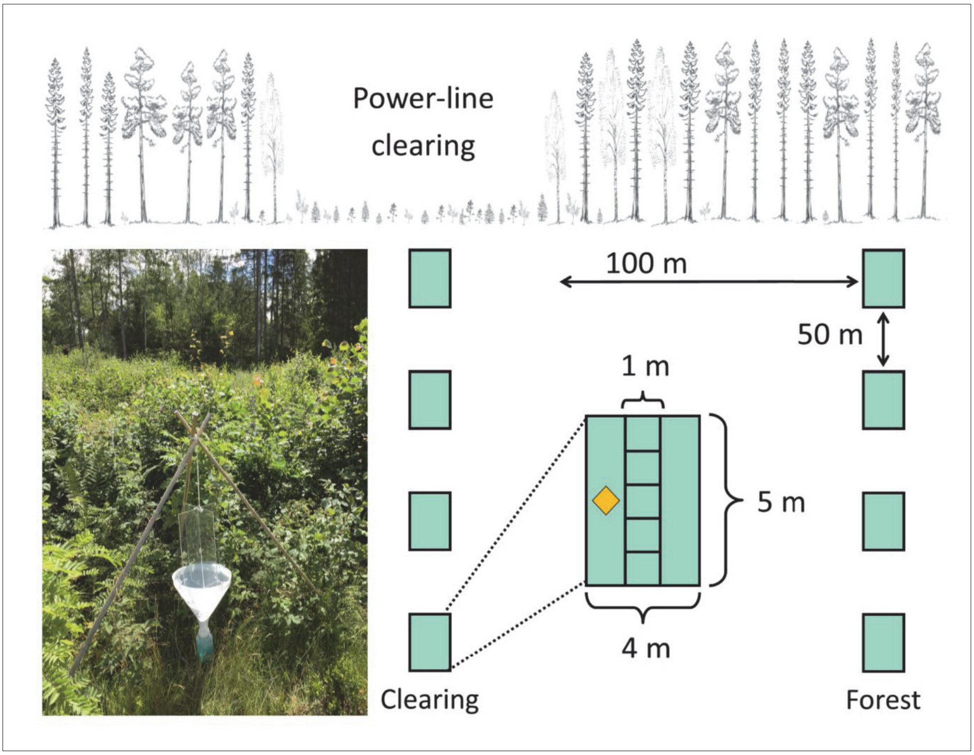

Figure 6: *Illustration of the study design in the observational study: 20 sites were situated along the main power-line grid in boreal production forests. We established four plots (4 × 5 m), 50 m apart in the center of the power-line clearing and four plots located in parallel, 100 m from the forest edge into adjacent forest. Bumble bees were sampled in one flight-interception trap (diamond) within each plot (10 traps each site), and flower resources were surveyed within five subplots (1m2) along the center of each plot (5 m2 x 10 plots). Photo: Mari Steinert*

2.4 Data preparation

2.4.1 Plant community responses (Paper I)

We selected flowering forb, dwarf shrub and shrub species, based on two criteria; plants known to be of importance to pollinators (Willmer 2011), and with an average height of no more than 1.5 m. Within each treatment plot, the observed plants in the nine $1m^2$ subplots were treated as one plant community, i.e. we used treatment plot as sampling unit in the statistical analyses. We calculated species richness, diversity and evenness, using the Vegan package in R (Oksanen et al. 2013). Richness was calculated by summing the number of species in the nine subplots in each treatment plot. If a species or a morphospecies was present more than once in one of the nine subplots, it was counted as one. A diversity index (Shannon diversity, H') was calculated for each treatment plot (Heip et al. 1998), based on the summarized abundance per species in the nine subplots. Evenness was calculated following Pielou (1966), using J= H'/log(s), where H' is the Shannon diversity and *s* is the number of species.

To quantify the floral resource diversity within the plant communities, we assigned nine functional effect traits to each plant species (Figure 7). The traits [extracted from Lid and Lid (2005)] were based on morphological characteristics of flowers of known importance for pollinators (**Paper I**, Appendix). We calculated two functional diversity indices: functional dispersion, as a measure of the variation in trait values within a community (Laliberté and Legendre 2010) and functional evenness, as a measure of the regularity of the distribution of abundance in functional trait space (Villéger et al. 2008, Laliberté and Legendre 2010, Mouchet et al. 2010, Mouillot et al. 2013). We used the number of subplots in which a species occurred as a measure of abundance. When calculating the indices, we used weighted abundances and the Cailliez correction for non-Euclidian distances because of the inclusion of categorical traits (Laliberté et al. 2014, Forrest et al. 2015). Both indices were calculated using the dbFD-function of the FD package in R (Laliberté et al. 2014).

Figure 7: *Photos demonstrating different floral traits and different wild bee species in our study, representing some of the functional traits. (A) Bombus pascuorum with the tongue (proboscis) out ready to gather nectar. Tongue length is an important wild bee trait related to the nectar tube (corolla) of the flowers. (B) A ground-nesting bee coming out of its nest. The majority of the solitary bees in Norway nest below-ground, a trait that favors bare ground and sandy soils. (C) B. lucorum s.str. with pollen baskets loaded with pollen, feeding on red clover (Trifolium pratense) a plant in the Fabaceae family with multiple flowers in one flower head. Fabaceae is an important flower resource with concealed flowers and long nectar tubes. (D) Eucera longicornis (female), a large bodied bee feeding on a Vicia sp. (Fabaceae). The solitary bees vary in body size, an important trait determining their dispersal ranges and their ability to colonize managed habitats. (E) B. soroeensis visiting a bluebell (Campanula rotundifólia), an important flower resource for this species. Some bumble bees prefer specific flowers, but because their adult activity period is long, they forage on different species throughout the season. (F) An Andrena sp. (solitary bee) feeding on a dandelion (Taraxacum sp.), an open flower with early season pollen and nectar resources for wild bees. Photos: Mari Steinert.*

2.4.2 Bee community responses (Paper II, III, IV)

We rarefied the solitary and bumblebee responses to account for the variation in number of successful trapping sessions between treatment plots and years, which ranged from nine to 15. The sampling intensity was standardized by estimating the number of species and individuals expected to be sampled in a treatment plot given nine sampling sessions (Chao et al. 2014). The rarefied species richness was calculated using the iNext package in R with sample size set to nine, and with 50 bootstrap replications (Hsieh et al. 2019). The rarefied abundance was calculated by randomly sampling nine traps within a treatment plot, repeated 1000 times, to estimate mean abundance of each bee species as the rarefied response. The species richness summed from the rarefied abundance matrix was identical to the raw species richness (non-rarefied). For solitary bees and bumble bees we used treatment plot as sampling unit in the statistical analyses.

For the bumble bee responses in power-line clearings and forest habitats (**Paper IV**), we calculated richness and abundance by summing the species and individuals in each sampling period and used sampling period from each trap as our unit in the statistical analyses (i.e. four periods throughout the season). To account for the uneven sampling, we chose to use the smallest sampling unit (sampling period) and selected a nested random effects structure.

2.4.3 Environmental conditions (paper I, II, III, IV)

Habitat characteristics

In each paper we recorded environmental conditions and habitat characteristics at site or plot-level. As a measure of dead wood (**Paper II**), we counted lying dead trees with a diameter at breast height (DBH) of >15 cm in transects of 2 × 20 m along both sides of the forest-edges of each treatment plot (i.e. dead trees of larger dimensions compared to the woody debris from the maintenance clearing). Site-level data on average monthly precipitation (**Paper I, III**), temperature in January, and average temperature in the growth season (**Paper I**) was provided by the Norwegian Meteorological Institute. We also recorded direction, slope and latitude in each treatment plot, to calculate the solar irradiation index (Oke 1987) as a measure of light availability, hereafter ‘irradiation index’. To assess a more accurate amount of available sunlight, in **Paper I**, we calculated the global light index (GLI) in the growing season (May-September), from photos taken with a fisheye lens (hereafter ‘canopy density’). The global light index is the weighted average of diffuse and direct radiation through the canopy (Schleppi 2017). The photos were taken in the approximate center of each treatment plot at each site, in July 2013 and in mid to late June 2014 and 2015. We used the software Hemisfer (Schleppi et al. 2007, Thimonier et al. 2010) to analyze the photos. The software distinguishes between pixels of sky and canopy and uses this together with coordinates, slope gradients and slope directions to calculate available sunlight (Hemisfer 2014). We used the global light index in the uncut treatment plots in 2013 as a measure of initial regrowth (hereafter ‘initial canopy density’) based on light availability within the site. Elevation is recognized as a strong environmental filter on functional traits and species diversity (Hoiss et al. 2012), and we therefore included elevation based on digital maps (Kartverket 2019) in all our models (**Paper I, II, III, IV**). To identify the dependency on the environmental context in **Paper IV**, we calculated the solar irradiance index (Oke 1987) from the recorded direction, slope and latitude in each plot, and elevation was obtained from digital maps (Kartverket 2019). Tree cover density (%) was extracted from remotely sensed images for each plot within each site (Copernicus Land Monitoring Service 2012).

Flower resources (Paper II, III)

To investigate the responses of wild bees to management practices, we used plant species richness, cover and functional traits as measures of flower resources; For **Paper II**, **III** and **IV**, we used forb species richness as an explanatory variable, because forbs are positively correlated to wild bees (Sydenham et al. 2016, Goulson et al. 2003) and allows us to identify habitats with a larger proportion of flower species associated with the cultural landscape (Eldegard et al. 2017). From the same plant data in **Paper I**, we calculated the species richness of forbs (**Paper II, III**), % cover of ericaceous dwarf shrub species, % cover of Salix species, and % cover of species with a nectar tube (**Paper III**) by summing the values in each subplot per treatment plot. When calculating functional trait indices, we followed the same methodology as in **Paper I**, with the nine traits. We calculated functional dispersion (FDis) of forbs (**Paper II, III**), based on the nine functional effect traits for each plant species (**Paper II**, Appendix). In **Paper III**, we also calculated FDis of single traits: FDis inflorescence, and FDis flower phenology. In **Paper IV**, to test the spatiotemporal use of habitats we calculated species richness of forbs and species richness of dwarf shrubs and cover of *Calluna vulgaris* (heather) and cover of *Vaccinium Myrtillus* (bilberry) per plot.

Landscape fragmentation and source habitat (Paper I, II, III)

To assess the landscape fragmentation and source habitat areas surrounding each site, we used ArcGIS (ESRI 2011) and Ar5 digital land use maps (Ahlstrøm et al. 2019). As a proxy for landscape fragmentation we used the total number of polygons of different land use types (11 in total). As a proxy for source habitat, we used the total area of non-forested landscape elements (i.e. non-tilled arable land (due to the associated field margins), semi-natural areas/pastures, open surfaces, and road-verges) that can function as potential source patches for wild bees in the power-line clearings (**Paper II, III**). For the plants (**Paper I)**, we also included the category 'arable land' as a potential source habitat. The land use types were measured at increasing radii around each site (150m, 300m, 500m, 1000m, 2000m). To account for collinearity between the radii around each site, the different scales were combined into one variable using a separate principal component analysis (PCA). For both variables, we extracted the first PCA axes and transformed to a scale of 0–1 (Dormann et al. 2013). As a measure of landscape fragmentation, a PCA was calculated of all radii up to 2000 m (**Paper I, II),** and Shannon diversity (Heip et al. 1998) was calculated, of all radii up to 2000 m (**Paper III**). As a measure of source habitats, we used all radii up to 2000m for the plants and bumble bees (**Paper I, III**), whereas due to the more restricted foraging range of solitary bees (Greenleaf et al. 2007), we used the radii up to 500 m (**Paper II**).

2.5 Statistical analyses

2.5.1 Methods specific to Paper I

To study the effects of different management practices on the plant communities, we used several measures of biological diversity (Table 1). We were not only interested the influence of management practices on the taxonomic diversity of plants, but also the functional diversity (i.e. the evenness of traits within a community, functional evenness (FEve), and the variation in functional traits within a community, functional dispersion (FDis)). For each response variable, we carried out a preselection of candidate variables (*P*-values ≤ 0.10) and tested each explanatory variable separately and in interaction with the three-level categorical variable treatment. Site identity was used as a random effect to account for the among-sites variation and repeated sampling (i.e. once per year).

We analyzed effects of the treatments on diversity, evenness, functional evenness and functional dispersion, by fitting a linear mixed effect model (LMM), with Gaussian-distributed errors and identity link. Effects of the treatments on species richness were analyzed by fitting a generalized linear mixed effect model (GLMM), with Poisson-distributed errors and a log-link function. Each response variable was tested separately and in a two-way and three-way interaction with the categorical variables; treatment and year. We carried out a preselection of candidate variables (P-values ≤ 0.10). Final models were selected by conducting stepwise backward elimination based on likelihood ratio tests (LRTs), until only significant variables remained (P ≤ 0.05).

Table 1: *Statistical analyses for insect-pollinated plants* ***Paper I:*** *To test for treatment effects on the insect-pollinated plants we fitted linear mixed effect models (LMMs) and generalized linear mixed effect model (GLMM). Site identity was used as a random effect. Candidate environmental co-variables included in final models in bold.*

Responses	**Explanatory variables**	**Model**
Richness	**Treatment (cut, cut-remove, uncut)** **Year (2013, 2014, 2015)** **Elevation** **Temperature** **Precipitation** **Radiation index** **Stem m^{-2}** Initial canopy density **Productivity** **Source habitat (PC1)** Landscape fragmentation (PC1)	GLMM
Evenness (H’/ log(species richness))		LMM
Diversity (H’)		LMM
Functional evenness (FEve)		LMM
Functional dispersion (FDis)		LMM

2.5.2 Methods specific to Paper II

To identify the conservation effects of management practices on solitary bees over the course of three years, we used both taxonomic and functional trait diversity in addition to species composition (beta diversity and turnover) of solitary bees (Table 2). We chose three traits known to influence bee responses to environmental conditions: nesting preference (above vs below-ground nesters), tongue-length and body size (Williams et al. 2010, Cariveau et al. 2016, Greenleaf et al. 2007). The trait values for nesting preference was obtained from the literature (Carrek 2016; Westrich 1990). We used body size as a measure of species mobility (Greenleaf et al. 2007), measuring the intertegular distance (ITD) of the bees (Cane 1987). The tongue length was estimated using the BeeIT package in R (Cariveau et al. 2016), which calculates the tongue length based on the taxonomic family and species-specific ITD. For the body size and the tongue length we calculated the community weighted mean (CWM) and functional dispersion (FDis) within each treatment plot (Laliberté and Legendre 2010). We used weighted abundances (rarefied) with the dbFD-function of the FD package in R (Laliberté et al. 2014).

To assess the temporal change in species composition within and among treatments, we used multivariate dispersions as a measure of beta diversity (Anderson et al. 2006). We calculated the dissimilarity component of turnover (BetaJTU, i.e. species replacement) in addition to the overall beta diversity (BetaJAC, i.e. the turnover and species loss and gain) (Baselga et al. 2010, 2012) using the Betapart package (Baselga et al. 2018). To emphasize the importance of rare species, we used Jaccard distance, which uses presence absences (Anderson et al. 2011). We extracted the distances to group centroids within each site as our responses, using the betadisper function of the Vegan package (Oksanen et al. 2013). We analyzed effects of treatments on solitary bees, by fitting linear mixed effect models (LMMs), with identity link, assuming a normal distribution of errors for the rarefied responses and the functional trait indices and the measures of species composition (turnover and beta diversity). To model the raw species richness, we fitted a generalized mixed effect model (GLMM), with a log link function, assuming Poisson-distributed errors. To model the proportion of below-ground nesters, we fitted a GLMM, with binomial distributed errors and a log link function. For each response variable we tested each explanatory variable separately and in a two-way and three-way interaction with the categorical variables; treatment and year. We carried out a preselection of candidate variables (P-values ≤ 0.10), and then performed a backwards elimination of variables using likelihood ratio tests. Site identity was used as a random effect.

Table 2: *Statistical analyses for* ***Paper II****: To test for treatment effects on solitary bees, we fitted linear mixed effect models (LMMs). Site identity was used as a random effect. Responses were log(y+1) transformed to fit a normal distribution if needed. Candidate environmental co-variables included in final models in bold. Abbreviations: FDis = functional dispersion, CWM = Community weighted mean.*

Response variables	**Explanatory variables**	**Model**	**Description**
Richness	**Treatment** **Year (2013, 2014, 2015)** **Elevation** **Richness forbs** **FDis forbs** Irradiation index **Dead wood** **Source habitat (PC1)** Landscape fragmentation (PC1)	LMM	rarefied
Raw species richness		GLMM	
Abundance log(y+1)		LMM	rarefied
Proportions below-ground nesters (above-ground nesters inverse)		GLMM binomial	Erica affiliated bees and cleptoparasites removed from the analyses
FDis Body size log(y+1)		LMM	
CWM body size		LMM	
FDis tongue length log(y+1)		LMM	
Turnover BETA$_{JTU}$		LMM	Jaccard distance
Beta diversity BETA$_{JAC}$		LMM	Jaccard distance

2.5.3 Methods specific to Paper III

To identify the effects of management practices on bumble bees, we used both taxonomic and functional trait groups. We used rarefied richness and rarefied abundance of bumble bees. We calculated a diversity index (Shannon diversity, H’) from the rarefied abundance matrix (Heip et al. 1998). In addition to identifying management practices that would increase the species-based diversity, we also aimed to understand to what degree these practices retain the functional diversity of bumble bee communities, to ensure the provision of complementary pollination services (Albrecht et al. 2012, Hoehn et al. 2008). By taking functional trait groups into account we were able to identify the effects on vulnerable species of special conservation concern. We chose life history and morphological traits for all bumble bees, likely to be influenced by the treatments and environmental context (Goulson et al. 2005, 2008, Williams et al 2009): tongue-length (i.e. long tongued vs short tongued bumble bees, based on taxonomy), phenology (early vs. late, based on month of emergence of queens), and nesting strategy (eusocial vs cuckoo bumble bees). We used the abundance of individuals in each trait group as the functional trait responses in the analyses. To identify the influence of management practices on eusocial bumble bees, we excluded the cuckoo bumble bees from the analyses of the functional trait groups, due to their diverging biology and host dependence. This could potentially mask effects of management practices on the trait groups of the eusocial bumble bee communities.

To test for treatment effects on bumble bee responses, we fitted linear mixed effect models (LMMs), with identity link, assuming a normal distribution of errors. LMMs were used for all the bumble bee response variables due to the rarefied responses consisting of non-integers. To achieve a normal distribution of the residuals we log(y+1) transformed overall abundance, and abundance of long-tongued bees, short-tongued bees, early emerging bees, late emerging bees, cuckoo bees, and bees belonging to the *B. lucorum s.str.* group. We carried out a preselection of candidate environmental co-variables (P-values ≤ 0.10); for each response variable, we tested each environmental variable separately and in a two-way interaction with the categorical variable 'treatment'. We used site identity as a random effect.

Table 3: *Statistical analyses of Paper III: To test for treatment effects on bumble bee responses, we fitted linear mixed effect models (LMMs). Responses were log(y+1) transformed to fit a normal distribution if needed. Candidate environmental co-variables included in final models in bold. Abbreviations: FDis = functional dispersion.*

Response variables	**Explanatory variables**	**Model**	**Description**
Richness	**Year (2013 and 2015)** **Treatment (cut, cut-remove, uncut)** **Precipitation** **Elevation** Irradiation index Source habitat area (PC1) Landscape fragmentation (H') **Richness forbs** **Cover Ericacea species** Cover Salix species **Cover nectar tube species** **FDis forbs** FDis flower phenology FDis inflorenscence	LMMs, linear mixed-effects models	Rarefied
Abundance log(y+1)			Rarefied
Diversity			Rarefied
Cuckoo bumble bees log(y+1)			Based on rarefied abundances
Long-tongued bumble bees log(y+1)			Based on rarefied abundances Cuckoo bumble bees were excluded from the analyses
Short-tongued bumble bees log(y+1)			
Early emerging bumble bees log(y+1)			
Late emerging bumble bees log(y+1)			
B. lucorum s.str. log(y+1)			Based on rarefied abundances

2.5.4 Methods specific to Paper IV

To analyze the spatial and temporal variation in bumble bees in the power-line clearings and forest habitats throughout their main activity period, we used richness and abundance of bumble bees. We analyzed the influence of floral resources, light availability, tree cover density and elevation on bumble bees at the plot level (Table 4).

To visualize the bumble bee communities at each site in the two habitats (clearing and forest) We calculated Nonmetric Multidimensional Scaling ordination (NMDS) (Oksanen et al. 2013). To identify the spatio-temporal use of habitats related to environmental characteristics on bumble bees, we fitted linear mixed effects models (LMMs) with Gaussian-distributed errors and identity link, with the random structure of plots nested in site (1|site) + (1|site: plot). We carried out a preselection of candidate environmental co-variables (P-values ≤ 0.10); for each response variable, we tested each environmental variable separately and in a two and three-way interaction with the categorical variables; 'habitat' and 'sampling period'.

Table 4: *Statistical methods used in **Paper IV:** To test the variation in bumble bee richness and abundance in the power-line clearings and forest habitats we used Nonmetric Multidimensional Scaling ordination (NMDS) and linear mixed effects models (LMMs). Candidate environmental co-variables included in final models in bold.*

<table>
<tr><th>Response variables</th><th>Explanatory variables</th><th>Specifications</th><th>Model</th><th>Description</th></tr>
<tr><td>Abundance</td><td></td><td>Bray-curtis
Square-root transformation
999 permutations</td><td>NMDS</td><td>Visualization of the variation of bumble bees in the two habitats in multidimensional space.</td></tr>
<tr><td>Richness</td><td rowspan="2">Habitat
Sampling period
Richness forbs
Richness dwarf shrubs
Cover heather
Cover bilberry
Irradiance index
Tree cover density
Elevation</td><td>Random effects:
(1|Site) +
(1|Site:Plot)</td><td>LMM</td><td rowspan="2">Two habitats, four sampling periods</td></tr>
<tr><td>Abundance log(y+1)</td><td>Random effects:
(1|Site) +
(1|Site:Plot)</td><td>LMM</td></tr>
</table>

3 Results and discussion

Overall, the studies presented in this thesis show that power-line clearings can be important habitats for communities of both insect-pollinated plants and wild bees, and that habitat quality can be enhanced with proper management. We found that cutting the vegetation had a positive effect on plants and wild bees compared to the uncut plots, regardless of woody debris removal (**Paper I, II, III**). However, the effect of management practices was context dependent. Under certain environmental conditions the removal of woody debris led to a higher functional diversity of plants (**Paper I**) which promoted a higher functional diversity of wild bees (**Paper II, III**). Different management practices also showed contrasting effects on different biological diversity measures of plants and wild bees. We found that the power-line clearings provide essential late-season foraging resources for bumble bees and demonstrate the negative effects of too dense forest stands (**Paper IV**). Together, the findings of this thesis represent a foundation for developing informed management strategies for conserving pollinators in power-line clearings in forest landscapes.

In the experimental study we recorded a total of 269 vascular plant species (of which 19 were morphospecies). Of the total plant communities, the insect-pollinated plants comprised 52% (141 species) forbs, 4% (11) shrubs, and 2.6% (7) dwarf shrubs (**Paper I**). Of the wild bees, we found 91 out of the 172 known solitary bee species (**Paper II**), and 22 species out of the 35 bumble bee species in Norway (**Paper III, IV**). We found a high variation and no significant temporal differences in the observed means of the richness or functional dispersion (FDis) of insect-pollinated plant communities among the three treatments. Although there was a tendency of a small increase in mean richness and FDis of insect-pollinated plants in the two cut treatments over time (Figure 8 A, B). The observed mean richness and abundance of solitary bees increased over time, with the most substantial increase in treatment cut-remove (Figure 8 C, D). In comparison, the observed means of bumble bee richness and abundance were higher in both cut and cut-remove treatments, compared to the uncut treatment, but without a clear temporal increase (Figure 8 E, F).

3.1 Paper I

How do the management practices (i.e. cut, cut-remove, uncut) in power-line clearings influence species based and functional trait diversity of insect-pollinated plants?

We found that the management clearing practices cut and cut-remove were both effective in increasing the species and functional diversity of insect-pollinated plants. But the effect sizes depended on the environmental context. We expected that removing the woody debris would show a higher increase in species and functional diversity of plants compared to the cut treatment, because biomass removal is thought to be beneficial for forbs and semi-natural grassland species (Hansson and Fogelfors 2000). But woody debris did not seem to influence species or functional diversity of forbs, shrubs and dwarf shrubs, except under certain environmental conditions.

Based on our results, the most important environmental variables with a positive influence on species and functional traits of flowering plants were low elevation, low precipitation, together with intermediate/high productivity and a high stem density (Figure 9). Some of the responses to the environmental conditions could be explained by the stress gradient hypothesis, where plant interactions shift from facilitative to competitive as environmental stress decreases (Callaway 2007). In light of this theory, we expected clearing of the woody vegetation to have a larger effect on the plant communities in less stressful environments, where competition is thought to be high (Callaway et al. 2002). Indeed, we found that species richness and plant diversity were higher in the cleared plots in areas of low environmental stress (i.e. low elevation and relatively low precipitation) (Figure 9A, 9B). A previous study also found that sites with a high stem density would benefit more from clearing (Rajaniemi 2003). We found that the cut and cut-remove treatments both increased the diversity and functional dispersion of plants in sites with higher number of stems per m^2

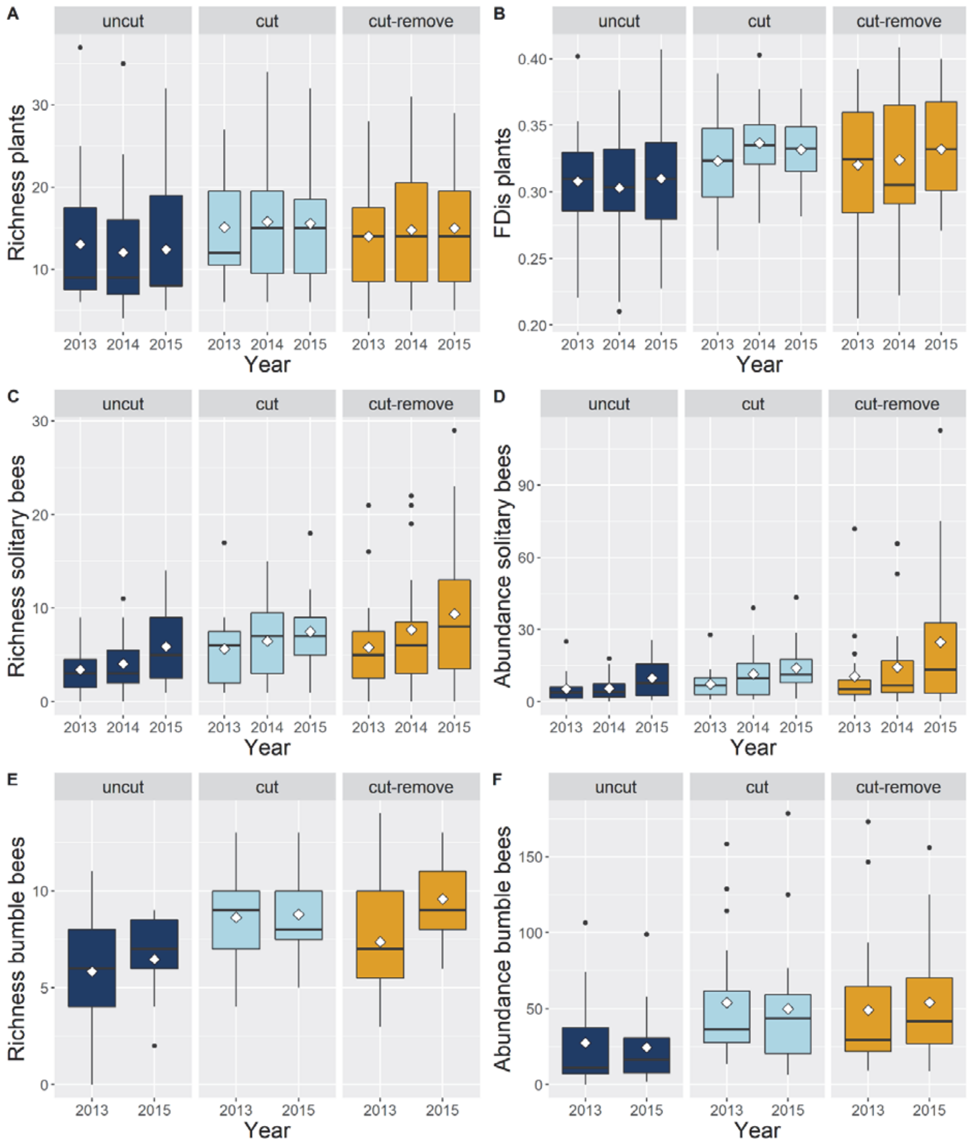

***Figure 8:** Observed species diversity of insect pollinated plants and wild bees in **Paper I, II, III**. Boxplots of (A) species richness and (B) functional dispersion (FDis) of insect-pollinated plants in the three treatments (uncut, cut, cut-remove) in power-line clearings over the course of three years (2013, 2014, 2015). (C) Species richness and (D) abundance of solitary bees in the three treatments in the three years. (E) Species richness and (F) abundance of bumble bees in the three treatments in 2013 and 2015. With mean (diamond) and median (mid-line).*

(Figure 9C, 9E). Yet, the cut treatment showed an even higher increase in both diversity and functional dispersion in sites with a high stem density, suggesting that the debris from a high number of stems is not necessarily inhibiting regeneration of many different species of insect-pollinated plants. We also found that Species richness, evenness and diversity increased with productivity across all treatments (Figure 9D). This is in accordance with the prediction that diversity should be highest at intermediate productivity (Rajaniemi 2003), because all our sites were located in areas with low to intermediate productivity. However, functional dispersion of plants increased with productivity when woody debris was removed, compared to a decrease with productivity when woody debris was left to decay. Previously, Winsa et al (2015) found that source habitats are important for establishment of semi-natural grassland species. We did not find a strong modifying effects of source habitat area on the plant communities in the different treatments. But this could be because the three species groups within the insect-pollinated plants (i.e. forbs, shrubs and dwarf shrubs) responded differently to migration from nearby source habitats.

The species and functional diversity metrics generally responded differently to the environmental context and showed contrasting treatment effects. These findings suggest that the ecosystem functioning of communities (mediated through the diversity of functional effect traits) is not necessarily predictable from the ecological processes behind the community assembly (i.e. species-based diversity) and provide empirical support for the theory of how functional trait indices should complement species-based diversities in community studies (Mouchet et al. 2010). According to Cadotte et al. (2011), the relationship between species richness and functional diversity is “complex and context dependent” and alterations in functional diversity, affecting ecosystem function, may occur without much change in species richness. Previous studies have argued that foraging traits are better predictors of pollination functions than species richness (Hoehn et al. 2008, Albrecht et al. 2012, Gagic et al. 2015). Thus, we suggest that emphasis should be placed on floral resource diversity if the aim is to enhance the habitat quality of power-line clearings for pollinating species. Nevertheless, when calculating functional trait indices based on multiple traits, the results need careful interpretation. Most of the species within the insect-pollinated plants were forbs, compared to few species of insect-pollinated shrubs and dwarf shrubs. Moreover, ericaceous dwarf shrubs are often dominating at low productive sites.

Therefore, a higher functional dispersion likely includes several forb species and a lower functional dispersion may be reflecting sites dominated by shrubs or dwarf shrubs.

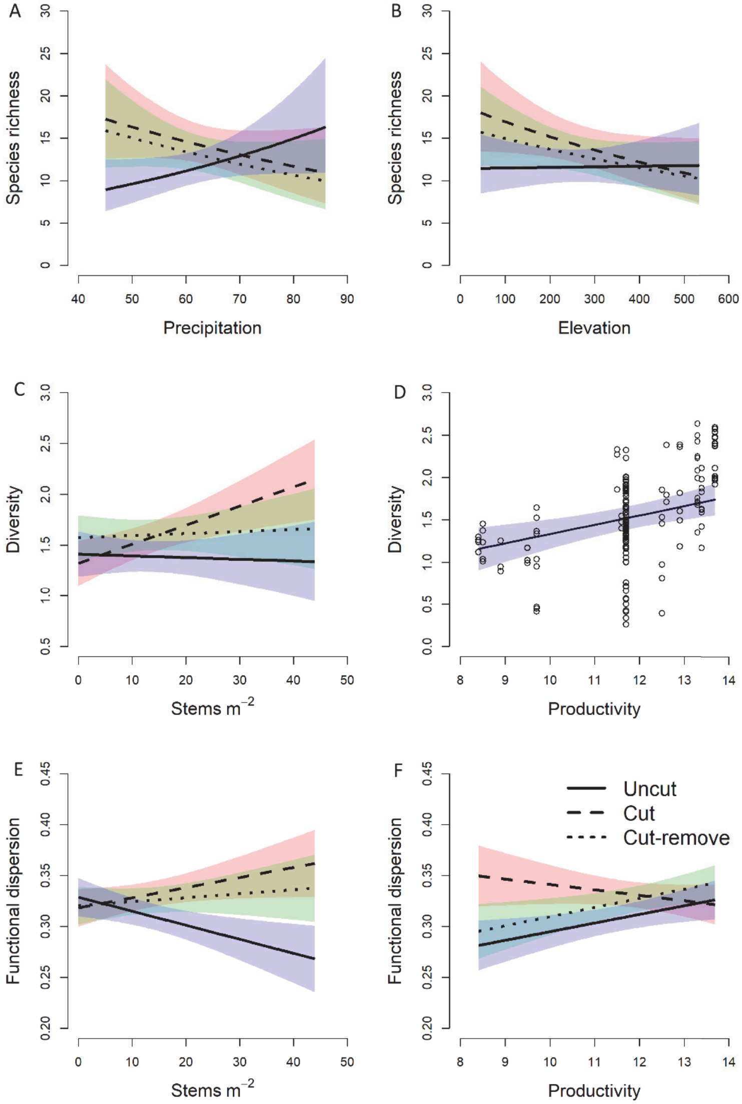

Figure 9: *Effects of management practices (uncut, cut, and cut-remove) on insect-pollinated plants in power-line clearings* ***(Paper I)****: Effects on species richness of plants were dependent on (A) precipitation and (B) elevation. Effects on diversity of plants in response to (C) stem density (stem m*$^{-2}$*) and (D) productivity. Effects on functional dispersion of plants in response to (E) stem density and (F) productivity. The shaded areas are 95% confidence intervals (CI). Uncut (solid lines) has blue CIs, cut (dashed line) has pink CIs and cut-remove (dotted line) has green CIs.*

3.2 Paper II

How do the management practices in power-line clearings influence the species-based diversity, functional trait diversity, and species composition of solitary bees?

We found that cutting the vegetation in power-line clearings was positive for solitary bee communities, and that woody debris removal further enhanced the positive effects on species richness, abundance and functional trait variation of solitary bees. The positive effect of removing the woody debris on the taxonomic and functional trait diversity of bees, was sustained over three years post treatment. However, we observed substantial among-sites variation in the temporal treatment effects for all the bee diversity measures, and some of this variation was attributed to abiotic and biotic environmental conditions. Particularly, the biotic variables, forb species richness or FDis of forbs, were important determinants for the solitary bees.

Cutting the vegetation substantially increased species richness and abundance of solitary bees, but the woody debris removal more than doubled the bee richness and abundance in areas with a higher forb richness (Figure 10a, 10d). The high richness of flower resources likely increases the habitat quality for bees by amplifying pollen and nectar rewards (Albrecht et al. 2007, Potts et al. 2003), which in turn enhance species richness as well as the frequency and stability of pollinator visits (Ebeling et al. 2008).

Removing the woody debris also had a larger positive effect on the functional trait diversity over time, by for example reducing the dominance of the most common trait group of below-ground nesters (Figure 10b), and by increasing the trait variation of tongue length within sites (Figure 10c). The FDis of tongue-length was dependent on source habitats, with a relatively higher positive effect on tongue length variation in the cut-remove treatment when more source habitat areas were available. More complex landscapes with ample adjacent source habitats may ensure a constant spillover of both plants and insects (Carrié et al. 2017). Likely, the woody debris removal facilitated immigration and subsequent recolonization of the power-line clearings from surrounding habitats, attracting species with a larger variety in tongue-length. Species richness, together with functional dispersion of body size substantially increased over time post clearing (Figure 11a, 11b), and at the same time functional dispersion of body size were much higher in the two cut treatments (Figure

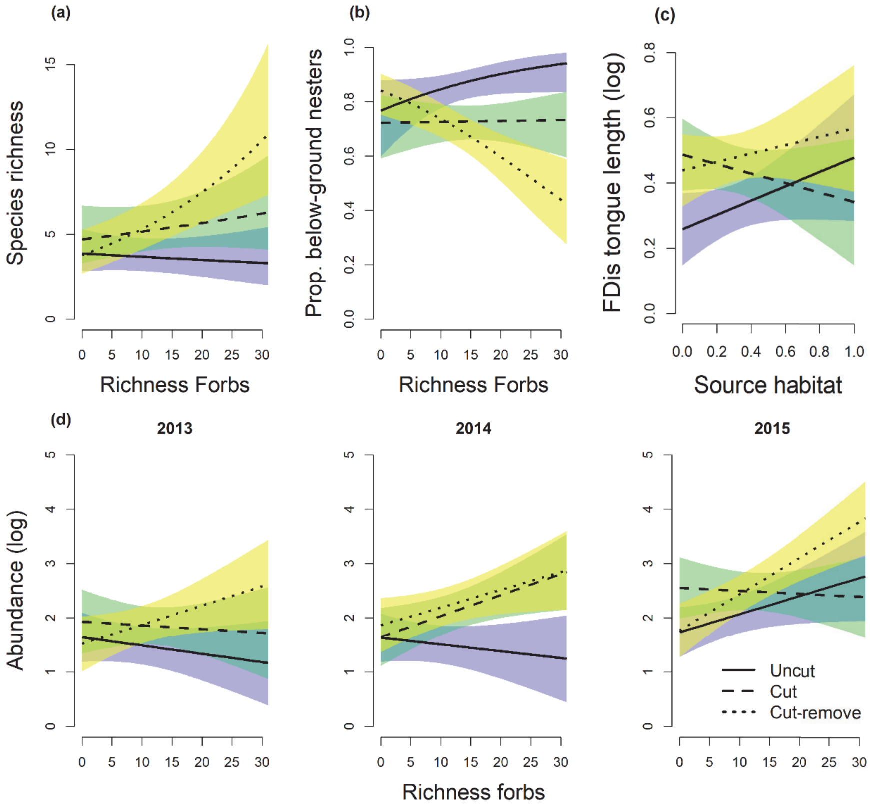

Figure 10: *Effects of management practices on solitary bees* ***(Paper II):*** *(a) Species richness of solitary bees in the three treatments (uncut, cut, cut-remove) in response to forb species richness. (b) Effects of treatments on proportion of below-ground nesters in response to forb species richness. The inverse proportion is the above-ground nesters. (c) Effects of treatments on the functional dispersion (FDis) of tongue length in the solitary bee communities in response to source habitat. (d) Effects of treatments on the abundance of solitary bees in response to forb species richness over the three years post maintenance clearing. FDis of tongue length and abundance was log(y+1) transformed. The shaded areas are 95% confidence intervals (CI). Uncut (solid lines) has blue CIs, cut (dashed line) has green CIs and cut-remove (dotted line) has yellow CIs.*

11c). These results show that cleared treatment plots attract more species each year, which suggest that it takes time for the solitary bees to colonize the habitats in the clearings. Particularly for small-bodied species the dispersal is thought to take longer time (Greenleaf et al. 2007). The proportion of above-ground nesters increased with the amount of dead wood when woody debris was removed, and sites with a higher amount of dead wood sustained communities with a higher functional dispersion of tongue length over time (**Paper II**). We anticipated a higher proportion of above-ground nesters to be attracted to sites with dead wood of larger dimensions and ground-nesting bees to be attracted when woody debris was removed, exposing the ground. Our findings suggest that woody debris removal enhanced the functional diversity of solitary bees by reducing the dominance of below-ground nesters, through providing both flower resources and nesting sites. Interestingly, we found that the species composition of solitary bees did not differ among the treatments and became more similar over the three years, resulting in a homogenization at the regional scale (Figure 11d). The beta diversity and turnover also decreased with forb species richness across the treatments in all years (Figure 11e, 11f), which may indicate that the availability of flower resources attracted a larger portion of species from the regional species pool. The decrease in beta diversity, together with the increase in bee species richness in the cut-remove and cut treatments over time may imply that the power-line clearings gradually attracted a larger portion of the regional species pool. This temporal decrease in beta diversity may signify a process where formerly rare or absent species become more common (Socolar et al. 2016), demonstrating the conservation value of the early successional habitats.

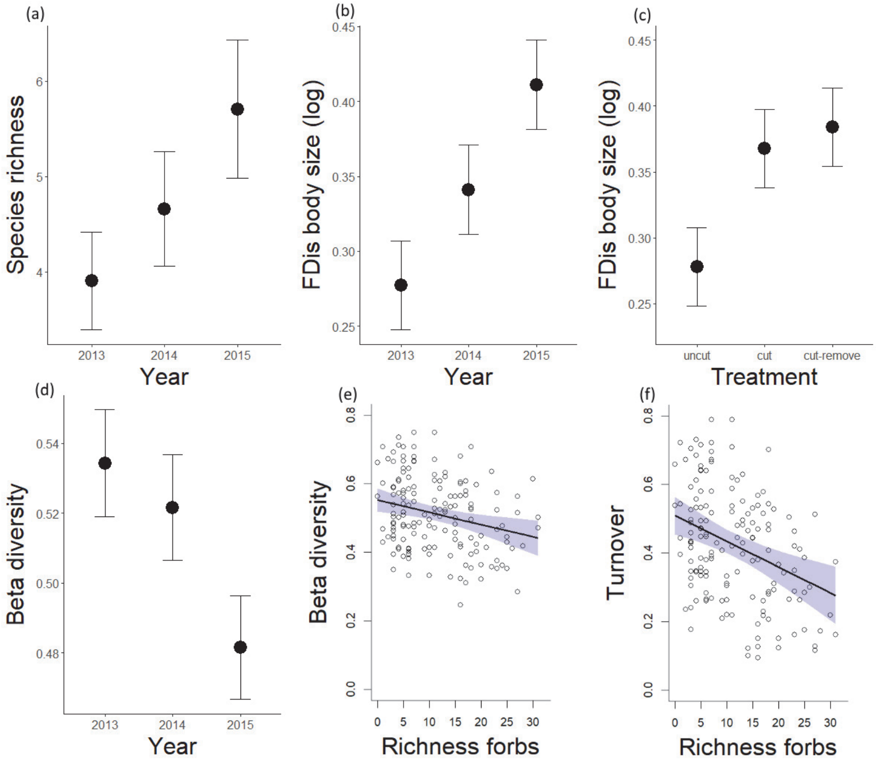

Figure 11: *Solitary bees in power-line clearings* ***(Paper II)****: (a) Species richness, (b) functional dispersion (FDis) and (c) beta diversity of solitary bees in the three years following maintenance clearing. (d) Functional dispersion of body size in the three treatments (uncut, cut, cut-remove). The variable was log(y+1) transformed. (e) Overall beta diversity and (f) turnover in response to species richness of forbs across all three treatments. Black dots and whiskers are predicted values and 95% CI limits. The shaded areas are 95% confidence intervals (CIs).*

3.3 Paper III

How do the management practices in power-line clearings influence the species diversity and functional trait groups of bumble bees?

We found that cutting the woody vegetation improved the habitat quality for bumble bees, whereas removal of the woody debris had little effect. However, the treatment effects were highly dependent on flower resources (Figure 12). Forb species richness enhanced the effect of the treatments on bumble bee species richness, abundance and diversity (Figure 12A). Particularly, the cover of forb species with nectar tube was positively associated with bumble bee species richness and abundance (Figure 12B). These results clearly demonstrate the positive effects of early successional habitats for bumble bees and support previous studies showing how flower rich early successional stands within clear-cuts in boreal forest landscapes are particularly important for wild bee species (Cartar 2005, Rubene et al. 2015). The early successional vegetation enhanced the habitat quality through increased forb richness, supporting previous studies documenting a higher bumble bee richness and abundance where there is an elevated species richness or cover of flowers (Carvell et al. 2004, Pywell et al. 2005, Rubene et al. 2015). Additionally, bumble bees have a large demand for nectar resources, and are well known for their preference for plants with high nectar content (Pywell et al. 2006, Goulson et al. 2005). Bumble bee richness increased with a higher functional trait variation in forb species (Figure 12C). A higher functional diversity of forbs likely reflects continuous flower resources throughout the foraging season with a variety of nectar and pollen resources, which is important to sustain species rich communities. The abundance of cuckoo bumble bees substantially increased with cover of forb species with nectar tube in the treatments where woody debris was removed, compared to the other two treatments (Figure 12D). This result is a strong indication of the increased habitat quality, given the cuckoo bees dependency on their host species (Sheffield et al. 2013).

Functional groups of special conservation concern, such as the long-tongued specialists and the late emerging species, were markedly more abundant in the two cleared treatment plots and in areas with a high functional diversity of floral traits (Figure 12E, 12F, 13C, 13D). These results show how vulnerable species prefer the early successional habitats after cutting, which is likely related to the availability of important floral resources (Persson

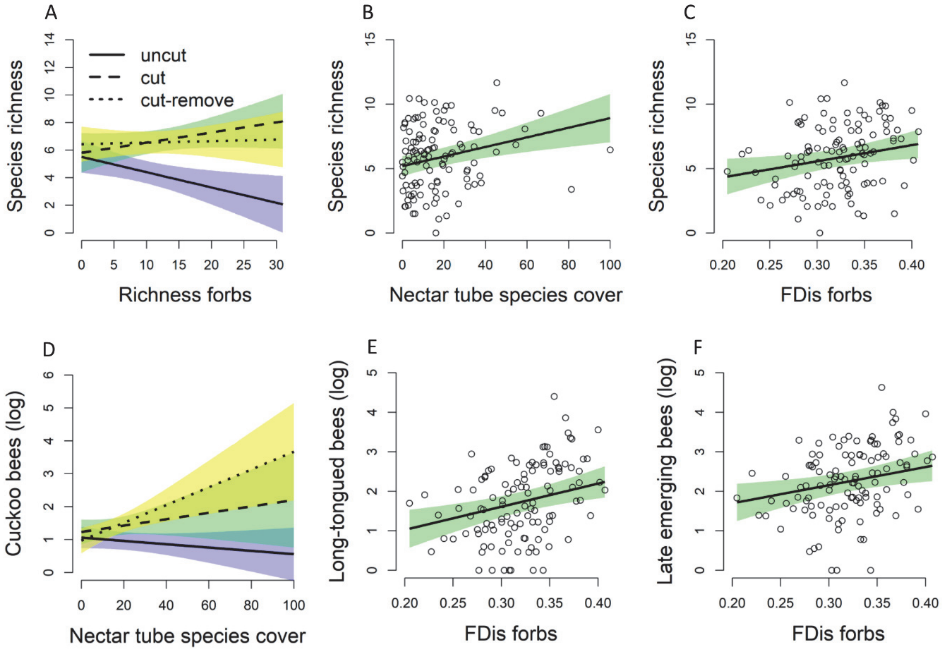

***Figure 12:** Effects of management practices on bumble bees in power-line clearings **(Paper III)**: Effects of treatments (uncut, cut, cut-remove) on (A) species richness of bumble bees in response to forb species richness. (B) Species richness of bumble bees in response to cover of forb species with nectar tube, and (C) species richness in response to functional dispersion (FDis) of forbs. (D) Effects of treatments on cuckoo bumble bees in response to cover of forb species with nectar tube. (E) Abundance of long-tongued bumble bees in response to FDis of forb species. (F) Abundance of bumble bees with late emerging queens in response to FDis of forb species. Cuckoo bees, Long-tongued bees and late emerging bees were log(y+1) transformed. The shaded areas are 95% confidence intervals (CI). (A, D) Uncut (solid lines) has blue CIs, Cut (dashed line) has green CIs and cut-remove (dotted line) has yellow CIs.*

et al. 2015). A larger variety of flower types increases bumble bee niche differentiation and reduces interspecific competition, particularly for the late-emerging species (Goulson et al. 2008). Variation in traits of both plants and bee species may be advantageous, allowing for different colonies to forage on separate parts of a rich flora (Persson et al. 2015).

Bumble bee richness and diversity increased over time (Figure 13A), suggesting that the less intensively managed habitats in power-line clearings – with early successional vegetation left undisturbed over several years – may be of great importance as alternative natural or semi-natural grassland habitats for bumble bees. In comparison, the long-tongued species were more abundant in the first year, compared to a substantial reduction three years post clearing (Figure 13B). This indicate how long-tongued species prefer shorter vegetation, which accords with typical grassland habitats where floral resources for the more specialized species can be found (Goulson et al. 2008). The lower levels of bumble bees found in the uncut treatment plots, demonstrate that the regrowth of trees reduces the habitat quality for bumble bees. Thus, our results indicate that a more frequent cutting would benefit bumble bee communities.

The contrasting response of the bumble bees (compared to solitary bees) to management practices (**Paper II**) is not surprising. Solitary bees and social bees respond differently to forest successional stages (Taki et al. 2013), and they require floral resources at different temporal and spatial scales (Murray et al. 2009). Thus, it could be that bumble bees do not respond as well to local habitat modifications, due to their potential for habitat searches at a landscape scale. Moreover, it is likely that bumble bees prefer nesting in sites with woody debris on the ground (Lanterman et al. 2019).

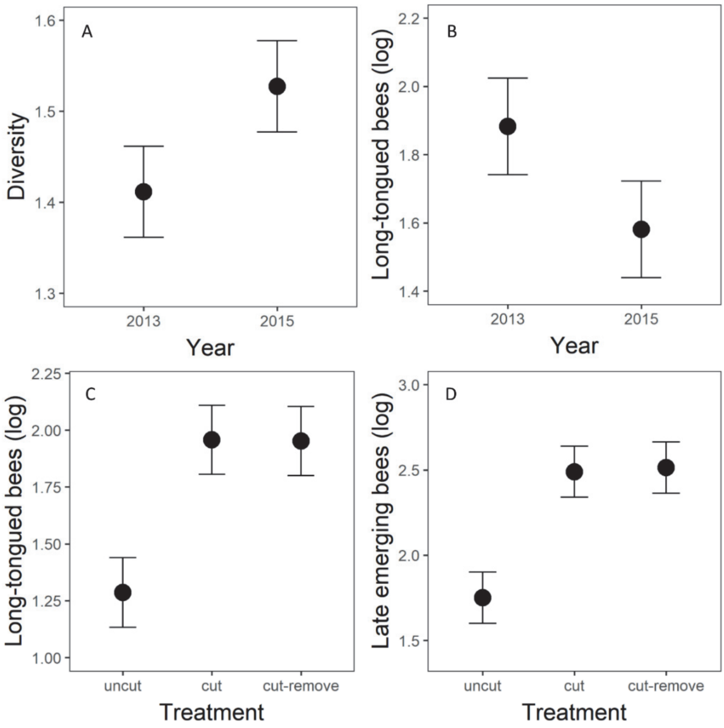

Figure 13: *Effects of management practices on bumble bees in power-line clearings over time (**Paper III**): (A) Diversity of bumble bees in the first (2013) and third (2015) year after cutting. (B) Abundance of long-tongued bumble bees over time after cutting. (C) Abundance of long-tongued bumble bees in the three treatments (uncut, cut, cut-remove). (D) Abundance of bumble bees with late emerging queens in the three treatments. Long-tongued bees and late emerging bees were log(y+1) transformed. Black dots and whiskers are predicted values and 95% CI limits.*

3.4 Paper IV

Is there a spatial and temporal variation in bumble bee communities – in power-line clearings and forest habitats – during their main foraging season?

This study showed how power-line clearings are valuable habitats for bumble bees in boreal production forests, because the clearings provide late season foraging resources. We found substantially more species and individuals in the power-line clearings, compared to the forest habitats. The spatiotemporal variation in richness and abundance of bumble bees was explained by the temporal availability of flower resources. Our results are in accordance with previous studies in forest landscapes showing that bee species are generally associated with flower resources in early successional forest openings (Carwell et al. 2004, Korpela et al. 2015, Roberts et al. 2017). In the power-line clearings we found both forest-dwelling bumble bees as well as bumble bee species associated with semi-natural grasslands. This indicates that power-line clearings may provide complementary flower resources for species foraging in the forest understory, in addition to providing a habitat for species solely dependent on semi-natural grasslands.

We found that bumble bees used power-line clearings and forest habitats to the same extent in spring and early summer, during the flower period of bilberry, but as the summer progressed the difference between the habitats increased. Towards the end of the summer bumble bee richness and abundance peaked in the power-line clearings (Figure 10), coinciding with the peak flowering period of heather (*Calluna vulgaris*). Heather is a light-tolerant species, associated with open habitats and open forest stands (Parlane et al. 2006). Our results demonstrate the importance of heather as a late season flower resource for bumble bees. The increase in richness and abundance towards the end of summer in July/August, also fits well with the anticipated increase in bumble bee population sizes, as most colonies reach maturity towards the end of summer. However, in contrast to the power-line clearings, there were no spatial or temporal pattern of bumble bees in the forest habitats, suggesting that the power-line clearings provide more attractive late season foraging resources for most of the bumble bees, also the forest-dwelling species. Wagner et al. (2019), similarly found substantial differences in wild bees between power-line clearings and adjacent closed canopy forests and concluded that many of the species found in the forest were also depended on nearby open habitats.

Boreal forest understory may provide abundant ericaceous dwarf shrub species, but in managed forests the stand-age and tree density may lead to a high variability in plant diversity, leading to spatial and temporal gaps in flower resource availability during the foraging season. This might be detrimental to bumble bee colony survival (Goulson et al. 2008). Our results indicate that the habitats in power-line clearings are even more important for provision of complementary flower resources for bumble bees in dense forests with reduced field layer vegetation. Maintaining early successional habitats in forested ecosystems may contribute to preserving mutually beneficial plant-pollinator interactions as plants in canopy gaps receive more pollinator visits than those in closed forests (Proctor et al. 2012). Thus, it is likely that an increased forest density, with the absence of forest openings, would be disadvantageous for native plant populations, their pollinators and associated ecosystem services.

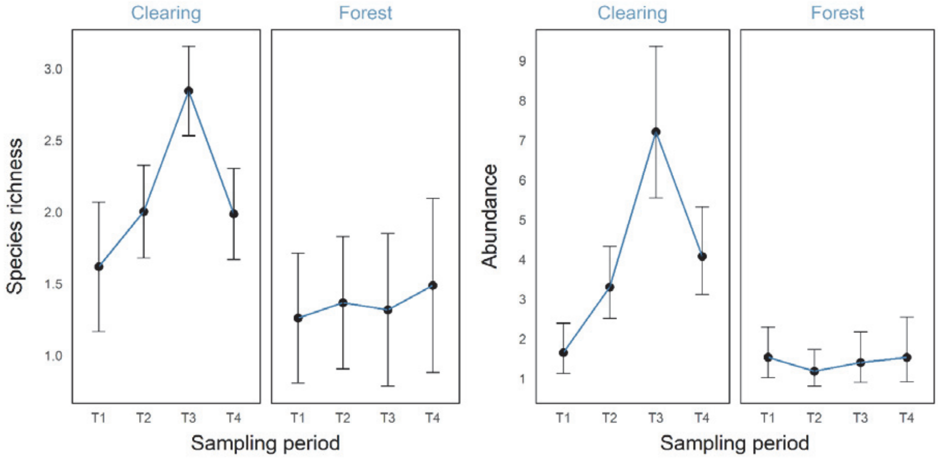

Figure 10: *Spatial and temporal variation in bumble bee communities in power-line clearings (and forest habitats during one foraging season (**Paper IV**): Mean (± 95% CI) species richness and abundance of bumble bees in power line clearings and production forest habitats in the four sampling periods during the main foraging season, where T1 is sampling period May/June, T2 is sampling period in June/July, T3 is sampling period in July/August, and T4 is sampling period in August/September.*

4 Management implications

4.1 Experimental management practices

The studies presented in this thesis demonstrate the potential value of power-line clearings for conservation of native plants and wild bees, and thus the ecosystem functions and services they provide. In forest landscapes, power-line clearings can function as alternative habitats for wild bees associated with semi-natural habitats, providing potential nesting substrates and enhanced foraging resources. Our findings show that the current practice of manual clearing of woody vegetation (i.e. cut) is beneficial for the insect-pollinated plants and the wild bees (**Paper I, II III**), when compared to the uncut treatments. But removing the woody debris after cutting (i.e. cut-remove) have the potential to promote a higher functional diversity of flower resources under certain environmental conditions (**Paper I**). A higher functional diversity of flower resources was found to sustain a higher diversity of wild bee species and functions (**Paper II, III**). Compared to the current routine practice we found that woody debris removal promoted a stronger positive increase in functional trait diversity of the solitary bee communities, which was sustained at least three years post clearing (**Paper II**). Bumble bees seemed to thrive in both cut treatments – irrespective of woody vegetation removal – and the effect of cutting was sustained over the three years, but bumble bee species of special conservation interest decreased the third year after clearing (**Paper III**). Thus, to improve habitat conditions for the solitary bees, removing the woody debris is highly recommended, whereas to improve habitat conditions for bumble bees, woody debris removal is beneficial, but not as important. Our results further indicate that solitary bees depend more strongly on management efforts at a local scale, compared to bumble bees, which appear to depend more on management efforts at a landscape scale. Recommendations for overall wild bee conservation would thus be to implement a mosaic of woody debris retention and removal in power-line clearings, to support diverse wild bee communities.

4.2 Environmental context

Our results also illustrate that the efficiency of management practices depend on the environmental context (**Paper I, II, III**). Which is supporting Scheper et al. (2013), who emphasized the importance of considering the environmental conditions prior to management scheme decisions. Given limited budgets, the implementation of the more costly treatment of woody debris removal should be allocated to carefully selected locations. For the insect-pollinated plant communities, woody debris removal should be implemented in areas of intermediate to high site productivity, with available source habitats in the surrounding landscape, and where the stem density is high. A continuation of business as usual would be beneficial for insect-pollinated plants in areas with low productivity, high stem density or high temperatures (**Paper I**). Management practices should aim at enhancing species and functional diversity of insect-pollinated plants to benefit both solitary and social bees (**Paper II, III**), and should particularly promote species with a nectar tube and late season flower resources, such as heather to benefit the bumble bees (**Paper III, IV**). Moreover, management practices should be allocated to areas according to geological conditions, as many ground-nesting bees favor nesting in sandy soils (Cane 1991). And management practices in power-line clearings would enhance their value for both plants and wild bees if there are sufficient source habitats in the surrounding landscape (**Paper I, II, III**). Elevation was also an important limiting factor in all studies (**Paper I, II, III, IV**). These environmental variables can easily be extracted from remote sensing data and may be used to predict geographical locations best suited for management implementation (Sydenham et al. 2020).

4.3 Management intensity

To promote wild bees, we suggest that more frequent cutting of the vegetation than the standard long intervals of up to 10-12 years, would be beneficial to sustain the floral vegetation in time and space for wild bees (**Paper I, II, III**). In order to preserve the functional diversity of insect-pollinated plants (**Paper I**), our results suggest that productive areas, with high stem density or high temperatures, could be cut more frequently, i.e. perhaps after 3-4 years. Wild bee communities were sustained at least three years post-clearing. The more vulnerable and extinction prone bumble bees also seemed to benefit from increasing the frequency of cutting, i.e. preventing the regrowth from outcompeting floral resources (**Paper III**).

On the other hand, we assume that less intensive management is precisely what makes the power-line clearings optimal early successional habitats for a wide range of plants and wild bees, compared to other habitats. In North America, Russel et al. (2018), also suggested that cutting the woody vegetation in combination with herbicide treatments or spot removal of invasive species, rather than mowing at shorter intervals, was found to be more beneficial for bees. Wagner et al. (2019), suggested that a five-year management cycle within power-line clearings would create large areas of suitable habitats for many wild bee species with a high trait diversity. These practices provide periods of undisturbed nesting habitat and potentially more stable provisions of floral resources, which may maintain species populations over time. Other human-modified habitats, such as road verges, field edges or meadows, are typically mowed or grazed more intensively, which may negatively affect both plants and pollinators (Hanula et al 2016, Sjödin et al. 2008). Furthermore, clear-cuts are similar to power-line clearings but may not provide as diverse and stable habitats. Over time power-line clearings may evolve into qualitatively different habitats compared to clear-cuts. The recurrent cutting of early successional vegetation in power-line clearings likely changes soil conditions for seedling establishment and thereby increase the plant diversity and the seed bank (Luken et al 1992). Clear-cuts also have much longer intervals between disturbances and replanting with tree seedlings speeds up regrowth of trees and canopy closure, which is not suitable for sustaining native plants and wild bees unless combined with other conservation efforts.

4.4 Wild bee management in forests

Wild bees in managed forests may be limited by a shortage of continuous flower resources throughout the foraging season. Our results indicate that the conservation of wild bees in forests requires an integrated strategy within forestry management related to early successional habitats in the landscape (**Paper IV**). Our findings suggest that less dense forest stands are positive for wild bees and highlight the importance of open canopy habitats. Roberts et al. (2017), suggested that the total proportion of the landscape converted into early successional habitat, rather than size of individual openings, were important for wild bee abundance and diversity. In forest management, open canopy habitats should be promoted within largely forested areas of dense stands, either by thinning (Taki et al. 2010, Romey et al. 2007), or careful rotation planning of clear-cuts. Dependent on the landscape matrix, conservation efforts in forestry should be implemented on a landscape scale, preferably near other existing early successional habitats to ensure immigration from source habitats (Ohwaki et al. 2018). However, the conservation value of open canopy habitats in power-line clearings is restricted to managed forests, which are even-aged stands that lack for example natural gap-forming dynamics. Constructing new power-line clearings through forests of high conservation value, with intact natural multi-layered forest structure, well developed field layer vegetation and 'natural' gaps, should be avoided.

4.5 Power-line clearings in the landscape

The power-line clearings constitute extensive areas of interconnected early successional habitats but may depend on other open-canopy or semi-natural habitats in the landscape to sustain diverse plant and wild bee communities. The conservation measures implemented at a local scale could contribute to increase the resource availability at a landscape scale, which is important for regional wild bee populations (Knight et al. 2005). When habitats in the power-line clearings are kept in early succession, they may generate local increases of pollinators, potentially acting as source habitats for native bee populations (Fransén et al. 2007, Russel et al. 2018). These source habitats may act as stepping stones connecting power-line clearings with other suitable pollinator habitat or cause a spillover effect through migration to adjacent fields and forests (Morandin and Kremen 2013; Roberts et al. 2017). This has the potential of redistributing pollinators in the landscape, which may lead to new stable and persistent pollinator populations (M'Gonigle et al. 2015). However, the effect of management practices may be dependent on the connectivity between power-line clearings and other suitable habitats in the landcsape (Baum et al. 2004, Lampinen et al. 2018). Connectivity is recognized as an essential factor for sustaining biodiversity in fragmented landscapes (Öckinger et al. 2012). The power-line clearings may function as dispersal corridors, independent of the surrounding landscape. But when power-line clearings are transecting managed forest landscapes, with few adjacent early successional habitats, there would be a low spatial flow of organisms to and from the habitat. Homogenous and dense forests may reduce the permeability of the landscape matrix and negatively influence the dispersal (Baum et al. 2004). Despite management efforts, the power-line clearings may remain sink patches, with species possibly disappearing in between maintenance clearings. In order to conserve native plants and wild bees species, the populations need to be maintained at a landscape level. Hence, management practices should be implemented in areas enabling connectivity and where the power-line clearings can function as source habitats in the landscape.

Power-line clearings as a dispersal corridor may also have a negative influence on native biodiversity, by facilitating the establishment and spread of invasive species (Lampinen et al. 2015). Therefore, management practices should be aware of potential invasions in the landscape, and a need for additional efforts of targeted removal of unwanted species may have to be considered.

4.6 Other taxa

The studies presented in this thesis focus on enhancing the habitat conditions for native plants and wild bee pollinators, and the management practices suggested here are not necessarily beneficial for all organisms. For example, removal of woody debris through harvesting biomass from the power-line clearings for biofuel may have a negative effect on species associated with dead wood, such as saproxylic species. Whereas leaving the woody debris collected in piles on site, as in our experiment, will create a more heterogenous environment, potentially benefitting both bees and species dependent on dead wood, thereby increasing the conservation value of the habitat interventions.

5 Future Perspectives

Future studies should aim to find the optimal timing for management practices in power-line clearings. This thesis is based on empirical data from three years post clearing; hence we do not have data to make clear recommendations regarding clearing frequency, particularly for the wild bees. We found that the power-line clearings seemed to be a vital habitat within managed forests for the wild bees, at least three years post-clearing, with a substantial increase over time (**Paper II, III**). But we do not yet know when this effect will level off or even decrease. Future studies should consider studying wild bee communities over a longer time period, alternatively monitoring wild bees in in sites of different intervals since last cutting (space-for-time substitution) (Pickett 1989).

To fully understand the conservation value of power-line clearings on wild bees, it would be interesting to know more about the actual population sizes of the wild bees, and whether the power-line clearings provide nesting habitats. Further it would be interesting to monitor the plant-pollinator interactions. This would require observations in field and closer monitoring of populations over time.

In order to truly understand how management of human modified landscapes may promote biodiversity, future studies should aim to identify effects at larger spatial scales. Considering the connectivity between several early successional habitats at a landscape scale would be informative for developing strategies to mitigate wild bee decline in habitats changed by human land use.

To improve our understanding of how human modified habitats should be included in conservation plans, several other organisms across different trophic levels should be included in future studies. Power-line clearings may be particularly valuable for a wide range of early successional species but do also have a potential for conserving saproxylic invertebrate species. Dead wood is found both in smaller and larger dimensions, both as woody debris from the maintenance clearings, and as large dead trees from e.g. wind felling along the edges of the clearings.

6 Conclusions

Our results suggest that in countries with a high proportion of boreal forest landscapes, the extensive networks of open-canopy habitats from power-line clearings can—with proper management—function as alternative habitats for native insect-pollinated plants and wild pollinators. Current management practices enhance habitat quality for early successional plants and wild bees and provide important late season foraging resources for bees associated with semi-natural grasslands but also for bees foraging in the forest understory. Removing the woody debris after cutting may promote pollination functions and services by enhancing the diversity of species and functional traits of flower resources. Woody debris removal is recommended to sustain species and functional diversity of solitary bees, whereas this is not necessary for bumble bees. However, management practices are context dependent and should take into account the local environmental conditions. The studies presented in this thesis support previous studies emphasizing the importance of early-successional human-modified habitats for conservation of native plants and wild bees (Hanula et al. 2016, Wagner et al. 2014b, 2019). And our results demonstrate that proper management of power-line clearings is a promising tool to mitigate ongoing declines in semi-natural grassland species.

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Outreach contributions

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Paper I

esa ECOSPHERE

Different cutting regimes improve species and functional diversity of insect-pollinated plants in power-line clearings

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Abstract. To mitigate biodiversity loss, it is essential to understand how areas altered by human land use can act as alternative habitats for functional groups of species, which are in decline. In forested landscapes, power-line clearings can be valuable habitats for early successional plant species, which in turn provide important food resources for pollinating insects. However, we know little about how management practices affect plant diversity, or how changes in species diversity translate into the functional diversity of floral resources. We conducted an experiment at 19 sites in power-line clearings across southeast Norway where the woody vegetation was (1) cut and left to decay, (2) cut and removed, or (3) uncut. We assessed the effects of treatments on species diversity (richness, evenness, diversity) and functional diversity (functional evenness, functional dispersion) of understory plant communities of insect-pollinated plants. We also investigated the influence of environmental conditions within the power-line clearings, the surrounding landscape, and climatic factors on species and functional diversity. We found that the cut and cut–remove treatments were effective in increasing biological diversity of insect-pollinated plants. The species and functional diversity showed contrasting responses to treatments, and the treatment effects depended on the environmental context. This shows that ecosystem functioning is not necessarily predictable from the ecological processes that drive species composition. The treatment effects on species diversity were partly explained by the stress-gradient hypothesis; species richness was higher in the cleared plots in areas of low environmental stress from precipitation and elevation. In contrast, the treatment effects on functional diversity were positively influenced by productivity, stem density, temperature, available source habitats, elevation, and canopy density. Functional diversity, based on effect traits, should be emphasized when the aim is to maintain a broad range of pollination functions and services in power-line clearings. This study shows that inclusion of power-line clearings in conservation plans can mitigate biodiversity decline in forested landscapes. We recommend the cut–remove treatment in productive areas with available source habitats and high stem density. In low productive areas, with high stem density and high temperatures, the standard cut treatment is sufficient, but a higher cutting frequency is recommended.

Key words: boreal forests; conservation; ecosystem functions; ecosystem services; effect traits; land use; management; plant communities.

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INTRODUCTION

The need for developing habitat management plans to conserve wild pollinators has recently gained increased recognition by governments and NGOs (Potts et al. 2016, Senapathi et al. 2017), with ~87.5% of flowering plants globally thought to be dependent on biotic pollination (Ollerton et al. 2011). Human disturbance, especially habitat destruction through land use changes, is considered one of the most important drivers of declines in wild pollinator populations (Goulson et al. 2008, Winfree et al. 2009, Potts et al. 2010). However, it is increasingly recognized that plant communities associated with human infrastructure, such as power-line clearings, can function as alternative habitats for pollinating insects (Wagner et al. 2014*a*, Berg et al. 2016, Hill and Bartomeus 2016, Sydenham et al. 2016, Russell et al. 2018). The woody vegetation under power lines is subject to frequent maintenance clearing, which keeps the plant communities at an early successional stage. Eldegard et al. (2015) suggested that with proper habitat management to promote conditions for wild pollinators, power-line clearings may contribute to ecosystem function and services. Yet, so far, there have been no experimental studies quantifying the effects of management practices on plant communities in power-line clearings, only observational approaches (Wagner et al. 2014*b*, Lampinen et al. 2015, Eldegard et al. 2017). Furthermore, previous studies have mainly used traditional species diversity response metrics and have not considered functional traits, which have the advantage of being linked more closely to ecosystem functions and services (Weiher 2011).

Understanding how plant communities change in response to management practices requires that we can link patterns of biodiversity to underlying ecological processes. Species may respond positively to management interventions, either directly because of improved abiotic conditions (e.g., improved light availability) or indirectly because of improved biotic conditions (e.g., reduced competition). The most commonly used species-based indices are species richness (number of species), evenness (the relative abundance), and proportional diversity index, for example, Shannon diversity (Magurran and McGill 2011). Ecological processes may alter diversity through changes in evenness without changes in species richness. Thus, we need to weigh species richness by relative abundance to get a more complete understanding of diversity (Wilsey et al. 2005). To predict ecosystem function, indices based on functional traits, rather than species identities, are increasingly being used in ecological studies (Reiss et al. 2009, Gagic et al. 2015). Functional diversity collectively refers to the richness, dissimilarity, and evenness of functional groups in an ecosystem identified by species traits and niches (Walker 1992, Naeem et al. 2012). To understand the links between species and ecosystem processes, a conceptual framework has been developed to distinguish between functional response traits and functional effect traits (Keddy 1992, Garnier et al. 2007, Suding et al. 2008, Cadotte et al. 2011). Response traits are related to the response of plant species to the environment (Pakeman 2011), whereas effect traits represent the contribution of species to ecosystem functioning (Chapin et al. 2000, Garnier et al. 2007, Suding et al. 2008). Effect traits are therefore particularly relevant for studies of ecosystem services, like pollination (Díaz et al. 2007, Violle et al. 2007, de Bello et al. 2010), but this has rarely been studied (Pakeman 2011).

In forested landscapes, maintenance clearing of the woody vegetation under power lines increases light availability and changes temperature and competition for resources (Facelli and Pickett 1991*a*). Within production forests, these open-canopy habitats are thought to benefit many native forb, dwarf shrub, and shrub species (Wagner et al. 2014*b*) and thereby provide otherwise limiting food resources for pollinators, such as local wild bee populations (Russell et al. 2005, Wagner et al. 2014*a*, Hill and Bartomeus 2016). Dwarf shrubs refer to short-growing woody plants, such as ericaceous species. Moreover, the species composition of plants in power-line clearings is likely to be influenced by the levels of landscape fragmentation (Fahrig 2003) and patches of available source habitats (Winsa et al. 2015), which influence the colonization rate of propagules. Power-line clearings may also function as dispersal corridors for plants, and previous studies have shown that the richness of native insect-pollinated plants is higher in power-line clearings than in the adjacent forest (Wagner et al. 2014*b*, Eldegard et al. 2017).

Previous studies have detected positive relationships between functional plant diversity and functionally linked pollinators (Biesmeijer et al. 2006, Winfree et al. 2011). Based on these findings, we are able to predict the ability of plant communities to sustain the diversity of pollinators by studying the functional diversity of flowering plants. An increased diversity of floral forms (effect traits) represents an increased variety of niches for pollinators to occupy. Effect traits that may attract different pollinators are, for example, flower shapes and flowers with variable pollen and nectar content (Lázaro et al. 2008). Species and trait diversity indices may show contrasting patterns to environmental conditions across space, and the biological diversity of pollinator-friendly plants will vary along environmental gradients (McGill et al. 2006, Hoiss et al. 2012). For instance, Hoiss et al. (2013) showed how the altered composition of plant species along elevation gradients also led to a shift in the proportion of pollinator-visited plants vs. graminoids. Therefore, understanding where and how to promote foraging resources is essential to conserve pollinators and the ecosystem services they provide.

The main aim of this study was to quantify the effect of different management practices (i.e., uncut, cut, and cut–remove of woody vegetation) on insect-pollinated plants (i.e., forbs, dwarf shrubs, and shrubs) in power-line clearings, using several measures of biological diversity (i.e., species richness, evenness, diversity, functional evenness, and functional dispersion). We hypothesized that:

1. The cleared plots (i.e., cut and cut–remove treatments) would have higher species-based and functional diversities of insect-pollinated plants than uncleared plots (i.e., uncut) because of altered space and resource availability (Pickett and White 1985, Muscolo et al. 2014);
2. The cut–remove treatment would show the highest increase in species-based and functional diversities, because removing woody debris may facilitate germination from the existing seed bank, increase colonization from surrounding areas, increase seedling survival, and increase evenness through a reduced competition for light and space (Pickett and White 1985, Facelli and Pickett 1991*a*);
3. The effects of management practices (experimental treatments) would depend on the environmental context, and species-based and functional diversities within the three treatments would respond differently to environmental factors, such as attributes of the power-line clearing, attributes of the surrounding landscape, and climatic factors.

METHODS

Study design and data collection

The large-scale field experiment was conducted within the main power-line grid in southeast Norway (Fig. 1). Sites were located between latitudes 59.33°–61.12° N and longitudes 08.95°–11.36° E at 45–535 masl. We identified 19 sites where there was a stretch of at least 200 m with substantial regrowth of trees underneath the power lines. Each site had been subjected to the same management regime with manual cutting (no use of chemicals) of all woody vegetation every 5–10 yr, dependent on the local productivity, with biomass left to decay on the ground. All sites were located below power lines in boreal forest systems consisting of varying proportions of the Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and birch (*Betula* spp.). At each site, we established three plots of ~30 × 60 m (corridor width), at least 20 m apart. At each study site (established autumn 2012 [$n = 16$] or spring 2013 [$n = 3$]), we deployed three plots and randomly assigned one of the three treatments to each plot: (1) uncut; (2) cut, all trees cut and left to decay in the clearing; and (3) cut–remove, all trees cut and removed from the plot (Fig. 1). Plant surveys were carried out at each site in late June/early July in 2013, 2014, and 2015. Within each treatment plot, we placed nine quadratic subplots of 1 m^2. The 1-m^2 subplots were regularly spaced within a 10 × 10 m quadrat located in the center of each treatment plot (Appendix S1: Fig. S1). Abundance of all vascular plants was visually quantified to the nearest 1% from the nine subplots during each sampling visit. If a species was present in a subplot, but had <1% cover, it was recorded as 0.001%. As some species of particular taxa are difficult to distinguish (e.g., *Taraxacum* sp., *Hieracium* sp., *Epilobium* sp., see species list, Appendix S1: Table S2), these observations were identified to genus and treated as morphospecies in the calculations and statistical analysis.

In each experimental treatment, we also measured environmental conditions and habitat characteristics (Table 1). At the start of the project, we scored site-specific potential productivity (hereafter, productivity) from the vegetation type of the adjacent forest and their associated site index classes (H_{40} index) in the Norwegian national

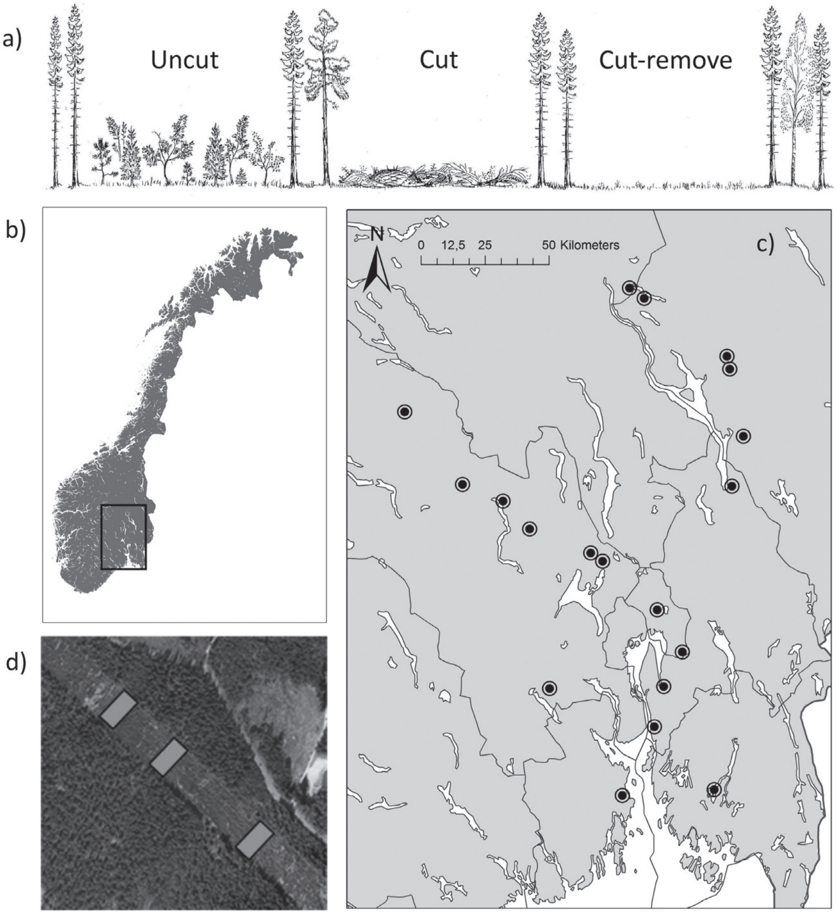

Fig. 1. (a) Schematic illustration of the experiment and (b, c) geographic distribution of the 19 study sites. There were three treatments at each site, where the woody vegetation was uncut: uncleared control; cut: all trees cut and left to decay in the clearing; and cut–remove: all trees cut and removed from the plot, exposing the ground. The distance between treatment plots was minimum 20 m. (d) Aerial photograph of one site with the three treatment plots. Plant data were collected in nine 1-m^2 subplots within each treatment plot.

forest inventory (Larsson and Søgnen 2003). We also calculated site-specific stem density (hereafter, stems/m^2), the number of trees/m^2, based on a count of stems in a radius of 4 m from the center of each uncut treatment plot in 2013. The Norwegian Meteorological Institute provided site-level data on temperatures and precipitation (Table 1). As a measure of light availability in each treatment plot, we recorded direction, slope, and latitude, which we used to calculate the solar radiation index (Oke 1987). In addition, to assess a more accurate amount of available sunlight, we calculated the global light index (GLI) in the growing season (May–September), from photographs taken

Table 1. The explanatory variables included in the analysis.

Variables in analysis	Variables included in PCA	Correlation (r) with PCA axis 1	Spatial scale	Categories	Measured values (min-max)	Measured values (mean)
Year				2013–2014–2015		
Treatment				Uncut, cut, and cut–remove		
Power-line clearing attributes						
Elevation (masl)			Site		45–535	260.3
Productivity			Site		8.4–13.7	11.7
Radiation index			Plot		−0.32 to 0.87	0.4
Canopy density			Plot		0.24–95.18	62.9
Initial canopy density			Site		4.73–76.73	29.5
Stems/m^2			Site		0–44	13.5
Landscape attributes						
Area (m^2) of polygons of potential source habitats (source habitat area)	Within 150 m radius	0.7	Site		0–114,20	
	Within 300 m radius	0.8	Site		0–104,933	
	Within 500 m radius	0.9	Site		0–326,588	
	Within 1000 m radius	0.9	Site		9123–1,717,195	
	Within 2000 m radius	0.7	Site		55672–7,169,672	
Number of polygons of area types (landscape fragmentation)	Within 150 m radius	0.4	Site		2–17	
	Within 300 m radius	0.9	Site		4–41	
	Within 500 m radius	0.9	Site		12–90	
	Within 1000 m radius	0.9	Site		45–341	
	Within 2000 m radius	0.7	Site		233–1280	
Climate attributes						
Average monthly temp. (°C) in January			Site		−9.7 to −2.9	−7.2
Average monthly temp. (°C) in growing season (June–August)			Site		10.8–15.5	13.5
Average monthly precipitation (mm)			Site		45–86	62.9

Notes: The spatial scale and measured values (range and mean) of power-line clearings, landscapes, and climate attributes. For description of the power-line clearing attributes, see *Methods*: *Study design and data collection*. The measured landscape attributes, (1) source habitat area and (2) landscape fragmentation, were combined in separate principal component analyses (PCA).

with a fisheye lens (hereafter, canopy density). The global light index is the weighted average of diffuse and direct radiation through the canopy (Schleppi 2017). The photographs were taken in the approximate center of each treatment plot at each site, in July 2013 and in mid-to-late June 2014 and 2015. We used the software Hemisfer (Schleppi et al. 2007, Thimonier et al. 2010) to analyze the photographs. The software distinguishes between pixels of sky and canopy and uses this together with coordinates, slope gradients, and slope directions to calculate available sunlight (Hemisfer 2014). We also calculated the global light index in all uncut treatment plots in 2013 as a measure of initial regrowth (hereafter, initial canopy density) based on light availability within the site (Table 1). To assess the landscape fragmentation and source habitat areas surrounding each site, we used ArcGIS (ESRI 2011) and Ar5 digital maps (Ahlstrøm et al. 2014). We used the total number of polygons of all different land use types as a measure of landscape fragmentation. As a measure of available source habitat area, we used the total (sum) area of selected land use types (i.e., arable land, non-tilled arable land, semi-natural areas, pastures, rocky surfaces, and roads) that can function as potential source patches or refuges for plants in the power-line clearings. Landscape fragmentation and source habitat area were measured at increasing radii around each site (Table 1). To account for collinearity between the radii around each site, the different scales were combined into one variable using a separate principal component analysis (PCA) for landscape fragmentation and source habitat area. For both variables, we used the first PCA axes, transformed on a scale of 0–1 (Dormann et al. 2013). Calculations were computed in R (R Development Core Team 2017) with the vegan package (Oksanen et al. 2013).

Data preparation

We selected flowering forb, dwarf shrub, and shrub species based on two criteria: plants known to be of importance to pollinators (Willmer 2011) and plants with an average height of no more than 1.5 m. Within each treatment plot, the observed plants in the nine 1-m^2 subplots were treated as one plant community; that is, we used treatment plot as sampling unit in the statistical analyses. We calculated species richness, diversity, and evenness, using the vegan package in R (Oksanen et al. 2013). Richness was calculated by summing the number of species in the nine subplots in each treatment plot. If a species or a morphospecies was present more than once in one of the nine subplots, they were counted as one. A diversity index (Shannon diversity, H') was calculated for each treatment plot (Heip et al. 1998), based on the summarized abundance per species in the nine subplots. Evenness was calculated following Pielou (1966), using $J = H'/\log(s)$, where H' is the Shannon diversity, and s is the number of species.

To quantify the floral resource diversity within the plant communities, we assigned nine functional effect traits to each plant species. The traits (extracted from Lid and Lid 2005) were based on morphological characteristics of flowers of known importance for pollinators (Appendix S1: Table S1, Table S2). We calculated two functional diversity indices by quantifying the distribution of functional traits in multidimensional trait space (Laliberté and Legendre 2010). We used functional dispersion, which, as the weighted mean distance of individual species to the centroid of all species in functional space, is a measure of the variation in trait values within a community (Laliberté and Legendre 2010). In addition, we used functional evenness, which is a measure of the regularity of the distribution of abundance in functional trait space (Villéger et al. 2008, Laliberté and Legendre 2010, Mouchet et al. 2010, Mouillot et al. 2013). We used the number of subplots in which a species occurred as a measure of abundance. When calculating the indices, we used weighted abundances and the Cailliez correction for non-Euclidian distances because of the inclusion of categorical traits (Laliberté et al. 2014, Forrest et al. 2015). The two functional diversity indices were selected because they are independent of species richness and can accept any number or type of traits (Mouchet et al. 2010, Laliberté et al. 2014). Both indices were calculated using the dbFD function of the FD package in R (Laliberté et al. 2014).

Statistical analyses

The response variables were species richness (mean = 14.2, min = 4.0, max = 37.0), evenness (mean = 0.6, min = 0.13, max = 0.9), diversity (mean = 1.53, min = 0.26, max = 2.64), functional evenness (mean = 0.76, min = 0.55, max = 1), and functional dispersion (mean = 0.32, min = 0.2, max = 0.41). For each response variable, we carried out a preselection of candidate variables (P-values ≤ 0.10) and tested each explanatory variable separately and in interaction with the three-level categorical variable treatment. Site identity was used as a random effect to account for the among-site variation and repeated sampling (i.e., once per year). Year and landscape fragmentation did not significantly influence any of the responses ($P \geq 0.1$). To deal with collinearity (Appendix S1: Table S3), we calculated the generalized variance inflation factor (GVIF) values for all variables in each candidate model (Fox and Monette 1992, Zuur et al. 2010) using the car package in R (R Development Core Team 2017). Only variables with a GVIF value of <3 were retained in the full model (Fox and Monette 1992, Zuur et al. 2010). Final models were selected by conducting stepwise backward elimination based on likelihood ratio tests (LRTs), until only significant variables remained ($P \leq 0.05$; Appendix S1: Table S4). The effects of the treatments on species richness were analyzed by fitting a generalized linear mixed-effect model (GLMM), with Poisson-distributed errors and a log-link function, using the function glmer of package lme4 (Bates et al. 2014). We tested the effect of treatments on diversity, evenness, functional evenness, and functional dispersion, by fitting a linear mixed-effect model (LMM), with Gaussian-distributed errors and identity link, using the function lmer of package lme4 (Bates et al. 2014). To validate the model fit, we visually assessed the plotted residuals against the fitted values for all explanatory variables and assessed the distribution of residuals using Q-Q plots. For the GLMM on species richness, we also checked for over-dispersion of the residuals (ϕ = 0.75; Zuur et al. 2013). All analyses were carried out in R version 3.2.5 (R Development Core Team 2017).

RESULTS

We recorded a total of 269 vascular plant species (of which 19 were morphospecies). Of these, forbs accounted for the highest number of species (52%), followed by graminoids (23.6%), deciduous trees (8.9%), ferns (7.7%), shrubs (4%), dwarf shrubs (2.6%), and coniferous trees (1.1%; Table 2). The mean (± standard deviation [SD]) species richness in treatment plots was 26.9 (± 12.5) for all vascular plants and 14.2 (± 7.4) for the selected group of insect-pollinated plants (forbs, dwarf shrubs, and shrubs). We found a large among-site variation in effects of the three experimental treatments on all the five biological diversity metrics. The variation was partly explained by differences in the environmental conditions, but the five response metrics were generally not influenced by the same set of environmental variables (Tables 3 and 4). Nevertheless, there were similar responses to environmental factors between species evenness and functional evenness, and between species diversity and functional dispersion.

Effects of treatments: species richness, diversity, and evenness

Overall, there was a higher species richness of insect-pollinated plants in the cut and cut–remove treatments than in the uncut treatments, but the effect size depended on the environmental context. The estimated species richness decreased by 58% and 60% from relatively dry (45 mm) to wet (86 mm) areas in cut and cut–remove, respectively, compared to an increase of 83% in uncut (Table 3, Fig. 2; treatment × precipitation: LRT = 33.24, df = 2, $P = 0.005$). Within the elevation range (45–535 m), species richness decreased by 71% in cut treatment and 53% in cut–remove treatment, compared to almost no effect (3% increase) in uncut (Table 3, Fig. 2; treatment × elevation: LRT = 10.77, df = 2, $P = 0.005$). Species richness also increased by 65% with site-specific productivity (range: 8.4–13.7), but this was unrelated to treatment (Fig. 3; LRT = 10.37, df = 1, $P = 0.001$). Evenness increased with elevation (from 45 to 535 m) in cut–remove (18%) and cut (20%), but decreased in uncut (19%) (Table 3, Fig. 2; treatment × elevation: LRT = 9.041, df × 2, $P = 0.01$). Overall evenness increased by 17% with productivity (range: 8.4–13.7), irrespective of treatment (Fig. 3; LRT = 2.86, df = 1, $P = 0.09$).

Species diversity increased 62% with stems/m^2 (range: 0–44) in the cut treatment, compared to a 6% increase in cut–remove and a decrease of 5% in the uncut treatment (Table 3, Fig. 3; treatment × stems/m^2: LRT = 23.13, df = 2, $P = <0.001$). An increase in site-specific productivity (8.4–13.7) increased diversity by 49% (Fig. 3; LRT = 10.33, df = 1, $P = 0.001$), but productivity did not interact with treatment. With an increase in precipitation (45–86 mm), diversity decreased by 58% in the cut treatment, whereas there was only a slight decrease (5%) in the cut–remove and a 40% increase in the uncut treatment (Table 3, Fig. 2; treatment × precipitation: LRT = 22.04, df = 2, $P = <0.001$). In addition, diversity

Table 2. The total and mean number of vascular plant species found in the treatment plots.

Vascular plant groups	Total No.	Mean no. ± standard deviation (SD) Uncut	Cut	Cut–remove
Forbs	141	12.6 ± 7.8	12.6 ± 7.3	11.4 ± 8.0
Dwarf shrubs	7	3.2 ± 1.5	2.4 ± 1.2	3.1 ± 1.9
Shrubs	11	1.0 ± 0.9	1.1 ± 0.6	0.9 ± 0.7
Ferns	21	2.0 ± 1.9	2.2 ± 1.5	2.1 ± 1.7
Graminoids	64	5 ± 2.7	6.4 ± 4.0	6.9 ± 4.4
Coniferous trees	3	0.5 ± 0.7	0.3 ± 0.6	0.4 ± 0.7
Deciduous trees	24	3.2 ± 2.0	3.3 ± 2.0	3.6 ± 1.9

Notes: The total number of species in each vascular plant groups across all sites ($n = 19$). Mean (±SD) number of plant species recorded in treatment plots: uncut, cut, and cut–remove ($n = 19$), in 2013, 2014, and 2015.

Table 3. The treatment effects and environmental context on species richness, diversity, and evenness of insect-pollinated plants in power-line clearings.

Response	β	σ	SE	SD	Obs	*z*	*t*	*P*	Sites
Species richness (GLMM)									
Intercept (uncut)	2.452		0.084			29.31		***	
Treatment cut	0.198		0.051			3.87		***	
Treatment cut–remove	0.112		0.053			2.09		*	
Precipitation	0.155		0.087			1.78		0.08	
Elevation	0.009		0.085			0.11		0.92	
Productivity	0.133		0.041			3.27		***	
Precipitation × treatment cut	−0.273		0.054			−5.09		***	
Precipitation × treatment cut–remove	−0.277		0.055			−5.02		***	
Elevation × treatment cut	−0.168		0.054			−3.12		**	
Elevation × treatment cut–remove	−0.136		0.055			−2.47		**	
Random effects									
Site identity		0.103		0.321	168				19
Evenness (LMM)									
Intercept (uncut)	0.568		0.027				21.416	***	
Treatment cut	0.025		0.024				1.053	0.29	
Treatment cut–remove	0.070		0.024				2.931	**	
Productivity	0.025		0.015				1.640	0.10	
Elevation	−0.029		0.026				−1.104	0.29	
Elevation × treatment cut	−0.002		0.024				−0.099	0.92	
Elevation × treatment cut–remove	0.061		0.024				2.565	**	
Random effects									
Site identity		0.008		0.089	168				19
Shannon diversity (LMM)									
Intercept (uncut)	1.391		0.077				18.177	***	
Treatment cut	0.185		0.058				3.191	**	
Treatment cut–remove	0.212		0.059				3.620	***	
Productivity	0.159		0.047				3.370	***	
Precipitation	0.116		0.079				1.460	0.16	
Radiation index	0.130		0.051				2.574	**	
Source habitat area	0.093		0.080				1.156	0.27	
Stems/m^2	−0.022		0.078				−0.275	0.79	
Precipitation × treatment cut	−0.277		0.061				−4.578	***	
Precipitation × treatment cut–remove	−0.131		0.059				−2.224	*	
Radiation index × treatment cut	−0.119		0.059				−2.032	*	
Radiation index × treatment cut–remove	0.030		0.064				0.456	0.65	
Source habitat area × treatment cut	0.041		0.060				0.682	0.50	
Source habitat area × treatment cut–remove	−0.124		0.058				−2.138	*	
Stems/m^2 × treatment cut	0.266		0.059				4.528	***	
Stems/m^2 × treatment cut–remove	0.047		0.059				0.807	0.42	
Random effects									
Site identity		0.079		0.281	168				19

Notes: Final model summary outputs from GLMMs, generalized linear mixed-effect models, and LMMs, linear mixed-effect models. Variables: treatment (uncut = reference level, cut, and cut–remove), productivity, elevation, average monthly precipitation, source habitat area, solar radiation index, stems/m^2. SD, standard deviation; SE, standard error.

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

increased twofold along the radiation index gradient (from −0.32 to 0.87) in the cut–remove treatment, compared to a 50% increase in the uncut and a 9% increase in the cut treatments (Table 3, Fig. 2; treatment × radiation index: LRT = 22.04, df = 2, P = <0.001). Moreover, diversity decreased by an average of 22% in the cut–remove treatment as source habitat area increased (from 0 to 1), whereas there was a 14% increase in the cut and a 17% increase in the uncut (Table 3, Fig. 2; treatment × source habitat area: LRT = 8.15, df = 2, P = 0.02).

Table 4. The treatment effects and environmental context on functional evenness and functional dispersion of insect-pollinated plants in power-line clearings.

Response	β	σ	SE	SD	Obs	*t*	*P*	Sites
Functional evenness (LMM)								
Intercept (uncut)	0.779		0.015			51.893	***	
Treatment cut	−0.005		0.018			−0.257	0.80	
Treatment cut–remove	−0.022		0.018			−1.227	0.22	
Canopy density	0.010		0.011			0.885	0.38	
Elevation	−0.021		0.011			−1.995	0.06	
Canopy density × treatment cut	−0.061		0.021			−2.944	**	
Canopy density × treatment cut–remove	−0.011		0.017			−0.658	0.51	
Elevation × treatment cut	0.021		0.013			1.640	0.10	
Elevation × treatment cut–remove	0.033		0.013			2.579	**	
Random effects								
Site identity		0.0005		0.022	168			19
Functional dispersion (LMM)								
Intercept (uncut)	0.310		0.006			48.346	***	
Treatment cut	0.022		0.005			4.311	***	
Treatment cut–remove	0.016		0.005			3.095	**	
Productivity	0.012		0.005			2.516	**	
Temperature	−0.021		0.007			−2.785	**	
Source habitat area	0.012		0.008			1.565	0.14	
Stems/m^2	−0.018		0.007			−2.736	*	
Productivity × treatment cut	−0.019		0.006			−3.337	***	
Productivity × treatment cut–remove	0.001		0.006			0.130	0.90	
Source habitat area × treatment cut	−0.014		0.006			−2.328	*	
Source habitat area × treatment cut–remove	−0.001		0.006			−0.139	0.89	
Stems/m^2 × treatment cut	0.031		0.005			5.977	***	
Stems/m^2 × treatment cut–remove	0.023		0.005			4.453	***	
Temperature × treatment cut	0.027		0.006			4.648	***	
Temperature × treatment cut–remove	0.018		0.006			3.159	**	
Random effects								
Site identity		0.0005		0.023	168			19

Notes: Final model summary outputs from LMMs, linear mixed-effect models. Variables: treatment (uncut = reference level, cut, and cut–remove), productivity, elevation, average monthly temperature in growth season, source habitat area, canopy density, and stems/m^2. SD, standard deviation; SE, standard error.

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Effects of treatments: functional evenness and functional dispersion

As for the species-based diversity indices, there was also an overall positive effect of the cut and cut–remove treatments on the functional diversity of flowers, and treatment-induced changes in the functional diversity also depended on the environmental context. The cut treatment decreased the estimated functional evenness by 23% when the canopy density increased from 0.24 to 95.18, whereas the cut–remove treatment showed a weak negative effect and the uncut treatment showed a week positive effect (Table 4, Fig. 4; treatment × canopy density: LRT = 8.67, df = 2, $P = 0.01$). There was a 5% increase in functional evenness over the elevation range (45–535 masl) in the cut–remove treatments, compared to a 9% decrease in the uncut treatments, and a week negative effect in the cut treatments (Table 4, Fig. 4; treatment × elevation: LRT = 6.96, df = 2, $P = 0.03$).

In both the cut–remove and the uncut treatments, the estimated functional dispersion increased with productivity (range: 8.7–13.7) by 16% and decreased by 9% in the cut treatments (Table 4, Fig. 4; treatment × productivity: LRT = 13.52, df = 2, $P = 0.001$). Functional dispersion also increased with source habitat area (range: 0–1) in the cut–remove treatments (12%) and in the uncut treatments (14%), compared to a 2%

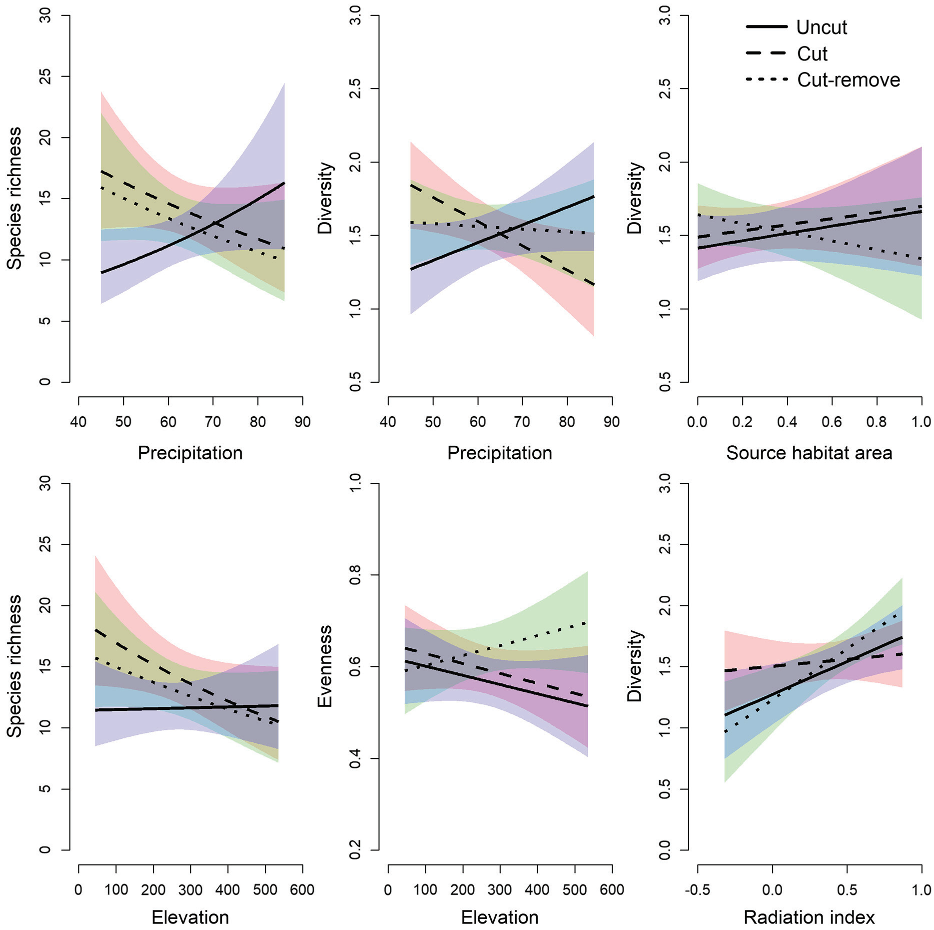

Fig. 2. The treatment effects in interaction with environmental variables on the species-based diversities, species richness × precipitation, diversity × precipitation, diversity × source habitat area, species richness × elevation, evenness × elevation, and diversity × radiation index. The shaded areas are 95% confidence intervals (CI). Uncut (solid line) has blue CIs, cut (dashed line) has pink CIs, and cut–remove (dotted line) has green CIs.

decrease in the cut treatments (Table 4, Fig 4; treatment × source habitat area: LRT = 7.56, df = 2, $P = 0.02$). In addition, in the cut and cut–remove treatments, functional dispersion increased by 14% and 5%, respectively, with number of stems/m^2 (range: 0–44), compared to a 22% decrease in the uncut treatments (Table 4, Fig. 4; treatment × stems/m^2: LRT = 36.76, df = 2, $P = <0.001$). The functional dispersion increased by 6% in the cut treatment with average temperature in growth season (10.8–15.5°C), compared to practically no difference (2% decrease) in the cut–remove treatment and a substantial decrease (24%) in the uncut treatment (Table 4, Fig. 4; treatment × temperature: LRT = 22.57, df = 2, $P = <0.001$).

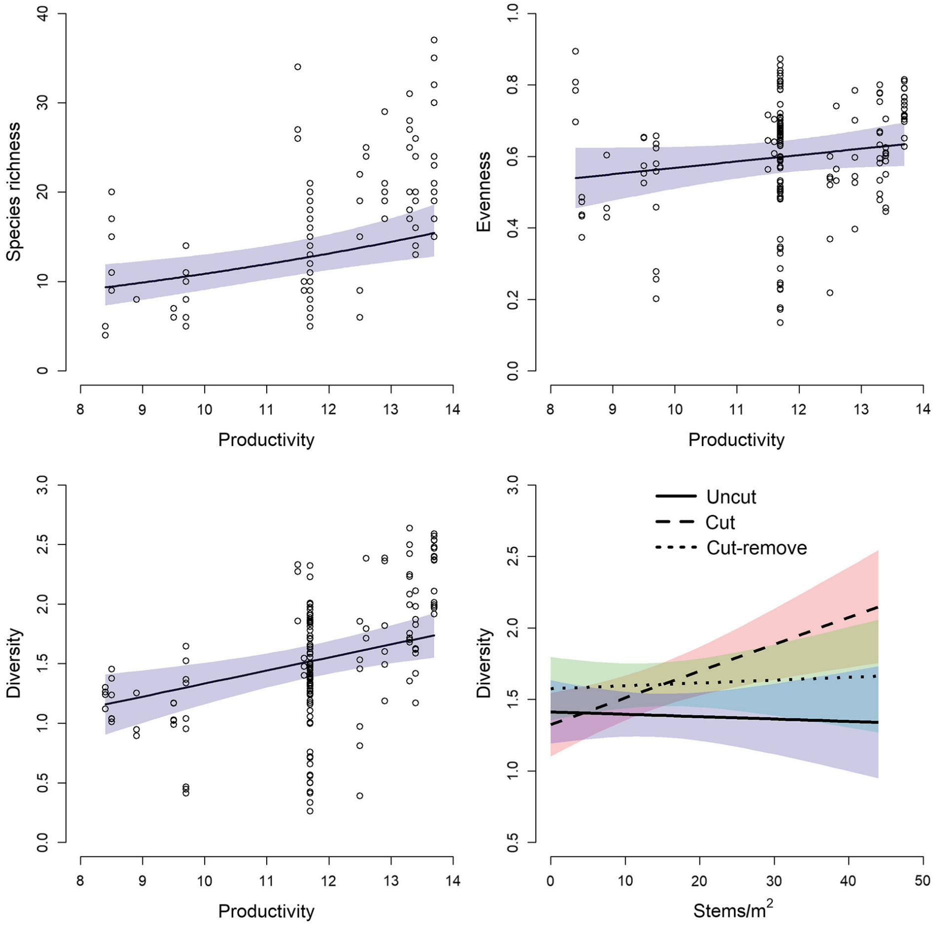

Fig. 3. The influence of productivity on the species-based diversities, species richness, evenness, and plant diversity, and the influence of stems/m^2 on plant diversity. The shaded areas are 95% confidence intervals (CIs). Uncut (solid line) has blue CIs, cut (dashed line) has pink CIs, and cut–remove (dotted line) has green CIs.

DISCUSSION

The management clearing practices cut and cut–remove were both effective in increasing the species and functional diversity of insect-pollinated plants. However, the effect sizes depended on environmental context. The cut–remove treatment clearly did not show a higher increase in species and functional diversity of insect-pollinated plants compared to the cut treatment, except under specific environmental conditions. The species and functional diversity metrics generally responded differently to the environmental context and showed contrasting treatment effects. These findings suggest that the ecological processes that shape the floral resources that pollinators depend on may be partly independent of the processes that

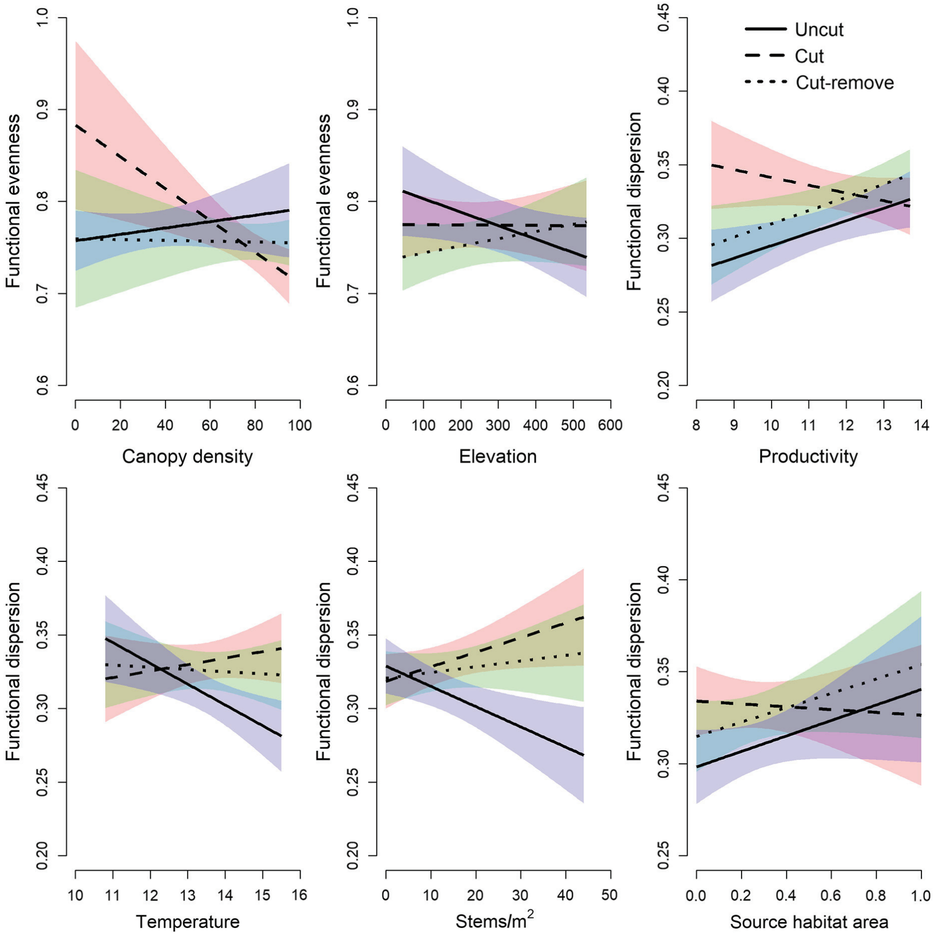

Fig. 4. The treatment effects in interaction with environmental variables on the floral resource diversities, functional evenness × canopy density, functional evenness × elevation, functional dispersion × productivity, functional dispersion × average temperature in growth season (June–August), functional dispersion × stems/m^2, and functional dispersion × source habitat area. The shaded areas are 95% confidence intervals (CIs). Uncut (solid lines) has blue CIs, cut (dashed line) has pink CIs, and cut–remove (dotted line) has green CIs.

determine the species-based diversity within plant communities.

Species-based responses to habitat management

Early successional forest can be valuable habitats for many species (King and Schlossberg 2014). Hence, we anticipated that plot clearance (i.e., treatments cut and cut–remove) would lead to an increase in the species-based indices, when compared to uncleared plots (i.e., uncut). We also expected a greater effect in the cut–remove treatment, because biomass removal is thought to be beneficial for forbs and semi-natural grassland species (Hansson and Fogelfors 2000). In contrast to our expectations, there were no significant effects of the treatments alone on species richness, evenness, or diversity, due to the context dependency of treatment effects. Our findings suggest that the abiotic and biotic factors within power-line clearings determine how the plant community—which is determined by environmental drivers and biotic interactions (HilleRisLambers et al. 2012)—will respond to habitat management practices.

According to the stress-gradient hypothesis, plant interactions shift from facilitative to competitive as environmental stress decreases (Callaway 2007). In light of this theory, we would expect clearing of the woody vegetation to have a larger effect on the plant communities in less stressful environments, where competition is thought to be high (Callaway et al. 2002). Indeed, we found that species richness and plant diversity were higher in the cleared plots in areas of low environmental stress (i.e., low elevation and relatively low precipitation; Fig. 2). These findings are in accordance with other studies, in which higher elevation posed a strong environmental filter (Stevens 1992) and high precipitation was a strong abiotic stressor due to soil erosion (Nearing et al. 2005) or late snowmelt (Wipf et al. 2009). The observed decline in richness with elevation was expected due to co-occurring environmental factors (e.g., productivity, temperature) increasing the harsh conditions (Hoiss et al. 2012). As hypothesized, evenness responded positively to the treatment cut–remove. The observed increase in evenness with elevation in cut–remove, compared to a decrease in the other two treatments (Fig. 2), suggests that in a stressful environment, cutting and removal of biomass leads to a more even distribution of species.

As expected, the species diversity was particularly high in the cut–remove treatment at a high radiation index (Fig. 2). This is also in accordance with the stress-gradient hypothesis (Callaway 2007), because it can be assumed that high solar radiation increases the interspecific facilitation within the plant community (Callaway et al. 2002, Maestre et al. 2009). Species diversity increased with stem density (stems/m^2) in the cut and cut–remove treatments, compared to a decreasing effect in the uncut treatment (Fig. 3). This was expected, since sites with a high stem density would benefit more from clearing (Rajaniemi 2003). The modifying effects of source habitat area on the treatment effects were statistically significant, but the effect sizes were generally weak and thus of minor practical importance (Fig. 2). Nevertheless, this may show that the surrounding source habitats are less important for colonizing plant species in the power-line clearings. Power-line clearings are old constructions and may function as dispersal corridors, independent of the surrounding landscape. The management history, that is, the age of the corridor, can potentially be a more important determinant of the species composition within the clearings (Bramble and Byrnes 1983, Eldegard et al. 2015, Lampinen et al. 2015). Species richness, evenness, and diversity increased with productivity across all treatments (Fig. 3). This is in accord with the prediction that diversity should be highest at intermediate productivity (Rajaniemi 2003), because all our sites were located in areas with low to intermediate productivity.

Functional diversity responses to habitat management

The treatment effects on floral resource diversity (i.e., functional diversity) indices depended to a large extent on other environmental conditions than the species-based indices (Tables 3–4, Figs. 2–4). The influence of environmental factors on functional dispersion was similar to the influence on species diversity but differed from species richness and evenness. Functional evenness and evenness had similar results. However, the five responses showed contrasting treatment effects. These findings suggest that the ecosystem functioning of communities (mediated through the diversity of functional effect traits) is not necessarily predictable from the ecological processes behind community assembly (i.e., species-based diversity) and provide empirical support for the theory of how functional trait indices should complement species-based diversities in community studies (Mouchet et al. 2010). According to Cadotte et al. (2011), the relationship between species richness and functional diversity is "complex and context dependent" and alterations in functional diversity, affecting ecosystem function, may occur without much change in species richness. Previous studies have argued that foraging traits are a better predictor of pollination functions than species richness (Hoehn et al.

2008, Albrecht et al. 2012, Gagic et al. 2015). Thus, we suggest that emphasis should be placed on floral resource diversity if the aim is to enhance the habitat quality of power-line clearings for pollinating species.

The treatment effects on the functional diversity were influenced by productivity, stems/m^2, temperature, source habitat areas, elevation, and canopy density (Table 4, Fig. 4). In contrast to the species-based indices, which increased in all treatments with increasing productivity, the treatment effects on functional dispersion depended on productivity (Fig. 4). We expected the removal of biomass (i.e., cut–remove) to be essential for increasing functional diversity, because high productivity potentially generates a larger amount of accumulated litter, which may function as a barrier for seedling and sprout emergence or the spread of seeds (Facelli and Pickett 1991*b*). According to Korpela et al. (2015), the cover of forbs increased as a response to logging but was negatively related to the amount of logging residue. Our results showed that unproductive sites could generate a high diversity of floral resources when cut, whereas productive sites could generate a high diversity of floral resources when cut with woody debris removed. Similar to the species diversity, we found that the cut and cut–remove treatments both increased the functional dispersion in sites with higher number of stems/m^2. This is in accordance with Åström et al. (2005), where the richness of forbs increased after clearcutting, irrespective of residue removal. Yet, the cut treatment showed an even higher increase in both diversity and functional dispersion in sites with a high stem density, suggesting that the debris from a high number of stems is not necessarily inhibiting regeneration of insect-pollinated plants. If the aim is to increase the functional diversity within a plant community, our results suggest that clearing the vegetation and removing the biomass is effective in dense and productive areas, whereas clearing without biomass removal is effective in low productive sites and where there is a high stem density.

The effects of the treatments on functional dispersion depended on average temperature in the growth season (June–August), but temperature was not a strong environmental driver on the functional dispersion in the cut or cut–remove treatments. In contrast, the uncut treatment had a negative impact on the functional dispersion with increased temperature, highlighting the importance of more frequent cutting in areas with high temperatures to minimize competition from dominant species (Rajaniemi 2003). Functional dispersion increased with source habitat area in the cut–remove treatment. Thus, when implementing the cut–remove management strategy, adequate available source habitat areas in proximity of the power-line clearing are important to promote a high floral resource diversity. Functional evenness was weakly affected by the cut and cut–remove treatments along the elevation gradient, compared to strong effects on species richness and evenness with elevation. However, there was a positive effect on the functional evenness of the plant communities in the cut treatment at low canopy density, revealing that woody debris in less dense habitats may lead to a more even distribution of functional traits in a community.

Multifunctional land use—power lines as alternative habitat for wild pollinators

National pollinator conservation strategies recently have been developed in a number of countries (Senapathi et al. 2017), with strategies typically focusing on field margins and semi-natural grasslands. The findings from our field experiment, as well as previous observational approaches (Hill and Bartomeus 2016), suggest that in countries with a high proportion of (boreal) forested landscapes, the extensive networks of open-canopy habitats from power-line clearings can—with proper management—function as alternative habitats for wild pollinators. Our results demonstrate the importance of using human-modified land for conservation of biodiversity (Russell et al. 2005, Eldegard et al. 2017). It has also been suggested that management of power-line clearings should complement agri-environmental schemes (AES) and contribute to conservation and ecosystem service provision (Hill and Bartomeus 2016). Our results also illustrate how the efficiency of management schemes depends on the environmental context, supporting Scheper et al. (2013), who emphasized the importance of considering the environmental conditions prior to management scheme decisions.

Our findings show that the current practice of manual clearing of woody vegetation (treatment cut) in many cases increases biological diversity of insect-pollinated plants. A continuation of this practice will particularly be beneficial for insect-pollinated plants in areas with low productivity, high stem density, or high temperatures. The differences in effect sizes between uncleared plots and the two cleared plots demonstrate how areas that are productive, have a high stem density, or have high temperatures should be cut more frequently to promote functional diversity of insect-pollinated plants. Given limited budgets, the implementation of the costlier treatment of residue removal (i.e., cut–remove) should be allocated to carefully selected locations, such as locations where a strong effect on the chosen response metric(s) is likely because of the environmental conditions. Specifically, in order to achieve a high floral resource diversity, we suggest that management practices including removal of the woody debris (cut–remove) should be implemented at locations of high or intermediate site productivity, with available source habitats in the surrounding landscape, and where the stems/m^2 are high. These environmental factors can easily be extracted from remote sensing data and could be transferred onto a distribution map of main-grid power-line clearings to more easily identify suitable locations.

CONCLUSIONS

Our results indicate that to enhance the value of plant communities for pollinators, a combination of cut and cut–remove management practices in power-line clearings—at carefully selected locations—would be optimal, both economically and through its effect on biological diversity. The contrasting effects of treatments on species and functional diversity highlight the importance of exploring not only traditional diversity measures when investigating ecosystem function, but also functional diversity, based on effect traits. Functional diversity should be emphasized when identifying valuable foraging habitats for pollinating insects, particularly when applying cut and removal of the woody debris, since it is the more costly and labor-intensive management practice. Targeted management schemes in areas already disturbed by humans can thereby contribute to the conservation of pollinators and pollination functions and services. Moreover, our study reveals how small adjustments of current management practices can directly promote pollination services by enhancing the diversity of floral resources. We recommend that the extensive geographical areas under power-line clearings should be included in conservation plans.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2509/full

Appendix

Ecosphere.

Different cutting regimes improve species and functional diversity of insect-pollinated plants in power-line clearings.

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Appendix S1: Supplementary material

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Appendix S1: Table S1: Functional traits. *Description of the plant functional traits and the value per trait.*

No.	Trait	Value/No. categories	Description
1.	Inflorescence	3	A: singular flowers B: singular flowers in a group C: multi flowers/pseudanthium
2.	Flower colors	16	color variations
3.	Exposed nectar/pollen	2	Exposed / not exposed
4.	Nectar tube	3	Short / medium / long
5.	Pollen per flower	2	few: less than 4 anthers per flower many: more than 4 anthers per flower
6.	Flowering period	4	vår = spring fso = early summer mso = mid summer sso = late summer
7.	Height	6.5 – 150	average potential height (cm)
8.	Floral symmetry	2	Actinomorphic / zygomorphic
9.	Life-strategy	3	Annual / biennial / perennial

Appendix S1: Table S2: Species list and corresponding functional traits. *Functional traits of forb, dwarf shrub and shrub species; 9 traits that were used to calculate the functional diversity indices (i.e. Functional evenness and functional dispersion). Nomenclature follows Artsdatabanken (2015). Traits are retained from Lid and Lid (2005). There are 158 species from 38 families.*

Family	**Species**	**Category**	**Functional traits**								
			Inflore -scence	**Flower colors**	**Life-strategy**	**Symmetry**	**nectar/ pollen**	**Nectar tube**	**Pollen per flower**	**First flowering**	**Average height (cm)**
Apiaceae	*Angelica sylvestris*	forb	C	white	perennial	actinomorphic	exposed	no	few	mso	125
Apiaceae	*Anthriscus sylvestris*	forb	C	white	perennial	actinomorphic	exposed	no	many	fso	100
Apiaceae	*Peucedanum palustre*	forb	C	white	biennial	actinomorphic	exposed	no	many	mso	80
Apiaceae	*Pimpinella saxifraga*	forb	C	white	perennial	actinomorphic	exposed	no	many	fso	35
Asparagaceae	*Convallaria majalis*	forb	B	white	perennial	actinomorphic	concealed	no	few	vår	20
Asteraceae	*Achillea millefolium*	forb	C	white-pink	perennial	actinomorphic	exposed	no	few	mso	35
Asteraceae	*Antennaria dioica*	forb	C	white-pink	perennial	actinomorphic	exposed	no	few	fso	15
Asteraceae	*Carduus vulgare*	forb	C	purple	biennial	actinomorphic	exposed	short	few	mso	95
Asteraceae	*Cirsium arvense*	forb	C	purple	perennial	actinomorphic	exposed	short	few	mso	80
Asteraceae	*Cirsium heterophyllum*	forb	C	purple	perennial	actinomorphic	exposed	short	few	mso	100
Asteraceae	*Cirsium palustre*	forb	C	purple	biennial	actinomorphic	exposed	short	few	mso	125
Asteraceae	*Gnaphalium* sp	forb	C	brown	perennial	actinomorphic	exposed	short	few	mso	27.5
Asteraceae	*Hieracium lactucella*	forb	C	yellow	perennial	actinomorphic	exposed	long	few	fso	20
Asteraceae	*Hieracium pilosella* sp	forb	C	yellow	perennial	actinomorphic	exposed	long	few	fso	17.5
Asteraceae	*Hieracium* sp	forb	C	yellow	perennial	actinomorphic	exposed	long	few	NA	NA
Asteraceae	*Hieracium sylvatica* sp	forb	C	yellow	perennial	actinomorphic	exposed	long	few	fso	37.5
Asteraceae	*Hierarcium umbellatum*	forb	C	yellow	perennial	actinomorphic	exposed	long	few	mso	42.5
Asteraceae	*Hierarcium vulgatum*	forb	C	yellow	perennial	actinomorphic	exposed	long	few	fso	50
Asteraceae	*Hypochaeris maculata*	forb	C	yellow	perennial	actinomorphic	exposed	long	many	fso	40
Asteraceae	*Lapsana communis*	forb	C	yellow	perennial	actinomorphic	exposed	long	few	mso	75
Asteraceae	*Leontodon autumnale*	forb	C	yellow	perennial	actinomorphic	exposed	long	few	mso	22.5
Asteraceae	*Leucanthemum vulgare*	forb	C	white-yellow	perennial	actinomorphic	exposed	short	few	fso	45
Asteraceae	*Omaloteca sylvatica*	forb	C	brown	perennial	actinomorphic	exposed	long	few	mso	27.5
Asteraceae	*Solidago canadensis*	forb	C	yellow	perennial	actinomorphic	exposed	long	many	sso	100
Asteraceae	*Solidago virgaurea*	forb	C	yellow	perennial	actinomorphic	exposed	long	many	mso	52.5

Asteraceae	*Tussilago farfara*	forb	C	yellow	perennial	actinomorphic	exposed	long	few	vår	12.5
Asteraceae	*Tanacetum vulgaris*	forb	C	yellow	perennial	actinomorphic	exposed	short	few	mso	95
Asteraceae	*Taraxacum* sp	forb	C	yellow	perennial	actinomorphic	exposed	long	many	NA	22.5
Balsaminaceae	*Impatiens noli-tangere*	forb	A	yellow	annual	zygomorphic	concealed	long	few	mso	55
Brassicaceae	*Cardamine amara*	forb	B	white	perennial	actinomorphic	exposed	short	few	vår	27.5
Brassicaceae	*Cardamine dentata*	forb	B	white-lilac	perennial	actinomorphic	exposed	short	few	fso	30
Brassicaceae	*Cardamine pratensis*	forb	B	white-lilac	perennial	actinomorphic	exposed	short	few	vår	35
Brassicaceae	*Thlaspi caerulescens*	forb	C	white-pink	perennial	actinomorphic	exposed	Short	many	vår	20
Campanulaceae	*Campanula persicifolia*	forb	A	blue	perennial	actinomorphic	exposed	no	few	mso	55
Campanulaceae	*Campanula rotundifólia*	forb	A	blue	perennial	actinomorphic	exposed	no	few	fso	30
Caprifoliaceae	*Linnaea borealis*	shrub	A	pink	perennial	actinomorphic	concealed	short	few	fso	7.5
Caprifoliaceae	*Succisa pratensis*	forb	C	blue-violet-lilac	perennial	actinomorphic	exposed	long	few	sso	40
Caprifoliaceae	*Valeriana sambucifolia*	forb	C	white-pink	perennial	zygomorphic	exposed	long	few	fso	110
Carophyllaceae	*Carophyllaceae* sp	forb	A	white	perennial	actinomorphic	exposed	no	many	NA	NA
Carophyllaceae	*Cerastium arvénse*	forb	A	white	perennial	actinomorphic	exposed	no	many	fso	20
Carophyllaceae	*Cerastium fontanum*	forb	A	white	perennial	actinomorphic	exposed	no	many	fso	25
Carophyllaceae	*Moehringia trinervia*	forb	A	white	annual	actinomorphic	exposed	no	many	fso	12.5
Carophyllaceae	*Silene dioica*	forb	A	pink	perennial	actinomorphic	exposed	long	many	fso	40
Carophyllaceae	*Silene rupestris*	forb	A	white	annual	actinomorphic	exposed	short	many	mso	12.5
Carophyllaceae	*Stellaria graminea*	forb	A	white	perennial	actinomorphic	exposed	no	many	fso	25
Carophyllaceae	*Stellaria longifolia*	forb	A	white	perennial	actinomorphic	exposed	no	many	fso	22.5
Carophyllaceae	*Stellaria media*	forb	A	white	annual/ biennial	actinomorphic	exposed	no	many	vår	22
Carophyllaceae	*Stellaria nemorum*	forb	A	white	perennial	actinomorphic	exposed	no	many	fso	30
Cichoriaceae	*Mycelis muralis*	forb	A	yellow	perennial	actinomorphic	exposed	long	few	mso	70
Clusiaceae	*Hypericum maculatum*	forb	B	yellow	perennial	actinomorphic	exposed	no	many	mso	85
Clusiaceae	*Hypericum perforatum*	forb	B	yellow	perennial	actinomorphic	exposed	no	many	mso	50
Convallariaceae	*Maianthemum bifolium*	forb	B	white	perennial	actinomorphic	exposed	no	few	vår	12.5
Cornaceae	*Chamaepericlymenum suecicum*	forb	A	white	perennial	actinomorphic	exposed	no	many	fso	12.5
Crassulaceae	*Sedum telephium*	forb	C	white-green	perennial	actinomorphic	exposed	no	many	mso	35

Dipsacaceae	*Knautia arvensis*	forb	C	pink	perennial	actinomorphic	exposed	long	few	mso	55
Empetraceae	*Empetrum nigrum*	Dwarf shrub	B	pink	perennial	actinomorphic	exposed	no	few	vår	17.5
Ericaceae	*Andromeda polifolia*	Dwarf shrub	B	pink	perennial	actinomorphic	concealed	no	few	fso	17.5
Ericaceae	*Calluna vulgaris*	Dwarf shrub	B	pink	perennial	actinomorphic	exposed	no	few	mso	30
Ericaceae	*Orthilia secunda*	Dwarf shrub	B	green-white	perennial	actinomorphic	concealed	no	few	fso	12.5
Ericaceae	*Pyrola minor*	Dwarf shrub	B	white-pink	perennial	actinomorphic	concealed	no	few	fso	12.5
Ericaceae	*Pyrola rotundifolia*	forb	B	white-pink	perennial	actinomorphic	concealed	no	many	fso	20
Ericaceae	*Pyrola media*	forb	B	white-pink	perennial	actinomorphic	concealed	no	many	fso	20
Ericaceae	*Vaccinium myrtillus*	Dwarf shrub	A	pink	perennial	actinomorphic	concealed	short	few	vår	30
Ericaceae	*Vaccinium oxycoccus palustris*	Dwarf shrub	A	red	perennial	actinomorphic	exposed	short	few	fso	65
Ericaceae	*Vaccinium uliginosum*	Dwarf shrub	A	white-pink	perennial	actinomorphic	concealed	no	few	vår	35
Ericaceae	*Vaccinium vitis-idaea*	Dwarf shrub	B	white	perennial	actinomorphic	concealed	no	few	vår	17.5
Fabaceae	*Lathyrus linifolius*	forb	A	purple-blue	perennial	zygomorphic	concealed	long	few	vår	20
Fabaceae	*Lathyrus pratensis*	forb	B	yellow	perennial	zygomorphic	concealed	long	few	fso	40
Fabaceae	*Lathyrus vernus*	forb	B	purple	perennial	zygomorphic	concealed	long	few	vår	30
Fabaceae	*Trifolium medium*	forb	C	pink	perennial	zygomorphic	concealed	long	few	fso	35
Fabaceae	*Trifolium pratense*	forb	C	pink	perennial	zygomorphic	concealed	long	few	fso	32.5
Fabaceae	*Trifolium repens*	forb	C	white-pink	perennial	zygomorphic	concealed	long	few	fso	25
Fabaceae	*Vicia cracca*	forb	B	blue-violet	perennial	zygomorphic	concealed	long	few	fso	50
Fabaceae	*Vicia sepium*	forb	B	purple	perennial	zygomorphic	concealed	long	few	fso	45
Fabaceae	*Vicia* sp	forb	B	pink-purple-blue	perennial	zygomorphic	concealed	long	few	NA	NA
Geraniaceae	*Geranium sylvaticum*	forb	A	purple	perennial	actinomorphic	exposed	short	many	fso	50
Grossulariaceae	*Ribes nigrum*	shrub	B	green-red	perennial	actinomorphic	concealed	short	few	vår	150
Grossulariaceae	*Ribes rubrum*	shrub	B	green-white	perennial	actinomorphic	exposed	no	few	vår	125
Grossulariaceae	*Ribes* sp	shrub	B	green-white-red	perennial	actinomorphic	exposed	no	few	vår	NA
Grossulariaceae	*Ribes spicatum*	shrub	B	green-red	perennial	actinomorphic	exposed	no	few	vår	125
Lamiaceae	*Ajuga pyramidalis*	forb	B	blue-violet	perennial	zygomorphic	exposed	long	few	vår	15

Lamiaceae	*Clinopodium vulgare*	forb	A	pink	perennial	zygomorphic	exposed	long	few	mso	40
Lamiaceae	*Galeopsis* sp	forb	B	purple-pink-white	annual	zygomorphic	concealed	long	few	mso	NA
Lamiaceae	*Glechoma hederacea*	forb	A	blue-violet	perennial	zygomorphic	concealed	long	few	vår	17.5
Lamiaceae	*Lamium purpureum*	forb	A	pink	annual	zygomorphic	concealed	long	few	vår	17.5
Lamiaceae	*Lamium* sp	forb	A	purple-pink	annual	zygomorphic	concealed	long	few	vår	22.5
Lamiaceae	*Prunella vulgaris*	forb	B	blue-violet	perennial	zygomorphic	concealed	long	few	mso	15
Lamiaceae	*Scutellaria gallericulata*	forb	A	blue-violet	perennial	zygomorphic	concealed	long	few	mso	22.5
Lamiaceae	*Stachys palustris*	forb	B	pink	perennial	zygomorphic	concealed	long	few	mso	60
Lamiaceae	*Stachys sylvatica*	forb	B	red-violet	perennial	zygomorphic	concealed	long	few	mso	75
Melanthiaceae	*Paris quadrifolia*	forb	A	yellow-green	perennial	actinomorphic	exposed	no	many	vår	25
Onagraceae	*Chamerion angustifolium*	forb	B	purple	perennial	actinomorphic	exposed	short	many	mso	125
Onagraceae	*Circaea alpina*	forb	B	white	perennial	zygomorphic	exposed	short	few	fso	12.5
Onagraceae	*Epilobium montanum*	forb	A	pink	perennial	actinomorphic	exposed	short	few	mso	60
Onagraceae	*Epilobium* sp	forb	A	pink	perennial	actinomorphic	exposed	short	few	NA	NA
Orchidaceae	*Dactylorhiza maculata*	forb	B	white-purple	perennial	zygomorphic	concealed	long	few	fso	25
Orchidaceae	*Epipactis atrorubens*	forb	B	red-violet	perennial	zygomorphic	exposed	long	few	mso	35
Orchidaceae	*Listera ovata*	forb	B	green	perennial	zygomorphic	exposed	long	few	fso	40
Orchidaceae	*Platanthera bifolia*	forb	B	white	perennial	zygomorphic	concealed	long	few	fso	32.5
Orobanchaceae	*Euphrasia* sp	forb	A	white-lilac	annual	zygomorphic	exposed	long	few	NA	NA
Orobanchaceae	*Euphrasia stricta*	forb	A	white-lilac	annual	zygomorphic	exposed	long	few	mso	15
Orobanchaceae	*Melampyrum pratense*	forb	A	yellow	annual	zygomorphic	exposed	long	few	fso	25
Orobanchaceae	*Melampyrum* sp	forb	A	yellow	annual	zygomorphic	exposed	long	few	NA	NA
Orobanchaceae	*Melampyrum sylvaticum*	forb	A	yellow	annual	zygomorphic	concealed	long	few	fso	25
Oxalidaceae	*Oxalis acetosella*	forb	A	white-lilac	perennial	actinomorphic	exposed	no	many	vår	7.5
Plantaginaceae	*Linaria vulgaris*	forb	B	yellow	perennial	zygomorphic	concealed	long	few	mso	42.5
Plantaginaceae	*Plantago lanceolata*	forb	C	brown	perennial	actinomorphic	exposed	short	few	fso	30
Plantaginaceae	*Veronica beccabunga*	forb	A	blue	perennial	actinomorphic	exposed	no	few	fso	25
Plantaginaceae	*Veronica chamaedrys*	forb	A	blue	perennial	actinomorphic	exposed	no	few	vår	17.5
Plantaginaceae	*Veronica officinalis*	forb	B	blue	perennial	actinomorphic	exposed	no	few	fso	20

Plantaginaceae	*Veronica scutellata*	forb	A	white-lilac	perennial	actinomorphic	exposed	no	few	fso	17.5
Polygalaceae	*Polygala* sp	forb	B	blue-violet	perennial	zygomorphic	concealed	long	few	NA	17.5
Polygalaceae	*Polygala vulgaris*	forb	B	blue-violet	perennial	zygomorphic	concealed	long	few	fso	20
Polygonaceae	*Bistorta vivipara*	forb	B	white	perennial	actinomorphic	exposed	no	few	fso	17.5
Polygonaceae	*Rumex acetosa*	forb	B	red	perennial	actinomorphic	exposed	no	few	fso	50
Polygonaceae	*Rumex acetosella*	forb	B	red	perennial	actinomorphic	exposed	no	few	fso	17.5
Primulaceae	*Lysimachia vulgaris*	forb	B	yellow	perennial	actinomorphic	exposed	no	few	mso	100
Primulaceae	*Trientalis europaea*	forb	A	white	perennial	actinomorphic	exposed	no	many	fso	12.5
Ranunculaceae	*Actaea spicata*	forb	B	white	perennial	actinomorphic	exposed	no	many	fso	50
Ranunculaceae	*Anemone nemorosa*	forb	A	white	perennial	actinomorphic	exposed	short	many	vår	20
Ranunculaceae	*Caltha palustris*	forb	A	yellow	perennial	actinomorphic	exposed	no	many	vår	22.5
Ranunculaceae	*Hepatica nobilis*	forb	A	blue	perennial	actinomorphic	exposed	no	many	vår	12.5
Ranunculaceae	*Ranunculus acris*	forb	A	yellow	perennial	actinomorphic	exposed	no	many	fso	47.5
Ranunculaceae	*Ranunculus auricomus*	forb	A	yellow	perennial	actinomorphic	exposed	no	many	vår	15
Ranunculaceae	*Ranunculus repens*	forb	A	yellow	perennial	actinomorphic	exposed	no	many	fso	27.5
Ranunculaceae	*Ranunculus* sp	forb	A	yellow	perennial	actinomorphic	exposed	no	many	NA	NA
Rosaceae	*Comarum palustre*	forb	A	red	perennial	actinomorphic	exposed	no	many	fso	30
Rosaceae	*Filipendula ulmaria*	forb	C	white	perennial	actinomorphic	exposed	no	many	fso	100
Rosaceae	*Fragaria ananássa*	forb	A	white	perennial	actinomorphic	exposed	no	many	fso	22.5
Rosaceae	*Fragaria vesca*	forb	A	white	perennial	actinomorphic	exposed	no	many	vår	12.5
Rosaceae	*Geum rivale*	forb	A	red-brown	perennial	actinomorphic	exposed	no	many	vår	30
Rosaceae	*Geum urbanum*	forb	A	yellow	perennial	actinomorphic	exposed	no	many	fso	50
Rosaceae	*Potentilla erecta*	forb	A	yellow	perennial	actinomorphic	exposed	no	many	fso	20
Rosaceae	*Rubus chamaemorus*	Dwarf shrub	A	white	perennial	actinomorphic	exposed	no	many	fso	12.5
Rosaceae	*Rubus saxatilis*	Dwarf shrub	A	white	perennial	actinomorphic	exposed	no	many	fso	25
Rosaceae	*Crataegus scandinavicus*	shrub	A	white	perennial	actinomorphic	concealed	no	few	vår	85
Rosaceae	*Rosa majalis*	shrub	A	pink	perennial	actinomorphic	exposed	no	many	fso	110
Rosaceae	*Rosa* sp	shrub	A	white-pink	perennial	actinomorphic	exposed	no	many	NA	NA
Rosaceae	*Rubus fruticosus coll.*	shrub	A	white	perennial	actinomorphic	exposed	no	many	mso	NA

Rosaceae	*Rubus idaeus*	shrub	A	white	perennial	actinomorphic	exposed	no	many	fso	100
Rosaceae	*Rubus* sp	shrub	A	white	perennial	actinomorphic	exposed	no	many	NA	NA
Rubiaceae	*Galium aparine*	forb	A	white	annual	actinomorphic	exposed	no	few	fso	95
Rubiaceae	*Galium boreale*	forb	B	white	perennial	actinomorphic	exposed	no	few	mso	27.5
Rubiaceae	*Galium palustre*	forb	B	white	perennial	actinomorphic	exposed	no	few	fso	25
Rubiaceae	*Galium uliginosum*	forb	B	white	perennial	actinomorphic	exposed	no	few	fso	22.5
Rubiaceae	*Galium verum*	forb	B	yellow	perennial	actinomorphic	exposed	short	few	fso	40
Saxifragaceae	*Chrysosplenium alternifolium*	forb	B	yellow-green	perennial	actinomorphic	exposed	no	many	vår	12.5
Scrophulariaceae	*Scrophularia nodosa*	forb	B	brown-red	perennial	zygomorphic	concealed	short	few	mso	70
Solanaceae	*Solanum dulcamara*	forb	B	violet	perennial	actinomorphic	exposed	no	many	fso	110
Thymelaeaceae	*Daphne mezereum*	shrub	B	red-violet	perennial	actinomorphic	exposed	long	few	vår	100
Urticaceae	*Urtica dioica*	forb	B	green	perennial	actinomorphic	exposed	no	few	fso	65
Urticaceae	*Urtica* sp	forb	B	green	perennial	actinomorphic	exposed	no	few	NA	NA
Violaceae	*Viola canina*	forb	A	blue	perennial	zygomorphic	exposed	short	few	fso	12.5
Violaceae	*Viola mirabilis*	forb	A	lilac	perennial	zygomorphic	exposed	short	few	vår	20
Violaceae	*Viola palustris*	forb	A	lilac	perennial	zygomorphic	exposed	short	few	vår	6.5
Violaceae	*Viola tricolor*	forb	A	violet-yellow-white	perennial	zygomorphic	exposed	short	few	vår	17.5
Violaceae	*Viola riviniana*	forb	A	blue-violet	perennial	zygomorphic	exposed	short	few	vår	15
Violaceae	*Viola* sp	forb	A	violet	perennial	zygomorphic	exposed	short	few	NA	NA

Appendix S1: Table S3: Correlation matrix: *Correlation table of each of the five responses; species richness, evenness, Shannon diversity, functional evenness and functional dispersion, and the explanatory variables selected for the full models.*

	Species richness	Canopy density	Stems m^{-2}	Precipitation	Elevation	Productivity	Radiation index	Source habitat area
Species richness	1	0.095	0.096	-0.011	-0.165	0.634	0.321	0.316
Canopy density	0.095	1	-0.116	0.135	0.202	-0.081	0.112	-0.202
Stems m^{-2}	0.096	-0.116	1	-0.114	-0.086	0.104	-0.171	-0.065
Precipitation	-0.011	0.135	-0.114	1	-0.306	-0.124	0.185	-0.205
Elevation	-0.165	0.202	-0.086	-0.306	1	-0.062	-0.165	-0.654
Productivity	0.634	-0.081	0.104	-0.124	-0.062	1	0.189	0.226
Radiation index	0.321	0.112	-0.171	0.185	-0.165	0.189	1	0.066
Source habitat area	0.316	-0.202	-0.065	-0.205	-0.654	0.226	0.066	1

	Evenness	Canopy density	Temperature January	Elevation	Precipitation	Productivity
Evenness	1	0.111	-0.002	0.025	-0.033	0.241
Canopy density	0.111	1	-0.144	0.202	0.135	-0.081
Temperature January	-0.002	-0.144	1	-0.690	0.569	0.077
Elevation	0.025	0.202	-0.690	1	-0.306	-0.062
Precipitation	-0.033	0.135	0.569	-0.306	1	-0.124
Productivity	0.241	-0.081	0.077	-0.062	-0.124	1

	Shannon diversity	Canopy density	Initial canopy density	Stems m^{-2}	Precipitation	Productivity	Radiation index	Source habitat area
Diversity	1	0.093	-0.320	0.235	-0.033	0.594	0.239	0.197
Canopy density	0.093	1	0.231	-0.116	0.135	-0.081	0.112	-0.202
Initial canopy density	-0.320	0.231	1	-0.646	-0.085	-0.348	0.090	-0.429
Stems m^{-2}	0.235	-0.116	-0.646	1	-0.114	0.104	-0.171	-0.065
Precipitation	-0.033	0.135	-0.085	-0.114	1	-0.124	0.185	-0.205
Productivity	0.594	-0.081	-0.348	0.104	-0.124	1	0.189	0.226
Radiation index	0.239	0.112	0.090	-0.171	0.185	0.189	1	0.066

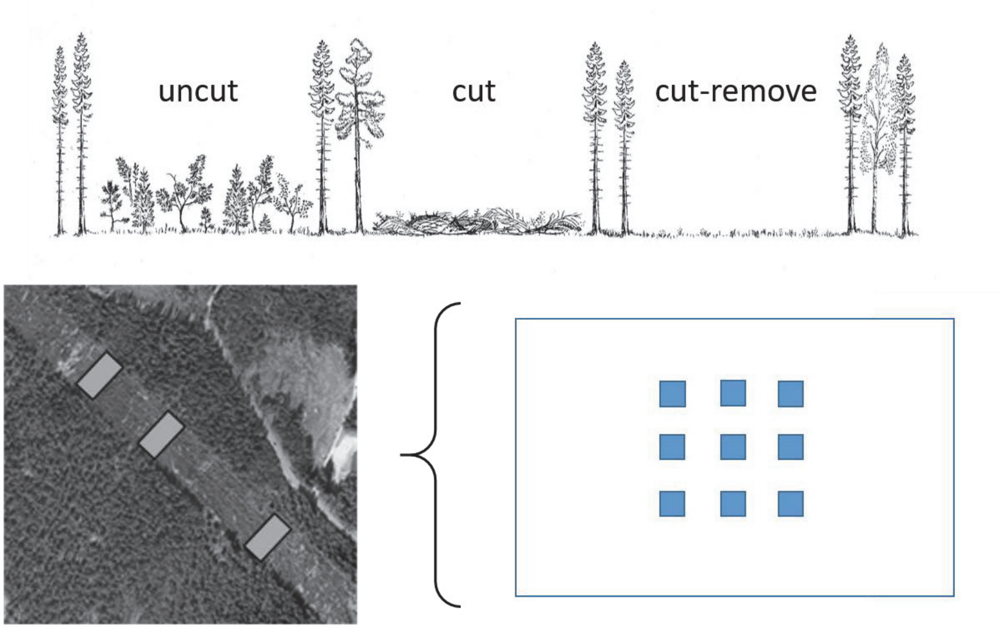
Source habitat area	0.197	-0.202	-0.429	-0.065	-0.205	0.226	0.066	1

	Functional evenness	Canopy density	Temperature January	Precipitation	Elevation	Productivity
Functional evenness	1	-0.070	0.199	0.140	-0.112	-0.059
Canopy density	-0.070	1	-0.144	0.135	0.202	-0.081
Temperature January	0.199	-0.144	1	0.569	-0.690	0.077
Precipitation	0.140	0.135	0.569	1	-0.306	-0.124
Elevation	-0.112	0.202	-0.690	-0.306	1	-0.062
Productivity	-0.059	-0.081	0.077	-0.124	-0.062	1

	Functional dispersion	Canopy density	Initial canopy density	Stems m^{-2}	Temperature growing season	Precipitation	Elevation	Productivity	Source habitat area
Functional dispersion	1	0.202	-0.019	-0.047	-0.014	-0.014	-0.177	0.186	0.243
Canopy density	0.202	1	0.231	-0.116	-0.131	0.135	0.202	-0.081	-0.202
Initial canopy density	-0.019	0.231	1	-0.646	-0.156	-0.085	0.374	-0.348	-0.429
Stems m^{-2}	-0.047	-0.116	-0.646	1	-0.126	-0.114	-0.086	0.104	-0.065
Temperature growing season	-0.014	-0.131	-0.156	-0.126	1	0.466	-0.776	0.040	0.390
Precipitation	-0.014	0.135	-0.085	-0.114	0.466	1	-0.306	-0.124	-0.205
Elevation	-0.177	0.202	0.374	-0.086	-0.776	-0.306	1	-0.062	-0.654
Productivity	0.186	-0.081	-0.348	0.104	0.040	-0.124	-0.062	1	0.226
Source habitat area	0.243	-0.202	-0.429	-0.065	0.390	-0.205	-0.654	0.226	1

***Appendix S1: Table S4: Likelihood ratio tests of final models** attained by backwards elimination of variables from the full models. Response variables were species richness, evenness, Shannon diversity, functional evenness and functional dispersion. For variables in the full models we used p-values < 0.1 as selection criterion, and for variables in the final models we used p-values <0.05 as selection criterion. Analyses were performed in R, package lme4. The model for species richness was fitted using GLMM with Poisson-distributed errors and a log-link function, while the models for the other responses were fitted using Gaussian distributed errors and identity link, with Site as a random effect.*

Response	**Explanatory terms**	**LRT**	**df**	***P***
Species richness	**Productivity**	**10.372**	**1**	**0.001**
	Treatment x Precipitation	**33.239**	**2**	**<0.0001**
	Treatment x Elevation	**10.768**	**2**	**0.005**
Evenness	**Productivity**	**2.864**	**1**	**0.091**
	Treatment x Elevation	**9.041**	**2**	**0.01**
Shannon diversity	**Productivity**	**11.828**	**1**	**0.001**
	Treatment x Precipitation	**21.542**	**2**	**<0.0001**
	Treatment x Radiation index	**6.461**	**2**	**0.04**
	Treatment x Source habitat area	**9.231**	**2**	**0.01**
	Treatment x stems m^{-2}	**23.131**	**2**	**<0.0001**
Functional evenness	**Treatment x Canopy density**	**8.672**	**2**	**0.01**
	Treatment x Elevation	**6.959**	**2**	**0.03**
Functional dispersion	**Treatment x Productivity**	**13.523**	**2**	**0.001**
	Treatment x Source habitat area	**7.557**	**2**	**0.02**
	Treatment x Stems m^{-2}	**36.759**	**2**	**<0.0001**
	Treatment x Temperature	**22.572**	**2**	**<0.0001**



Appendix S1: *Fig. S1: Aerial photo of three treatment plots within one Site (left), each randomly assigned the treatments uncut, cut or cut-remove. Within each treatment plot, the plant data was visually assessed in nine 1m^2 subplots (right, blue boxes). The subplots were regularly spaced within a 10m × 10m quadrat located in the center of each treatment plot.*

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Paper II

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Original Research Article

Conservation of solitary bees in power-line clearings: Sustained increase in habitat quality through woody debris removal

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ABSTRACT

Declining populations of wild pollinators have increased the interest in the management of human-modified landscapes for pollinator conservation. Modified landscape features, such as power-line clearings, may provide valuable habitats with increased floral resources for insect pollinators and solitary bees in particular. However, whether the effects of costly habitat interventions on bee communities in power-line clearings are sustained over time, is poorly understood. We conducted an experiment in 19 sites in power-line clearings across southeast Norway where the woody vegetation was; 1) cut and left to decay, 2) cut and removed, or 3) uncut. We assessed the temporal effects of habitat interventions and environmental factors on species richness, abundance, functional groups of nesting preference, body size, tongue-length, and species composition. Species richness and abundance of solitary bees increased substantially with time in both the cleared treatments. But compared to leaving the woody debris to decay, woody debris removal more than doubled estimated bee richness and abundance in areas with a higher forb richness and increased the trait variation in areas with high functional trait variation of forbs, dead wood, and available source habitats. The positive effect of woody debris removal on the species and functional trait diversity of bees was sustained during three years post-treatment, but the effect was dependent on abiotic and biotic environmental conditions. Over time the sites increasingly attracted bees from the regional species pool, showing how power-lines may benefit bee populations at a regional scale, through maintenance of temporary refugia in a forested landscape. The current routine practice (cut and left to decay) improves habitat quality for many bee species through alterations to early succession. However, our results indicate that the more costly woody debris removal is a more effective conservation measure for solitary bee communities over time and is to be recommended when funds are available. Removing the woody debris after routine maintenance clearing at specific sites may further enhance the diversity and persistence of bee populations over time, contributing to more diverse and stable bee communities.

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1. Introduction

Human induced modifications of landscapes are considered one of the main causes of biodiversity decline, through fragmentation, degradation and destruction of native habitats (Sánchez-Bayo and Wyckhuys, 2019; Winfree et al., 2009). Consequently, to reduce biodiversity loss (Pimm et al., 2014) there is a growing interest in the management of modified landscapes for conserving and restoring biodiversity (Villemey et al., 2018). Human-modified landscape features aligning infrastructure and other intensively used land, such as road-verges, railway lines, hedgerows, field margins or power-line clearings, may provide important habitats for several invertebrate taxa (Hanula et al., 2016; Wojcik and Buchmann, 2012). Wild bees constitute an important component of terrestrial biodiversity and are one of the most efficient groups of pollinators, contributing to vital pollination services for both crops and wild plants (Klein et al., 2007; Ollerton et al., 2011). Declining populations of wild pollinators (e.g. Biesmeijer et al., 2006; Potts et al., 2010) has led to an increased focus on wild bee conservation (IPBES, 2016).

Routine clearing of trees and shrubs along infrastructure networks maintain large areas in an early successional phase. Below high-voltage power-lines, the vegetation is cleared regularly to prevent trees from reaching the aerial lines, with clearing intervals ranging from five to ten years depending on rate of regrowth. This creates open-canopy habitats, which promote early successional vegetation of forbs and shrubs (Steinert et al., 2018) typically associated with semi-natural grasslands (Eldegard et al., 2017), which – in turn – provide a more stable nectar and pollen resource for bees in space and time (Potts et al., 2003). Bee species in forested landscapes are generally associated with patches of land in early succession forest openings (New, 2012, Roberts et al., 2017). Semi-natural grasslands, which typify diverse bee habitats, are often scarce in forested landscapes, and are considered a critically endangered nature type in Norway (Hovstad et al., 2018). Consequently, power-line clearings – commonly transecting forests managed for timber production – have gained increased attention the last two decades (Hanula et al., 2016). Particularly, there has been a recognition of their potential conservation value for wild bees (Hill and Bartomeus, 2016; Russel et al. 2005, 2018; Sydenham et al., 2016; Wagner et al., 2014, 2019). However, few experimental studies have been conducted that allow assessing whether wild bee habitat interventions in power line clearings persist over time.

Vegetation clearing is costly and time consuming, and a better understanding of the spatio-temporal effects of clearing on wild bee communities will aid in optimizing the timing and frequency of vegetation clearing in different areas (Hanula et al., 2016). In current routine maintenance clearing, all woody debris is left to decay. However, studies in forest clear-cuts have found that in order to promote flowering species and flower-visiting insects, the logging residue should be removed (Korpela et al., 2015; Rivers et al., 2018). Bees are characterized by complex life histories and specific habitat requirements (Westrich, 1990). Removing woody debris may increase plant diversity, through reduced competition for light and space, and alter ground-level microclimatic conditions of solar irradiation, temperature and moisture (Weng et al., 2007), beneficial for the many bees favoring warm and dry areas (Westrich, 1996). In boreal forests at northern latitudes, solitary bees generally have a short activity span, with marked seasonal patterns (Oertli et al., 2005) and generally low population growth rates (Danforth et al., 2019; Minckley and Danforth, 2019). Moreover, facultatively social species are typically solitary (Soro et al., 2010). Solitary bees are also central-place foragers with short dispersal distances (Franzén et al., 2009; Greenleaf et al., 2007) and respond to land use intensification at small spatial scales (Steffan-Dewenter et al., 2002). The modified habitats following different clearing practices may attract different species from the local species pool, and we may expect the emigration to and the colonization of the modified habitats in the power line clearings to show a temporal response (e.g. it may take more than one season).

The effects of habitat interventions often depend on the environmental context (Scheper et al., 2013; Sydenham et al., 2016). Diversity of flower resources is an important determinant for structuring bee communities (Gathmann et al., 1994). Removing the woody vegetation is expected to increase forb species, because of altered space and resource availability (Pickett and White, 1985). Enhanced species richness of forbs would support more bee species (Pywell et al., 2011), because of species-specific preferences and a better availability of nectar and pollen resources in space and time (Potts et al., 2003). Moreover, the functional diversity of flower resources (e.g. flower shapes, pollen and nectar content) may potentially better explain the functional diversity of pollinators (Cadotte et al., 2011), since a high functional diversity of floral forms represents a high variety of niches for the solitary bees. The effects of habitat management may also depend on abiotic environmental variables such as elevation (climate; Scheper et al., 2013), landscape fragmentation and the amount of source habitats in the surrounding landscape (Carrié et al., 2017), or factors associated with nesting preferences, such as dead wood and light availability (Murray et al., 2009).

To assess effects of habitat interventions, several measures of bee community responses should be considered, since they may reflect contrasting responses to habitat modifications (Forrest et al., 2015). Functional trait-based indices may better explain the impact of habitat quality on bee communities, compared to species-based indices (Díaz and Cabido, 2001; Gagic et al., 2015; Hooper et al., 2005). Species traits and niches determine functional trait groups, which may better reveal features of ecosystem properties (Hooper et al., 2005). Conservation efforts should preferably promote an increase in richness and abundance accompanied by a broad functional trait diversity. Some of the most important traits structuring bee communities are nesting preference (Potts et al., 2005; Williams et al., 2010), flower specialization (Cariveau et al., 2016; Gathmann et al., 1994) and foraging range which increases with body size (Greenleaf et al., 2007; Torné-Noguera et al., 2014). Understanding the effects on the species composition may also contribute to practical management decisions (Socolar et al., 2016). Beta diversity is the spatial variability in species composition across sites (Anderson et al., 2006, 2011), and beta diversity partitioning may give additional insight into spatial variability in bee communities compared with total beta diversity alone (Soininen et al., 2018). Changes in beta diversity or species turnover (i.e. species replacement) between bee communities provide insight into how the management practices contribute to maintaining regional diversity (Socolar et al., 2016).

The main aim of this study was to assess the potential for adjusting management practices in power-line clearings to improve habitat quality for solitary bees. We assessed whether the effect on bee communities was sustained over three years, giving bee populations time to disperse between and populate the cleared habitat patches created by experimental treatments. We conducted a large-scale field experiment to study effects on bee communities in response to different maintenance clearing practices (treatments): (1) cut, i.e. all trees cut and left to decay in the clearing; (2) cut-remove, i.e. all trees cut and removed from the plot; and (3) uncut. We measured effects of treatments on the bee community for three years post-treatment and studied whether temporal patterns depended on environmental context. We asked the following questions:

1) How do the treatments (i.e. cut, cut-remove, uncut) affect species richness and abundance of solitary bees within power-line clearings over the course of three years?
2) Do the treatments lead to a change in functional trait-diversity over time, by modifying relative proportions of below vs. above ground nesters, or trait variation in body size and tongue length?
3) How do the treatments affect bee species composition over time? Do beta diversity or species turnover vary between or within treatments over time?
4) Are temporal patterns of the bee diversity measures – in response to different management practices – modified by abiotic and biotic environmental conditions?

2. Methods

2.1. Experimental design

We conducted a large-scale field experiment within the main power-line grid in southeast Norway (Fig. 1). We identified 19 sites below power-lines located between latitudes 59.33°–61.12°N and longitudes 08.95°–11.36°E at 45–535 masl, where there was a stretch of at least 200 m with substantial regrowth of trees. All sites were located in boreal forest systems consisting of mixed stands of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula* spp.). Each site had been subjected to the same management regime with manual cutting (no use of chemicals and without disturbing the ground layer) of all woody vegetation every 5–10 years, dependent on the site productivity, with biomass (fine woody debris <10 cm in diameter) left to decay on the ground. The cut vegetation in the clearings comprised trees in an early successional phase. Productive sites were dominated by a substantial regrowth of deciduous trees, together with shrubs and forbs. Low-productive sites were dominated by ericaceous dwarf shrubs. At each site, we established three treatment plots of approx. 30 m × 60 m [corridor width], with an average distance of 120 m apart (min = 50, max = 345) (established autumn 2012 [n = 16] or early spring 2013 [n = 3]). Within each site, we randomly assigned one of the three treatments to each plot: (1) cut:

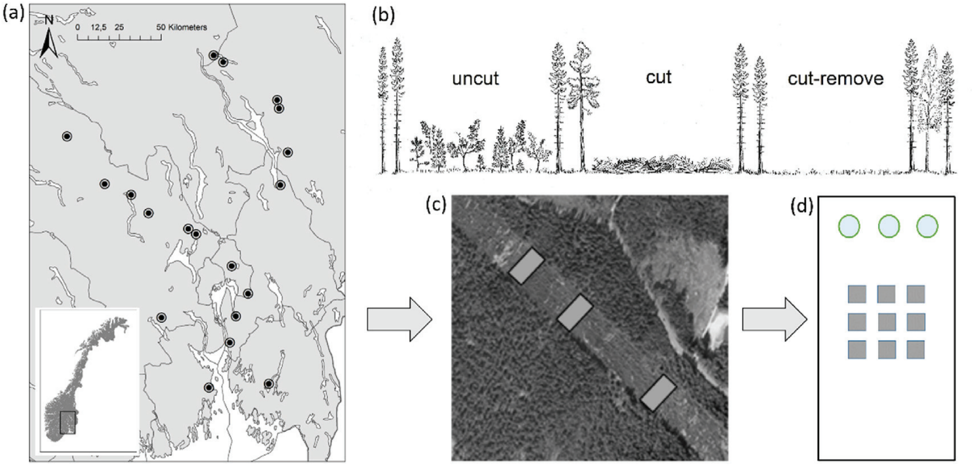

Fig. 1. (a) Geographic distribution of the 19 study sites. (b) Illustration of the three experimental treatments at each site, where the woody vegetation was uncut: uncleared control; cut: all trees cut and left to decay in the clearing; and cut-remove: all trees cut and removed from the plot, exposing the ground. (c) Aerial photograph of one site with the three treatment plots. The distance between treatment plots was minimum 20 m. (d) Three flight interception traps were placed along the northernmost side of each treatment plot (circles). Plant data were collected in nine 1-m^2 subplots within each treatment plot (squares).

all trees cut and left to decay in the clearing; (2) cut-remove: all trees cut and removed from the plot, (3) uncut (Fig. 1). The woody debris in the cut-remove treatment was moved and assembled into a pile at one of the edges of the treatment plot. We expected that the initial responses to habitat interventions would occur at the behavioral level of individuals within the bee communities (Wong and Candolin, 2015). Nevertheless, differences in species and individuals among the treatments likely reflect habitat preferences by bees from the local species pool. If one habitat is used more than the other this should be reflected in the collected material and should mirror the suitability of the habitat. The preference or avoidance of species to differently managed habitat patches within the spatial scale of the community can therefore reveal which of the clearing practices may enhance the habitat quality for bees. We assume that improved habitat conditions will ultimately increase bee populations, but in this study, we are only reporting the preference of bees for the different treatments.

2.2. Data collection

We used flight interception traps to sample the solitary bee communities within the power-line clearings (Moretti et al., 2009; Ulyshen et al., 2010; Rubene et al., 2015), to ensure a collection of representative data of the bee communities (Oertli et al., 2005). This sampling procedure enabled a continuous and consistent sampling intensity throughout the whole foraging activity season of bees in the three subsequent years. Although pan-trapping or vane traps are considered more effective for trapping bees (Westphal et al., 2008; Hall, 2018), pan-traps would be inefficient in our sites, due to large temporal and spatial coverage, and vane traps were not recognized as a standard sampling procedure at the time we started our data collection. We installed three flight interception traps (window traps) within each treatment plot (19 sites, 3 treatments), placed along the northernmost end of the treatment plot, to maximize sun exposure (Fig. 1). The traps consisted of two transparent Plexiglas screens (370 mm × 210 mm), that formed a cross, with a funnel and container attached to it (Fig. A1). The container was filled with 50:50 mixture of water and green propylene glycol and a drop of detergent. Bees were sampled continuously throughout their main foraging-activity season. Traps were installed immediately after snowmelt (April/May) and removed in early autumn (September). We emptied traps four times in 2013 and 2014 and five times in 2015, due to an earlier onset of snowmelt. The collected material was stored in 80% ethanol before pinning and identification. All bees were identified using regional identification keys (Schmid-Egger and Scheuchl 1997; Amiet et al., 1999; 2001; Scheuchl, 2000, 2006; Amiet, 2004). Voucher specimens are preserved in the entomological collection at the Norwegian University of Life Sciences.

In each treatment plot, we surveyed the plant community (floral resources), the environmental conditions and habitat characteristics (Table 1). Plant surveys were carried out in late June and early July in 2013, 2014 and 2015, covering all flowering species (insect-pollinated forbs) throughout the season. We spaced nine quadratic subplots of 1 m^2 regularly within a 10 × 10 m quadrat in the center of each treatment plot. We identified all forbs to species and visually estimated the abundances to the nearest 1% from the nine subplots during each sampling visit. If a species was present in a subplot, but had <1% cover, it was recorded as 0.001%. As a measure of dead wood, we counted lying dead trees with a diameter at breast height (DBH) of >15 cm in transects of 2 × 20 m along both sides of the forest-edges of each treatment plot (i.e. dead trees of

Table 1
Variables in the analyses. Response variables and candidate explanatory variables for the analyses of the full regression models. Measured values (range) of the bees, the functional trait groups and beta diversity components. Spatial scale and measured values (range/levels) of the plant community (floral resources), the environmental conditions and habitat characteristics. Variables in bold were included in the full (most complex) models. For description of the variables, see methods chapter, under 'Data collection 'and 'Data preparation'.

Variables in analysis	Spatial scale	Range/levels (mean)
Response variables		
Species richness		**0–29.0 (6.2)**
Rarefied richness		**0–6 .7 (1.3)**
Abundance		**0–112.8 (11.5)**
Prop. below-ground nesters		**0–1 (0.65)**
Functional dispersion (FDis) body size		**0–1 (0.44)**
Community weighted mean body size		**1–3.1 (2.0)**
Functional dispersion (FDis) tongue length		**0–1.65 (0.57)**
Turnover (Beta$_{JTU}$)		**0.1–0.83 (0.45)**
Jaccard (Beta$_{JAC}$)		**0.25–0.75 (0.51)**
Explanatory variables		
Year	**Site**	**2013– 2014– 2015**
Treatment	**Plot**	**uncut, cut, cut-remove**
Dead wood	**Site**	**0–45 (10.5)**
Elevation (m.a.s.l.)	**Site**	**45–535 (260)**
Richness forbs	**Plot**	**0–31 (10.8)**
Functional dispersion (FDis) forbs	**Plot**	**0.20–0.41 (0.32)**
Irradiation index	Plot	−0.32 − 0.87 (0.39)
Source habitat area	**Site**	**0–1 (0.32)**
Landscape fragmentation	Site	0–1 (0.34)

larger dimensions compared to the woody debris from the maintenance clearing). The dead wood typically originates from wind felling or manually felled trees (in danger of reaching the aerial lines) along the edges of the corridor.

To assess the landscape fragmentation and source habitat areas surrounding each site, we used ArcGIS (ESRI, 2011) and Ar5 digital land use maps (Ahlstrøm et al., 2019). Total number of polygons of different land use types (11 in total) was used as a *proxy* for landscape fragmentation. We used the total area of non-forested landscape elements (i.e. non-tilled arable land (due to the associated field margins), semi-natural areas/pastures, open surfaces, and road-verges) that can function as potential source patches for bees in the power-line clearings, as a *proxy* for available source habitat areas. The land use types were measured at increasing radii around each site (150 m, 300 m, 500 m, 1000 m, 2000 m). To account for collinearity between the radii around each site, the different scales were combined into one variable using a separate principal component analysis (PCA). For both variables, we extracted the first PCA axes, transformed on a scale of 0–1 (Dormann et al., 2013). For landscape fragmentation all radii up to 2000 m were used, and for source habitat area, the radii within 500 m were used – based on known foraging range of bees (Greenleaf et al., 2007). Elevation for each site was obtained from digital maps (Kartverket, 2019).

2.3. Data preparation

To calculate bee species richness and abundance we pooled all bee specimens sampled within one treatment plot in a given year and used treatment plots as our sampling unit in the statistical analyses. The number of successful trapping sessions varied between treatment plots and between years, ranging from nine to 15. To account for uneven sampling between years, we standardized the sampling intensity by estimating the number of species and individuals expected to be sampled in a treatment plot given nine sampling sessions (Chao et al., 2014). To calculate the rarefied species richness measure (q0) (hereafter 'rarefied richness') we used the iNext package in R with sample size set to nine, and with 50 bootstrap replications (Hsieh et al., 2019). For the abundance we randomly sampled nine of the traps within a treatment plot and calculated total richness and abundance of each bee species. We repeated the random sampling 1000 times and calculated mean abundance of each bee species within each treatment plot. The mean values were used as the rarefied abundance (hereafter 'abundance'). The species richness summed from the rarefied abundance matrix was identical to the raw species richness. The presence of cleptoparasitic species are host dependent and are found to persist only if there are relatively stable and healthy populations of their hosts (Sheffield et al., 2013). In order to determine the relationships between the environment and the solitary bee communities, we excluded the cleptoparasites (i.e. within the families Coelioxys, Nomada, Stelis and Sphecodes) before the statistical analyses, as they are only indirectly associated with local habitat conditions.

We compiled trait information for three traits known to influence bee responses to environmental conditions: nesting preference (above vs below-ground nesters), tongue-length and body size (Table A1). The trait values for nesting preference was obtained from the literature (Carreck, 2016; Westrich, 1990). As a measure of species mobility (Greenleaf et al., 2007), we used the intertegular distance (ITD) of the bees (Cane, 1987), hereafter 'body size'. We obtained measures of female species specific ITDs from Sydenham et al. (2015) and from specimens in our collected material. We supplemented the ITD measures using specimens from the Natural History Museum in Oslo, Norway, to obtain a mean of minimum five specimens per species. The ITD was rounded to the nearest mm to account for the intraspecific variation in sizes. The tongue length was estimated using the BeeIT package in R (Cariveau et al., 2016), which calculates the tongue length based on the taxonomic family and species-specific ITD. For the body size and the tongue length we calculated the community weighted mean (CWM) and functional dispersion (FDis) within each treatment plot. The CWM is a measure of the dominant trait value within a species community and the FDis is a measure of the variation in trait values within a community (Laliberté and Legendre, 2010). When the FDis is calculated from a single numerical trait, it equals the mean absolute Euclidean distance of trait values found within the species assemblage to the CWM. We used weighted abundances (rarefied) with the dbFD-function of the FD package in R (Laliberté et al., 2014). Because the treatments were expected to improve the habitat quality for the solitary bees associated with semi-natural environments, we wanted to test the responses on functional trait diversity of bees associated with open habitats. From a previous study we found that forest-dwelling species, such as the Ericacea affiliated bees (i.e. *Andrena fuscipes*, *A. lapponica* and *Colletes succinctus*) showed limited response to the treatments and factors that have been identified as important for structuring bee communities in open habitats (Sydenham et al., 2015). Also, when modeling the effects on the abundance of Ericacea specialists versus the abundance of the other bees, we found that they showed contrasting responses to both forb species richness, elevation and changes over time (Fig. A2). To enable the identification of the effects on the solitary bees that were associated with the expected habitat improvement we excluded the Ericacea affiliated bees before the analyses of the functional traits.

To calculate species richness and functional dispersion (FDis) of forbs we used treatment plots as sampling units in the statistical analyses. Taxa identified only to genus were treated as morphospecies. To quantify floral resource diversity within the plant communities, we assigned nine functional effect traits to each plant species (Table A2). The traits [extracted from Lid and Lid (2005)] were based on morphological characteristics of flowers of known importance for pollinators (Table A3). The FDis of forbs, a measure of the variation in trait values within a community (Laliberté and Legendre, 2010), were calculated from the abundance, using the dbFD function of the FD package in R (Laliberté et al., 2014). We used the number of subplots in which a species occurred as a measure of abundance, to account for the dominant species in each treatment plot. When calculating the indices, we used weighted abundances and the Cailliez correction for non-Euclidian distances because of the inclusion of categorical traits (Forrest et al., 2015; Laliberté et al., 2014). As a measure of light availability in each treatment plot, we used the aspect slope and latitude, to calculate the solar irradiation index (Oke, 1987), hereafter ‘irradiation index’. All calculations were computed in R (R Development Core Team, 2017).

2.4. Statistical analyses

Our measures of biological diversity of bees, i.e. our response variables, were species richness, abundance, proportions of below-ground nesters, FDis and CWM of body size, FDis of tongue length, in addition to turnover and overall beta diversity (Table 1). To assess the underlying patterns of beta diversity, we used the dissimilarity component of turnover (Beta_{JTU}, i.e. species replacement) in addition to the overall beta diversity (Beta_{JAC}, i.e. the turnover and species loss and gain) (Baselga, 2010; 2012). We carried out a preselection of candidate variables ($P\text{-values} \leq 0.10$). For each response variable we tested each explanatory variable separately and in a two-way and three-way interaction with the categorical variables; treatment and year. Explanatory variables were elevation, richness forbs, FDis forbs, irradiation index, dead wood, source habitat, and landscape fragmentation. For each model, site identity was used as a random effect to account for the among-sites variation and repeated sampling (i.e. three treatment plots sampled once per year). We scaled all numerical variables. We calculated the generalized variance inflation factor (GVIF) values for all variables in each candidate model (Fox and Monette, 1992; Zuur et al., 2010) using the car package in R (Fox et al., 2019). Only variables with a GVIF value of <3 were retained in the full model (Zuur et al., 2010). Final models were selected by conducting stepwise backward elimination based on likelihood ratio tests (LRTs), until only significant variables remained ($P \leq 0.05$) (Table A4). We compared the models with and without the outliers, which did not qualitatively change the models (Zuur et al., 2010).

2.4.1. Species richness and abundance

To test for temporal effects of the treatments on the rarefied richness and abundance of bees, we fitted linear mixed effect models (LMMs), with identity link, assuming a normal distribution of errors. We also fitted a model for the raw species richness, using a generalized mixed effect model (GLMM), with a log link function, assuming Poisson-distributed errors. The final models for rarefied richness and raw richness were qualitatively similar, thus we chose to present the raw richness (hereafter ‘species richness’) in the paper and the rarefied richness in the appendix.

2.4.2. Nesting preference, tongue length and body size

We tested for temporal treatment effects on nesting preference using the proportions of below-ground nesting bees as a response variable. We chose to carry out the analysis on the relative proportions of the dominant trait group (i.e. below-ground nesters). When interpreting the results, we also used the inverse proportion of the trait group (i.e. above-ground nesters). We used a GLMM, with binomial distributed errors and a log link function and the optimizer ‘bobyqua’ of the optimx package (Nash and Varadhan, 2011) to model the proportion of below-ground nesters. The temporal treatment effects on the FDis and CWM of body size, and the FDis of tongue length were analyzed by fitting linear mixed effect models (LMMs).

2.4.3. Bee species composition

To assess the temporal change in species composition within and among treatments, we used multivariate dispersions as a measure of beta diversity (Anderson et al., 2006). The calculations were based on the Jaccard dissimilarity of presence-absence data (Anderson et al., 2011) using the function beta.pair of the betapart package (Baselga et al., 2018). We chose to use presence-absence based distances to emphasize the importance of rare species, since the majority of species are rare in most communities (Magurran and McGill, 2011). To obtain the responses of turnover (Beta_{JTU}) and beta diversity (Beta_{JAC}) dissimilarities, we calculated the distances to group centroids, using the betadisper function of the vegan package (Oksanen et al., 2013). We used sites as groups, to express the variation in community structure in the treatments within sites over time. Communities that are more similar will have shorter distances to the group centroid (Anderson et al., 2006). We used LMMs to model both beta diversity indices, with identity link, assuming a normal distribution of errors.

For all the final models, we visually assessed model fit by plotting residuals against the fitted values for all explanatory variables and assessed the distribution of residuals using QQ-plots. For the GLMMs we also tested for over-dispersion of the residuals (species richness: $\phi = 0.8$; proportion of below-ground nesters: $\phi = 1.27$ (Zuur et al., 2013). The binomial model on below-ground nesters was slightly over-dispersed, but the visual inspection of the graphical diagnostic plots indicated adequate model fit. We log $(y+1)$ transformed rarefied richness, abundance, FDis body size and FDis tongue length to achieve a normal distribution of the residuals. All models were fitted using the lme4 library in R (Bates et al., 2019), and all analyses were carried out in R version 3.2.5 (R Development Core Team, 2017).

3. Results

In total, we collected 3126 individuals comprising 91 species of solitary bees from 21 different genera, of which 24 species were cleptoparasites (i.e. from the genera *Coelioxys, Nomada*, *Sphecodes* and *Stelis*). After removing the cleptoparasites, 67 species were included in the study (Table A1), comprising 2887 individuals, of which 20.1% were found in uncut, 31.2% in cut, and 48.7% in cut-remove (Table A5, Fig. A3).

3.1. Species richness and abundance

Species richness was on average 30% higher in the cut-remove and cut treatments, compared to the uncut treatment, and the effect was sustained over the three-year study period (Tables A5 and A6, Fig. A4). The treatment effect on the species richness of bees was dependent on forb species richness, with a significantly larger effect in the cut-remove treatment (Table A6, Fig. 2). In sites with more than 10 forb species, bee species richness increased twofold along the forb species gradient in the cut-remove treatment, compared to a minor increase in the cut treatment and a negative trend in the uncut treatment

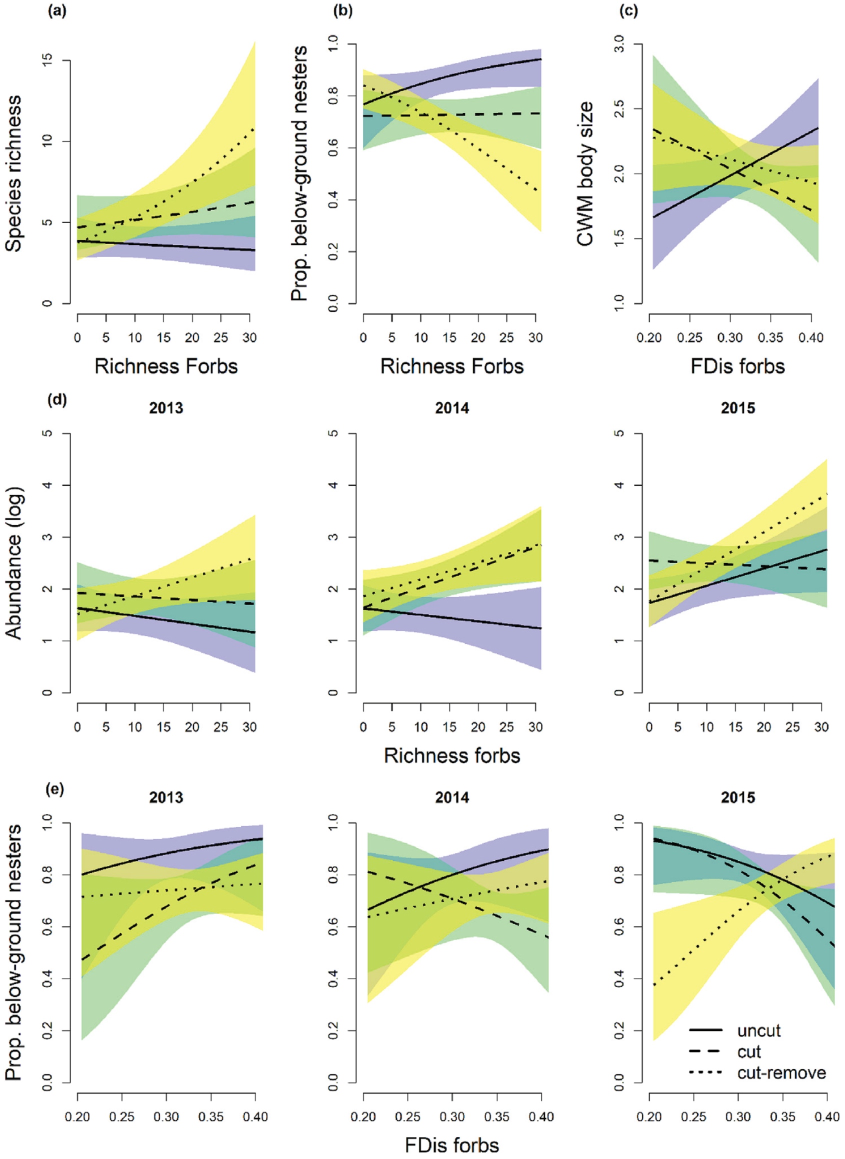

Fig. 2. The effects of treatment (uncut, cut and cut-remove) and forb species richness on (a) species richness, and (b) the proportion of below-ground nesters; (c) the effects of treatment and functional dispersion (FDis) of forbs on the community weighted mean (CWM) of body size; (d) the effects of treatment, year and forb species richness on the abundance (log (y+1)); (e) the effects of treatment, year and functional dispersion of forbs on the proportion of below-ground nesters. The shaded areas are 95% confidence intervals (CIs). Uncut (solid lines) has blue CIs, cut (dashed line) has green CIs, and cut-remove (dotted line) has yellow CIs. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

over the course of the study (treatment × forb richness: LRT = 15.38, df = 2, P < 0.001, Table A6, Fig. 2). The final model for the rarefied species richness is presented in the appendix (Tables A4, A6, Fig.A5). Bee species richness increased significantly over the three years (year × species richness: LRT = 24.63, df = 2, P < 0.001; year × rarefied richness: LRT = 48.34, df = 2, P < 0.001), but the temporal pattern did not differ between treatments. For species richness there was an estimated average increase of one species per year (Table A6, Fig. 4), and for the rarefied richness we found an increase of 18% from the first to second year, and then an increase of 32% from the second to the third year (Table A6, Fig. A5).

On average, the abundance of bees was more than twice as high in the cut-remove treatment, and almost twice as high in the cut treatment, compared to the uncut treatment over the three-year study period (Table A5, Fig. A5). Bee abundance increased along the forb richness gradient in the cut-remove treatment in all years with a threefold increase in the first two years (from low to high forb richness; 3.6–13 individuals in 2013; 5.5–16.8 individuals in 2014), followed by a nine-fold increase the last year (4.9–45.3 individuals in 2015) (Table A6, Fig. 2). In the cut treatment, forb species richness affected bee abundance positively only in the second year. In the uncut treatment, bee abundance decreased by 50% along the forb species richness gradient the first two years after treatments, and almost tripled in the third year (year × treatment × forb richness, Table A6, Fig. 2, LRT = 11.96, df = 4, P = 0.018). However, t-tests showed no significant differences in abundance between cut-remove and the other two treatments (Table A6). Both bee species richness (elevation, LRT = 10.57, df = 1, P = 0.001) and abundance (elevation, LRT = 7.9, df = 1, P = 0.005) decreased with increasing elevation (from 45 to 535 m) across all treatments (Table A6, Fig. A7).

3.2. *Functional trait groups*

The treatment effect on the relative proportions of below vs above-ground nesters depended on the forb species richness (treatment × forb richness, LRT = 20.16, df = 2, P < 0.001). Proportion of below-ground nesters was reduced by 50% along the forb richness gradient in the cut-remove treatment, compared to an estimated increase of about 1.4% in the cut treatment, and 23% increase in the uncut treatment (Table A7, Fig. 2). In sites with higher amounts of dead wood, proportion of below-ground nesters was reduced by 36% in the cut-remove treatment, and by 33% in the uncut treatment, compared to a negligible change in proportions in the cut treatment (treatment × dead wood, Table A7, Fig. 3, LRT = 6.09, df = 2, P = 0.048). The temporal treatment effect on proportion of below-ground nesters was also modified by the FDis of forbs (year × treatment × FDis forbs, LRT = 16.83, df = 4, P = 0.002). Proportion of below-ground nesters increased in the cut-remove treatment in all years with FDis of forbs. Cut-remove had generally high proportions of below-ground nesters, with minor increases the first two years, but increased from 36 to 88% during the third year, along the FDis of forbs gradient. In the cut treatment, there was almost a twofold increase the first year, before a decrease in the second and third year, by 31% and 44%, respectively, along the FDis of forbs gradient. In the uncut treatment, proportion of below-ground nesters increased in the first two years, compared to a decrease in the third year along the FDis of forbs gradient. However, the proportion of below-ground nesters was high (Table A7, Fig. 2).

FDis of body size was significantly higher in the two cut treatments compared to the uncut treatment, with a slightly higher response when the vegetation was cut and removed (treatment, Table A7, Fig. 4, LRT = 12.64, df = 2, P = 0.002). There was a significant temporal increase in FDis body size from the first to the second (23%) and from the second to the third year (21%), irrespective of treatments (year, Table A7, Fig. 4, LRT = 18.30, df = 2, P < 0.001). FDis of body size also decreased along the elevational gradient (elevation, Table A7, Fig. A7, LRT = 13.58, df = 1, P < 0.001). CWM of body size decreased with increasing amounts of dead wood (from 2.2 to 1.6 mm) (Table A7, Fig. 3, LRT = 4.54, df = 1, P = 0.03). The treatment effect on CWM of body size was modified by the FDis of forbs (Table A7, Fig. 2). The CWM was larger in both the cut treatments in areas with low functional trait variation of forbs, with a 16% decrease in cut-remove and 28% in cut, compared to a 43% increase in the uncut treatment along the FDis of forbs gradient (LRT = 8.90, df = 2, P = 0.01). Also, we found a large inter-annual variation in the temporal treatment effects on the CWM of body size in response to elevation (Table A7, Fig. A8). CWM of body size increased in all treatments with elevation in the first year, with significantly smaller bees in the cut treatment, compared to the uncut treatment at lower elevations. The second year, CWM of body size increased with elevation in the uncut treatment, whereas it was relatively unchanged in the cut treatment, compared to a decrease in the cut-remove treatment along the elevational gradient. In the third year there was a decrease in CWM of body size with elevation in the uncut treatment, and an increase from 2.0 to 2.3 mm in both the cut treatments with increased elevation (year × treatment × elevation, LRT = 11.56, df = 4, P = 0.02).

The treatment effect on FDis of tongue length was modified by source habitat areas (Table A7, Fig. 3). FDis of tongue length was higher in both the cut treatments compared to the uncut when there were few source habitat areas, and the variation in tongue length increased by 29% in the cut-remove treatment, compared to a decrease of 29% in the cut treatment with more source habitat areas available (treatment × source habitat, LRT = 9.86, df = 2, P = 0.007). In addition, we found a large inter-annual variation in the temporal treatment effects on the FDis of tongue length in response to dead wood (Table A7, Fig. 3). In the cut-remove treatment, FDis of tongue length decreased the first year with increasing amounts of dead wood (33%) but increased by 143% and 100% in the second and third year, respectively. In the cut treatment, FDis of tongue length more than doubled (127%) the first year with increasing amounts of dead wood, but decreased by 35% the second year, and increased by 25% the third year. In contrast, FDis of tongue length was lower in the uncut treatment in all years, with a slight increase the first two years and decrease in the third year, along the dead wood gradient (year × treatment × dead wood, LRT = 17.38, df = 4, P = 0.002). FDis of tongue length also decreased with elevation (Table A7, Fig. A7, LRT = 9.03, df = 1, P = 0.003).

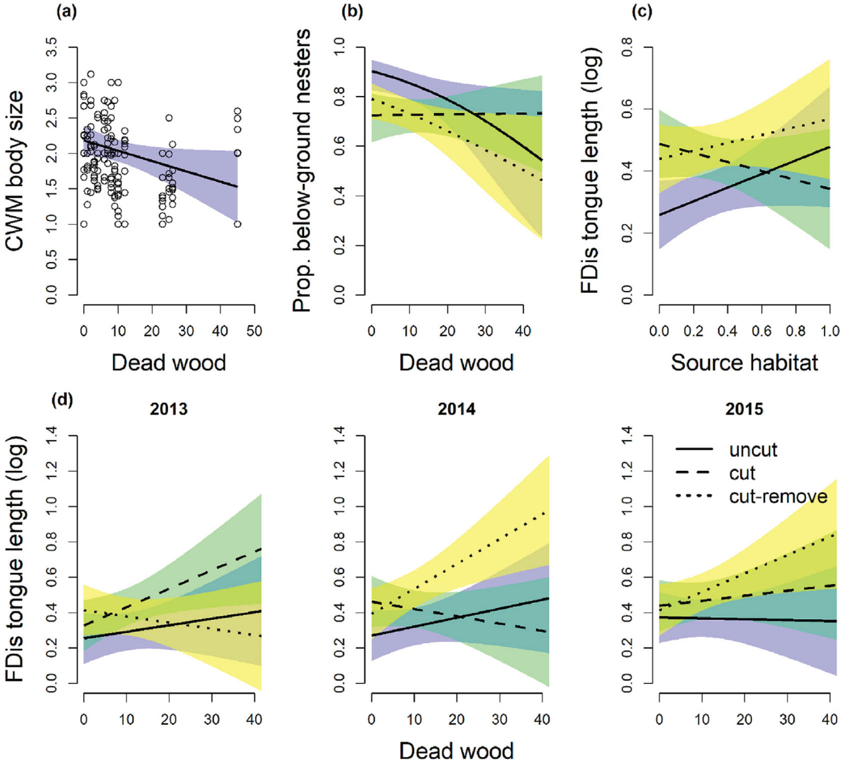

Fig. 3. (a) The effects of dead wood on the community weighted mean (CWM) of body size; (b) the effects of treatment (uncut, cut and cut-remove) and dead wood on the proportions of below-ground nesters; (c) the effects of treatment and source habitat on functional dispersion (FDis) of tongue length (log (y+1)); (d) the effects of treatment, year and dead wood on the functional dispersion of tongue length (log). The shaded areas are 95% confidence intervals (CIs). Uncut (solid lines) has blue CIs, cut (dashed line) has green CIs, and cut-remove (dotted line) has yellow CIs. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.3. *Bee species composition*

The species composition changed over the years, but we did not find any effects of the treatments on either the overall beta diversity or the turnover. Both the overall beta diversity (Beta_{JAC}) and the turnover (Beta_{JTU}) decreased over the years (Table A8). The beta diversity decreased significantly from the first to the third year (by 16%) ($LRT = 7.78$, $df = 2$, $P = 0.02$, Fig. 4). The temporal pattern of the turnover (Beta_{JTU}) was not significant ($LRT = 5.48$, $df = 2$, $P = 0.065$). Both the overall beta diversity ($LRT = 6.68$, $df = 1$, $p = 0.01$) and turnover ($LRT = 11.22$, $df = 1$, $P < 0.001$) also decreased with an increasing gradient of forb species richness, by 25% and 80%, respectively (Table A8, Fig. 4).

4. Discussion

We found that species richness and abundance of solitary bees substantially increased with time in both the cleared treatments, but the woody debris removal more than doubled the bee richness and abundance in areas with a higher forb richness. Compared to the cut treatment, removing the woody debris also had a positive effect on the functional trait diversity over time, by reducing the dominance of the most common trait group of below-ground nesters, and by increasing the trait variation of body size and tongue length within sites. In addition, the positive effect of removing the woody debris after maintenance clearing, on the taxonomic and functional trait diversity of bees, was sustained over three years post treatment. However, we observed substantial among-sites variation in the temporal treatment effects on all the bee diversity measures, and some of this variation was attributed to abiotic and biotic environmental conditions. Particularly, the biotic variables, forb species richness or FDis of forbs, were important determinants of all the measured bee community responses, except for the FDis of body size. The functional trait responses were predominantly affected by amount of dead wood and functional trait variation of forbs. Elevation was also an important determinant of all the measured bee community responses. The species composition did not differ among the treatments and became more homogenous among sites over time.

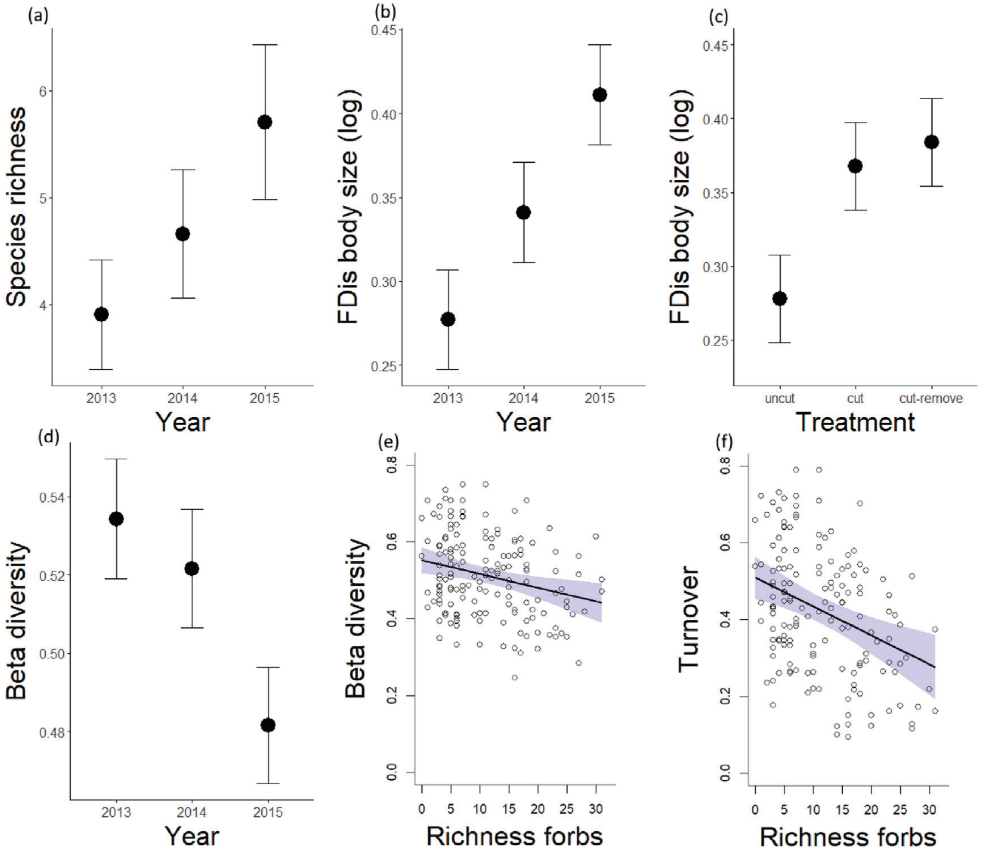

Fig. 4. The effects of year (three-year study period, 2013–2015) on (a) species richness and (b) functional dispersion (FDis) of body size (log (y+1)); (c) the effects of treatment (uncut, cut and cut-remove) on the FDis of body size (log (y+1)); (d) the effects of year on overall beta diversity ($Beta_{JAC}$). Black dots and whiskers are predicted values and 95% CI limits. (e) Overall beta diversity and (f) turnover ($Beta_{JTU}$) in response to forb species richness. The shaded areas are 95% confidence intervals (CIs).

4.1. Species richness and abundance

Our findings are in line with previous studies showing that the diversity of bees is positively associated with the presence of early-successional habitat in forest landscapes (Roberts et al., 2017), and that bee diversity increases with the diversity of flowering plants (Potts et al., 2003; Roberts et al., 2017; Rubene et al., 2015; Torné-Noguera et al., 2014). Plant species richness may also more generally enhance pollinator species richness as well as the frequency and stability of pollinator visits (Ebeling et al., 2008). The increase in richness of flower resources likely increases the habitat quality for bees by amplifying pollen and nectar rewards (Potts et al., 2003).

In forested landscapes, abundance and diversity of bees may decrease with vegetation height (Roberts et al., 2017). The regrowth in the power-line clearings depends on productivity, but within the first few years, both the cut and cut-remove treatments could potentially reach similar vegetation densities. However, we observed stronger positive effects on bee communities in the cut-remove treatment – as compared to the cut treatment – possibly due to higher amounts of solar irradiance reaching the field layer of plants and bare ground where the debris was removed.

There was an overall increase in bee richness in all treatments the third year. On site-scale, this could be due to a spillover effect; i.e. that the increase in bee abundance in the cleared treatment plots affected the entire site. Alternatively, it may simply reflect inter-annual variation, consistent with other studies showing how bee communities may display substantial spatio-temporal variation in abundance and composition among years (Tylianakis et al., 2005; Williams et al., 2001). Species richness and abundance decreased with elevation, which shows the importance of implementing conservation plans for solitary bees within their distributional range at lower elevations (Hoiss et al., 2012).

4.2. Functional trait groups

The dominance of the most common trait group of below-ground nesters was reduced and the trait variation of body size and tongue-length was increased in both the cut and the cut-remove treatment plots, resulting in more functionally diverse bee communities in these treatments over time, dependent on the environmental context. Two of the functional trait measures were dependent on richness and FDis of forbs. These findings corroborate the importance of flower resources as an important predictor of both species and functional community structure (Gathmann et al., 1994) and demonstrate that a higher functional diversity of bees can persist in anthropogenic habitats, provided that host plants are available to them.

4.2.1. Above vs below-ground nesters

Both the cut-remove and cut treatments had a positive effect on bee species nesting above-ground, which are less common than below-ground nesters. We expected the woody debris removal to attract a larger portion of the below-ground nesters (Rivers et al., 2018), due to the sun exposed bare ground, and we expected the woody debris left on the ground to attract a larger portion of the above-ground nesters, due to available nesting substrates (i.e. hollow stems and dead wood). In contrast, there was a positive effect of woody debris removal on the proportion of above-ground nesters that was further accentuated by high species richness of forbs and dead wood. Below-ground nesting bees have been found to prefer nesting sites with high sun exposure (Willmer, 2011). However, the overall light availability was probably greater in the clearings (in all the treatments) compared to the closed-canopy adjacent forests. In addition, below-ground nesters may be more dependent on the specific soil properties (Potts et al., 2005), than on sun exposure. The amount of dead wood was expected to have a positive effect on the above-ground nesters, since nesting sites are considered a limiting factor for these bees (Steffan-Dewenter and Schiele, 2008). Thus, for the above-ground nesters the amount of dead wood was potentially important when woody debris was removed due to the absence of other nesting substrates. Another explanation could be that the above-ground nesters were attracted to food resources in the power-line clearings and nesting substrates were more likely to be used when sufficient flower resources were present. However, there was a temporal positive effect on the above-ground nesters in the second and third year, when leaving the woody debris to decay in areas of higher functional trait variation of forbs. A higher trait variation in forbs reflects a floral resource complementarity throughout the season in addition to other flower traits of importance for e.g. specialist species, which together with available nesting substrate and less competition from below-ground nesters may have enhanced the proportion of above-ground nesters over time. Above-ground nesters may also respond more negatively to isolation from natural or semi-natural habitats compared to below-ground nesters (Williams et al., 2010), which likely explains the delayed positive effect in the temporal pattern.

4.2.2. Body size

We found a treatment effect on the FDis of body size, with a markedly higher variation in size in both the cut-remove and cut treatments, compared to the uncut. Bees are central-place foragers, but the altered habitats in the forest opening may provide valuable resources, which likely attracts species of different foraging ranges. Larger bees may show a behavioral response to the treatments, whereas the smaller species are more likely to use the habitat for nesting as well (Greenleaf et al., 2007). The FDis of body size also increased over time, which may be ascribed the ability of colonizing the altered habitats by bees of different body sizes. Larger bodied bees are found to have a better dispersal ability, compared to smaller sized bees (Williams et al., 2010). The community weighted mean of body size decreased where there was a larger functional trait variation of forbs in both the cleared treatments, and the mean body size decreased with amount of dead wood. Smaller bees require more diverse resources per unit area compared to larger species with greater foraging distances (Murray et al., 2009). Cleared treatments are likely to provide heterogenous resources preferred by smaller sized bees, by provision of functionally diverse foraging resources and available dead wood with preferred cavities for nesting (Sydenham et al., 2016).

4.2.3. Tongue length

There was a temporal treatment effect on the FDis of tongue length with the presence of dead wood. The first year after maintenance clearing there was a positive effect on the tongue length variation when woody debris was left on the ground, compared to a negligible effect in the next years. But where the woody debris was removed, we found the opposite pattern with a negative response on tongue length variation the first year and a positive effect in the second and third year. According to Hass et al. (2018), a high structural and floral diversity may be advantageous for long-tongued bees. Suggesting how the removal of woody debris enhances the occurrence of suitable floral resources for long-tongued bees, in addition to creating a preferred higher structural vegetation, in the second and third season after clearing. The FDis of tongue-length was also dependent on source habitats, with a relatively higher positive effect on tongue length variation in the cut-remove treatment when more source habitat areas were available. More complex landscapes with ample adjacent source habitats may ensure a constant spillover of both plants and insects (Carrié et al., 2017). Likely, the woody debris removal facilitated immigration and subsequent recolonization of the power-line clearings from surrounding habitats, attracting species with a larger variety in tongue length.

4.3. Species composition

In boreal forest landscapes, typical bee habitats of early succession are short-lived and ephemeral (Moretti et al., 2009; Rubene et al., 2015). As the plant succession progresses these habitats quickly lose their value for many solitary bees (Moretti et al., 2009). To sustain viable metapopulations, bees therefore have to locate and recolonize early successional habitats like forest clearings, when they become available. We found that the bee communities became more similar over the three years, resulting in a homogenization at the regional scale. The decrease in beta diversity, together with the increase in bee species richness in the cut-remove and cut treatments over time may imply that the power-line clearings gradually attracted a larger portion of the regional species pool. Our finding accords with Griffin et al. (2017) who found that the main driver of wild bee communities was the gradual accumulation of species. Moreover, a temporal decrease in beta diversity may signify a process where formerly rare or absent species become more common (Socolar et al., 2016), highlighting the potential conservation value of the habitats in the power-line clearings.

As for species richness, we found no treatment effects on beta-diversity or turnover, which may be ascribed to some “spillover effect” between the treatments. To a certain extent, within-site differences in species composition could be masked because treatment plots were placed within distances of averagely 120 m apart, which is within the foraging range of at least the largest bee species (Franzén et al., 2009; Gathmann et al., 1994; Greenleaf et al., 2007). The beta diversity and turnover also decreased with forb species richness across the treatments in all years, which may indicate that the availability of flower resources attracted a larger portion of species from the regional species pool. Bees may rapidly colonize restored habitats (M'Gonigle et al., 2015) and we may expect the early successional habitats in the power-line clearings to attract additional species from the surrounding landscape. Consequently, species' occupancy in subsequent years is the net outcome of the ability of bees to colonize vacant sites and persist in already colonized sites over time. Thus, the increased richness and abundance, in addition to a reduced beta diversity, suggests that the power line clearings may act as temporary refugia for bees at a landscape scale at least the first three years after clearing.

5. Conclusions and management implications

Compared to the current routine practice, we found that woody debris removal promoted a stronger positive increase in species richness and abundance in addition to a larger variety of functional traits within bee communities, which was sustained over the three-year study period. Likely, removal of debris improved the habitat quality through allowing more sunlight to reach the ground and field layer vegetation, which leads to enhanced floral resources (Pickett and White, 1985), in addition to a favorable alteration of the microclimate for bees (Westrich, 1996). Woody debris removal increases sun-exposure, resulting in a warmer and drier field-layer (Weng et al., 2007), compared to when woody debris is left to decay.

However, the occurrence of bees from the regional species pool increased in the power-lines during the three-year study period, irrespective of treatment type. This suggests that power-line clearings – when reset to early succession with or without woody debris removal – may benefit bee populations on a regional scale due to an increased habitat quality, with spillover effects through migration to adjacent fields and forests in the surrounding landscape (Morandin and Kremen, 2013; Roberts et al. 2017). Moreover, a more frequent clearing of productive sites in power-line clearings may enhance plant species associated with semi-natural grasslands habitat (Eldegard et al., 2017). Consequently, habitat interventions aimed at promoting early successional vegetation should be indicative of improving the conditions for solitary bees through provision of floral resources. Also, we found that positive effects of clearing were sustained at least over the course of three years. Power-line clearings on productive soils can have substantial regrowth a few years after cutting, which rapidly develop into dense vegetation with reduced light conditions at the ground and field layer. Thus, future studies should assess temporal effects of habitat interventions beyond three years.

Our results demonstrate that adjustments to the standard management practice (i.e. implementation of woody debris removal) may enhance the positive effects of maintenance clearings on the habitat quality for bees over time. But this study was only focusing on enhancing the habitat conditions for solitary bees. Removal of woody debris is not necessarily positive for all other organisms, such as saproxylic species. For example, harvesting biomass from the power-line clearings for biofuel may have a larger negative impact on the total biodiversity of the clearings. Whereas leaving the woody debris collected in piles on site, as in our experiment, will create a more heterogenous environment, potentially benefitting both bees and species dependent on dead wood, thereby increasing the conservation value of the habitat interventions.

Because managers typically have limited budgets, we recommend targeting the more costly practice of removing the woody debris after cutting to areas where the potential effect – in terms of enhanced bee species and functional diversity – is highest; i.e. to areas with a high forb species richness, with available dead wood and source habitats in the surrounding landscape, and at lower elevations. Site-specific local conservation efforts may contribute to maintain regional species and functional diversity along already existing power-line corridors in otherwise forested landscapes. The woody debris removal may have a positive impact on the provisioning of pollination functions at a landscape scale through enhancing the persistence of bee populations between seasons and thus contributing to more stable bee communities. Moreover, the extensive networks of power-line clearings may, given appropriate management, function as highly valuable habitats, and should therefore be included in conservation plans.

Author contribution

MS performed the analyses, wrote the first draft of the manuscript and led the writing of the manuscript. KE and SRM designed and initiated the experiment. MAKS identified all the solitary bees. All authors discussed the results and contributed to previous drafts and the final manuscript.

Declaration of competing interest

None declared.

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Appendix A. Supplementary data

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Appendix

Global Ecology and Conservation

Title: **"Conservation of solitary bees in power-line clearings: Sustained increase in habitat quality through woody debris removal "**

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Appendix: Supplementary material

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Table A1: List of solitary bees and the corresponding functional traits; Nesting preference, i.e. below-ground nesters (1) vs. above-ground nesters (0); Mean bee body size, the intertegular distance (ITD), rounded off to nearest mm (1-4); The tongue length (short vs. long), cleptoparasitic (TRUE, FALSE).

Number	Family	Species	Short	Nesting preference	ITD (mm)	Tongue-length	Cleptoparasite
1	Andrenidae	*Andrena bicolor*	*Andrebicol*	1	2	2.06	FALSE
2	Andrenidae	*Andrena carantonica*	*Andrecaran*	1	3	3.04	FALSE
3	Andrenidae	*Andrena cineraria*	*Andreciner*	1	3	3.04	FALSE
4	Andrenidae	*Andrena clarkella*	*Andreclark*	1	3	3.04	FALSE
5	Andrenidae	*Andrena coitana*	*Andrecoita*	1	2	2.06	FALSE
6	Andrenidae	*Andrena denticulata*	*Andredenti*	1	2	2.06	FALSE
7	Andrenidae	*Andrena fucata*	*Andrefucat*	1	2	2.06	FALSE
8	Andrenidae	*Andrena fulvida*	*Andrefulvi*	1	2	2.06	FALSE
9	Andrenidae	*Andrena fuscipes*	*Andrefusci*	1	2	2.06	FALSE
10	Andrenidae	*Andrena haemorrhoa*	*Andrehaemo*	1	3	3.04	FALSE
11	Andrenidae	*Andrena helvola*	*Andrehelvo*	1	2	2.06	FALSE
12	Andrenidae	*Andrena intermedia*	*Andreinter*	1	2	2.06	FALSE
13	Andrenidae	*Andrena lapponica*	*Andrelappo*	1	3	3.04	FALSE
14	Andrenidae	*Andrena nigriceps*	*Andrenigri*	1	2	2.06	FALSE
15	Andrenidae	*Andrena praecox*	*Andrepraec*	1	2	2.06	FALSE
16	Andrenidae	*Andrena ruficrus*	*Andrerufic*	1	2	2.06	FALSE
17	Andrenidae	*Andrena scotica*	*Andrescoti*	1	3	3.04	FALSE
18	Andrenidae	*Andrena semilaevis*	*Andresemil*	1	1	1.06	FALSE
19	Andrenidae	*Andrena subopaca*	*Andresubop*	1	2	2.06	FALSE
20	Andrenidae	*Andrena tibialis*	*Andretibia*	1	3	3.04	FALSE
21	Andrenidae	*Andrena vaga*	*Andrevaga*	1	3	3.04	FALSE
22	Apidae	*Anthophora furcata*	*Anthofurca*	0	3	6.12	FALSE
23	Apidae	*Ceratina cyanea*	*Ceratcyane*	0	1	2.13	FALSE
24	Megachilidae	*Chelostoma campanularum*	*Chelocampa*	0	1	1.87	FALSE
25	Megachilidae	*Chelostoma florisomne*	*Cheloflori*	0	2	3.64	FALSE
26	Colletidae	*Colletes cunicularius*	*Collecunic*	1	4	3.25	FALSE

27	Colletidae	*Colletes daviesanus*	*Colledavie*	1	3	2.47	FALSE
28	Colletidae	*Colletes succinctus*	*Collesucci*	1	3	2.47	FALSE
29	Halictidae	*Dufourea dentiventris*	*Dufoudenti*	1	2	2.68	FALSE
30	Halictidae	*Halictus rubicundus*	*Halicrubic*	1	2	2.68	FALSE
31	Halictidae	*Halictus tumulorum*	*Halictumul*	1	1	1.38	FALSE
32	Megachilidae	*Heriades truncorum*	*Heriatrunc*	0	2	3.64	FALSE
33	Megachilidae	*Hoplitis claviventris*	*Hopliclavi*	0	2	3.64	FALSE
34	Megachilidae	*Hoplitis tuberculata*	*Hoplituber*	0	2	3.64	FALSE
35	Colletidae	*Hylaeus angustatus*	*Hylaeangus*	0	1	0.86	FALSE
36	Colletidae	*Hylaeus annulatus*	*Hylaeannul*	0	1	0.86	FALSE
37	Colletidae	*Hylaeus brevicornis*	*Hylaebrevi*	0	1	0.86	FALSE
38	Colletidae	*Hylaeus communis*	*Hylaecommu*	0	1	0.86	FALSE
39	Colletidae	*Hylaeus confusus*	*Hylaeconfu*	0	1	0.86	FALSE
40	Colletidae	*Hylaeus hyalinatus*	*Hylaehyali*	0	1	0.86	FALSE
41	Colletidae	*Hylaeus incongruus*	*Hylaeincon*	0	2	1.67	FALSE
42	Colletidae	*Hylaeus rinki*	*Hylaerinki*	0	1	0.86	FALSE
43	Halictidae	*Lasioglossum albipes*	*Lasioalbip*	1	2	2.68	FALSE
44	Halictidae	*Lasioglossum calceatum*	*Lasiocalce*	1	2	2.68	FALSE
45	Halictidae	*Lasioglossum fratellum*	*Lasiofrate*	1	1	1.38	FALSE
46	Halictidae	*Lasioglossum fulvicorne*	*Lasiofulvi*	1	1	1.38	FALSE
47	Halictidae	*Lasioglossum leucopus*	*Lasioleuco*	1	1	1.38	FALSE
48	Halictidae	*Lasioglossum morio*	*Lasiomorio*	1	1	1.38	FALSE
49	Halictidae	*Lasioglossum rufitarse*	*Lasiorufit*	1	1	1.38	FALSE
50	Melittidae	*Macropis europaea*	*Macroeurop*	1	3	3.04	FALSE
51	Megachilidae	*Megachile alpicola*	*Megacalpic*	0	3	5.37	FALSE
52	Megachilidae	*Megachile centuncularis*	*Megaccentu*	0	3	5.37	FALSE
53	Megachilidae	*Megachile circumcincta*	*Megaccircu*	1	3	5.37	FALSE
54	Megachilidae	*Megachile lapponica*	*Megaclappo*	0	3	5.37	FALSE
55	Megachilidae	*Megachile nigriventris*	*Megacnigri*	0	4	7.08	FALSE

56	Megachilidae	*Megachile versicolor*	*Megacversi*	0	3	5.37	FALSE
57	Megachilidae	*Megachile willughbiella*	*Megacwillu*	0	4	7.08	FALSE
58	Melittidae	*Melitta haemorrhoidalis*	*Melithaemo*	1	3	3.04	FALSE
59	Megachilidae	*Osmia bicornis*	*Osmiabicor*	0	3	5.37	FALSE
60	Megachilidae	*Osmia caerulescens*	*Osmiacaeru*	0	2	3.64	FALSE
61	Megachilidae	*Osmia inermis*	*Osmiainerm*	0	3	5.37	FALSE
62	Megachilidae	*Osmia leaiana*	*Osmialeaia*	0	3	5.37	FALSE
63	Megachilidae	*Osmia nigriventris*	*Osmianigri*	0	3	5.37	FALSE
64	Megachilidae	*Osmia parietina*	*Osmiaparie*	0	2	3.64	FALSE
65	Megachilidae	*Osmia uncinata*	*Osmiauncin*	0	2	3.64	FALSE
66	Andrenidae	*Panurgus banksianus*	*Panurbanks*	1	2	2.06	FALSE
67	Andrenidae	*Panurginus romani*	*Panurroman*	1	2	2.06	FALSE
68	Megachilidae	*Coelioxys conica*	*Coeliconic*	-	-	-	TRUE
69	Megachilidae	*Coelioxys inermis*	*Coeliinerm*	-	-	-	TRUE
70	Megachilidae	*Coelioxys lanceolata*	*Coelilance*	-	-	-	TRUE
71	Megachilidae	*Coelioxys rufescens*	*Coelirufes*	-	-	-	TRUE
72	Megachilidae	*Coelioxys elongata*	*Coelielong*	-	-	-	TRUE
73	Halictidae	*Sphecodes ferruginatus*	*Sphecoferrug*	-	-	-	TRUE
74	Halictidae	*Sphecodes geoffrellus*	*Sphecogeoff*	-	-	-	TRUE
75	Halictidae	*Sphecodes hyalinatus*	*Sphecohyali*	-	-	-	TRUE
76	Halictidae	*Sphecodes crassus*	*Sphecocrassu*	-	-	-	TRUE
77	Halictidae	*Sphecodes pellucidus*	*Sphecopellu*	-	-	-	TRUE
78	Megachilidae	*Stelis ornatula*	*Steliornat*	-	-	-	TRUE
79	Apidae	*Nomada alboguttata*	*Nomadalbog*	-	-	-	TRUE
80	Apidae	*Nomada flava*	*Nomadflava*	-	-	-	TRUE
81	Apidae	*Nomada flavoguttata*	*Nomadflavo*	-	-	-	TRUE
82	Apidae	*Nomada fulvicornis*	*Nomadfulvi*	-	-	-	TRUE
83	Apidae	*Nomada lathburiana*	*Nomadlathb*	-	-	-	TRUE
84	Apidae	*Nomada marshamella*	*Nomadmarsh*	-	-	-	TRUE

85	Apidae	*Nomada opaca*	*Nomadopaca*	-	-	-	TRUE
86	Apidae	*Nomada roberjeotiana*	*Nomadroberj*	-	-	-	TRUE
87	Apidae	*Nomada leucophthalma*	*Nomadleucop*	-	-	-	TRUE
88	Apidae	*Nomada obscura*	*Nomadobscu*	-	-	-	TRUE
89	Apidae	*Nomada panzeri*	*Nomadpanze*	-	-	-	TRUE
90	Apidae	*Nomada ruficornis*	*Nomadrufic*	-	-	-	TRUE
91	Apidae	*Nomada rufipes*	*Nomadrufipe*	-	-	-	TRUE

Table A2: Functional traits of forbs**.** Description of the functional traits and the value per trait.

No.	Trait	Value/No. categories	Description
1.	Inflorescence	3	A: singular flowers B: singular flowers in a group C: multi flowers/pseudanthium
2.	Flower colors	16	color variations
3.	Exposed nectar/pollen	2	Exposed / not exposed
4.	Nectar tube	3	Short / medium / long
5.	Pollen per flower	2	few: less than 4 anthers per flower many: more than 4 anthers per flower
6.	Flowering period	4	vår = spring fso = early summer mso = mid summer sso = late summer
7.	Height	6.5 – 125	average potential height (cm)
8.	Floral symmetry	2	Actinomorphic / zygomorphic
9.	Lifenastrategy	3	Annual / biennial / perennial

Table A3: List of forb species and the corresponding functional traits; 9 functional traits that were used to calculate the functional diversity indices (i.e. functional dispersion). Nomenclature follows Artsdatabanken (2015)*. Traits are retained from Lid and Lid (2005)**.

Family	**Species**	**Functional traits**								
		Inflore-scence	**Flower colors**	**Life-strategy**	**Symmetry**	**nectar/ pollen**	**Nectar tube**	**Pollen per flower**	**First flowering**	**Average height (cm)**
Apiaceae	*Angelica sylvestris*	C	white	perennial	actinomorphic	exposed	no	few	mso	125
Apiaceae	*Anthriscus sylvestris*	C	white	perennial	actinomorphic	exposed	no	many	fso	100
Apiaceae	*Peucedanum palustre*	C	white	biennial	actinomorphic	exposed	no	many	mso	80
Apiaceae	*Pimpinella saxifraga*	C	white	perennial	actinomorphic	exposed	no	many	fso	35
Asparagaceae	*Convallaria majalis*	B	white	perennial	actinomorphic	concealed	no	few	vår	20
Asteraceae	*Achillea millefolium*	C	white-pink	perennial	actinomorphic	exposed	no	few	mso	35
Asteraceae	*Antennaria dioica*	C	white-pink	perennial	actinomorphic	exposed	no	few	fso	15
Asteraceae	*Carduus vulgare*	C	purple	biennial	actinomorphic	exposed	short	few	mso	95
Asteraceae	*Cirsium arvense*	C	purple	perennial	actinomorphic	exposed	short	few	mso	80
Asteraceae	*Cirsium heterophyllum*	C	purple	perennial	actinomorphic	exposed	short	few	mso	100
Asteraceae	*Cirsium palustre*	C	purple	biennial	actinomorphic	exposed	short	few	mso	125
Asteraceae	*Gnaphalium sp*	C	brown	perennial	actinomorphic	exposed	short	few	mso	27.5
Asteraceae	*Hieracium lactucella*	C	yellow	perennial	actinomorphic	exposed	long	few	fso	20
Asteraceae	*Hieracium pilosella sp*	C	yellow	perennial	actinomorphic	exposed	long	few	fso	17.5
Asteraceae	*Hieracium sp*	C	yellow	perennial	actinomorphic	exposed	long	few	NA	NA
Asteraceae	*Hieracium Sylvatica sp*	C	yellow	perennial	actinomorphic	exposed	long	few	fso	37.5
Asteraceae	*Hierarcium umbellatum*	C	yellow	perennial	actinomorphic	exposed	long	few	mso	42.5
Asteraceae	*Hierarcium vulgatum*	C	yellow	perennial	actinomorphic	exposed	long	few	fso	50
Asteraceae	*Hypochaeris maculata*	C	yellow	perennial	actinomorphic	exposed	long	many	fso	40
Asteraceae	*Lapsana communis*	C	yellow	perennial	actinomorphic	exposed	long	few	mso	75
Asteraceae	*Leontodon autumnale*	C	yellow	perennial	actinomorphic	exposed	long	few	mso	22.5
Asteraceae	*Leucanthemum vulgare*	C	white-yellow	perennial	actinomorphic	exposed	short	few	fso	45
Asteraceae	*Omaloteca sylvatica*	C	brown	perennial	actinomorphic	exposed	long	few	mso	27.5
Asteraceae	*Solidago canadensis*	C	yellow	perennial	actinomorphic	exposed	long	many	sso	100
Asteraceae	*Solidago virgaurea*	C	yellow	perennial	actinomorphic	exposed	long	many	mso	52.5
Asteraceae	*Tussilago farfara*	C	yellow	perennial	actinomorphic	exposed	long	few	vår	12.5

Asteraceae	*Tanacetum vulgaris*	C	yellow	perennial	actinomorphic	exposed	short	few	mso	95
Asteraceae	*Taraxacum sp*	C	yellow	perennial	actinomorphic	exposed	long	many	NA	22.5
Balsaminaceae	*Impatiens noli-tangere*	A	yellow	annual	zygomorphic	concealed	long	few	mso	55
Brassicaceae	*Cardamine amara*	B	white	perennial	actinomorphic	exposed	short	few	vår	27.5
Brassicaceae	*Cardamine dentata*	B	white-lilac	perennial	actinomorphic	exposed	short	few	fso	30
Brassicaceae	*Cardamine pratensis*	B	white-lilac	perennial	actinomorphic	exposed	short	few	vår	35
Brassicaceae	*Thlaspi caerulescens*	C	white-pink	perennial	actinomorphic	exposed	Short	many	vår	20
Campanulaceae	*Campanula persicifolia*	A	blue	perennial	actinomorphic	exposed	no	few	mso	55
Campanulaceae	*Campanula rotundifólia*	A	blue	perennial	actinomorphic	exposed	no	few	fso	30
Caprifoliaceae	*Succisa pratensis*	C	blue-violet-lilac	perennial	actinomorphic	exposed	long	few	sso	40
Caprifoliaceae	*Valeriana sambucifolia*	C	white-pink	perennial	zygomorphic	exposed	long	few	fso	110
Carophyllaceae	*Carophyllaceae sp*	A	white	perennial	actinomorphic	exposed	no	many	NA	NA
Carophyllaceae	*Cerastium arvénse*	A	white	perennial	actinomorphic	exposed	no	many	fso	20
Carophyllaceae	*Cerastium fontanum*	A	white	perennial	actinomorphic	exposed	no	many	fso	25
Carophyllaceae	*Moehringia trinervia*	A	white	annual	actinomorphic	exposed	no	many	fso	12.5
Carophyllaceae	*Silene dioica*	A	pink	perennial	actinomorphic	exposed	long	many	fso	40
Carophyllaceae	*Silene rupestris*	A	white	annual	actinomorphic	exposed	short	many	mso	12.5
Carophyllaceae	*Stellaria graminea*	A	white	perennial	actinomorphic	exposed	no	many	fso	25
Carophyllaceae	*Stellaria longifolia*	A	white	perennial	actinomorphic	exposed	no	many	fso	22.5
Carophyllaceae	*Stellaria media*	A	white	annual/ biennial	actinomorphic	exposed	no	many	vår	22
Carophyllaceae	*Stellaria nemorum*	A	white	perennial	actinomorphic	exposed	no	many	fso	30
Cichoriaceae	*Mycelis muralis*	A	yellow	perennial	actinomorphic	exposed	long	few	mso	70
Clusiaceae	*Hypericum maculatum*	B	yellow	perennial	actinomorphic	exposed	no	many	mso	85
Clusiaceae	*Hypericum perforatum*	B	yellow	perennial	actinomorphic	exposed	no	many	mso	50
Convallariaceae	*Maianthemum bifolium*	B	white	perennial	actinomorphic	exposed	no	few	vår	12.5
Cornaceae	*Chamaepericlymenum suecicum*	A	white	perennial	actinomorphic	exposed	no	many	fso	12.5
Crassulaceae	*Sedum telephium*	C	white-green	perennial	actinomorphic	exposed	no	many	mso	35
Dipsacaceae	*Knautia arvensis*	C	pink	perennial	actinomorphic	exposed	long	few	mso	55
Ericaceae	*Pyrola rotundifolia*	B	white-pink	perennial	actinomorphic	concealed	no	many	fso	20
Ericaceae	*Pyrola media*	B	white-pink	perennial	actinomorphic	concealed	no	many	fso	20
Fabaceae	*Lathyrus linifolius*	A	purple-blue	perennial	zygomorphic	concealed	long	few	vår	20

Fabaceae	*Lathyrus pratensis*	B	yellow	perennial	zygomorphic	concealed	long	few	fso	40
Fabaceae	*Lathyrus vernus*	B	purple	perennial	zygomorphic	concealed	long	few	vår	30
Fabaceae	*Trifolium medium*	C	pink	perennial	zygomorphic	concealed	long	few	fso	35
Fabaceae	*Trifolium pratense*	C	pink	perennial	zygomorphic	concealed	long	few	fso	32.5
Fabaceae	*Trifolium repens*	C	white-pink	perennial	zygomorphic	concealed	long	few	fso	25
Fabaceae	*Vicia cracca*	B	blue-violet	perennial	zygomorphic	concealed	long	few	fso	50
Fabaceae	*Vicia sepium*	B	purple	perennial	zygomorphic	concealed	long	few	fso	45
Fabaceae	*Vicia sp*	B	pink-purple-blue	perennial	zygomorphic	concealed	long	few	NA	NA
Geraniaceae	*Geranium sylvaticum*	A	purple	perennial	actinomorphic	exposed	short	many	fso	50
Lamiaceae	*Ajuga pyramidalis*	B	blue-violet	perennial	zygomorphic	exposed	long	few	vår	15
Lamiaceae	*Clinopodium vulgare*	A	pink	perennial	zygomorphic	exposed	long	few	mso	40
Lamiaceae	*Galeopsis sp*	B	purple-pink-white	annual	zygomorphic	concealed	long	few	mso	NA
Lamiaceae	*Glechoma hederacea*	A	blue-violet	perennial	zygomorphic	concealed	long	few	vår	17.5
Lamiaceae	*Lamium purpureum*	A	pink	annual	zygomorphic	concealed	long	few	vår	17.5
Lamiaceae	*Lamium sp*	A	purple-pink	annual	zygomorphic	concealed	long	few	vår	22.5
Lamiaceae	*Prunella vulgaris*	B	blue-violet	perennial	zygomorphic	concealed	long	few	mso	15
Lamiaceae	*Scutellaria gallericulata*	A	blue-violet	perennial	zygomorphic	concealed	long	few	mso	22.5
Lamiaceae	*Stachys palustris*	B	pink	perennial	zygomorphic	concealed	long	few	mso	60
Lamiaceae	*Stachys sylvatica*	B	red-violet	perennial	zygomorphic	concealed	long	few	mso	75
Melanthiaceae	*Paris quadrifolia*	A	yellow-green	perennial	actinomorphic	exposed	no	many	vår	25
Onagraceae	*Chamerion angustifolium*	B	purple	perennial	actinomorphic	exposed	short	many	mso	125
Onagraceae	*Circaea alpina*	B	white	perennial	zygomorphic	exposed	short	few	fso	12.5
Onagraceae	*Epilobium montanum*	A	pink	perennial	actinomorphic	exposed	short	few	mso	60
Onagraceae	*Epilobium sp*	A	pink	perennial	actinomorphic	exposed	short	few	NA	NA
Orchidaceae	*Dactylorhiza maculata*	B	white-purple	perennial	zygomorphic	concealed	long	few	fso	25
Orchidaceae	*Epipactis atrorubens*	B	red-violet	perennial	zygomorphic	exposed	long	few	mso	35
Orchidaceae	*Listera ovata*	B	green	perennial	zygomorphic	exposed	long	few	fso	40
Orchidaceae	*Platanthera bifolia*	B	white	perennial	zygomorphic	concealed	long	few	fso	32.5
Orobanchaceae	*Euphrasia sp*	A	white-lilac	annual	zygomorphic	exposed	long	few	NA	NA
Orobanchaceae	*Euphrasia stricta*	A	white-lilac	annual	zygomorphic	exposed	long	few	mso	15
Orobanchaceae	*Melampyrum pratense*	A	yellow	annual	zygomorphic	exposed	long	few	fso	25

Orobanchaceae	*Melampyrum sp*	A	yellow	annual	zygomorphic	exposed	long	few	NA	NA
Orobanchaceae	*Melampyrum sylvaticum*	A	yellow	annual	zygomorphic	concealed	long	few	fso	25
Oxalidaceae	*Oxalis acetosella*	A	white-lilac	perennial	actinomorphic	exposed	no	many	vår	7.5
Plantaginaceae	*Linaria vulgaris*	B	yellow	perennial	zygomorphic	concealed	long	few	mso	42.5
Plantaginaceae	*Plantago lanceolata*	C	brown	perennial	actinomorphic	exposed	short	few	fso	30
Plantaginaceae	*Veronica beccabunga*	A	blue	perennial	actinomorphic	exposed	no	few	fso	25
Plantaginaceae	*Veronica chamaedrys*	A	blue	perennial	actinomorphic	exposed	no	few	vår	17.5
Plantaginaceae	*Veronica officinalis*	B	blue	perennial	actinomorphic	exposed	no	few	fso	20
Plantaginaceae	*Veronica scutellata*	A	white-lilac	perennial	actinomorphic	exposed	no	few	fso	17.5
Polygalaceae	*Polygala sp*	B	blue-violet	perennial	zygomorphic	concealed	long	few	NA	17.5
Polygalaceae	*Polygala vulgaris*	B	blue-violet	perennial	zygomorphic	concealed	long	few	fso	20
Polygonaceae	*Bistorta vivipara*	B	white	perennial	actinomorphic	exposed	no	few	fso	17.5
Polygonaceae	*Rumex acetosa*	B	red	perennial	actinomorphic	exposed	no	few	fso	50
Polygonaceae	*Rumex acetosella*	B	red	perennial	actinomorphic	exposed	no	few	fso	17.5
Primulaceae	*Lysimachia vulgaris*	B	yellow	perennial	actinomorphic	exposed	no	few	mso	100
Primulaceae	*Trientalis europaea*	A	white	perennial	actinomorphic	exposed	no	many	fso	12.5
Ranunculaceae	*Actaea spicata*	B	white	perennial	actinomorphic	exposed	no	many	fso	50
Ranunculaceae	*Anemone nemorosa*	A	white	perennial	actinomorphic	exposed	short	many	vår	20
Ranunculaceae	*Caltha palustris*	A	yellow	perennial	actinomorphic	exposed	no	many	vår	22.5
Ranunculaceae	*Hepatica nobilis*	A	blue	perennial	actinomorphic	exposed	no	many	vår	12.5
Ranunculaceae	*Ranunculus acris*	A	yellow	perennial	actinomorphic	exposed	no	many	fso	47.5
Ranunculaceae	*Ranunculus auricomus*	A	yellow	perennial	actinomorphic	exposed	no	many	vår	15
Ranunculaceae	*Ranunculus repens*	A	yellow	perennial	actinomorphic	exposed	no	many	fso	27.5
Ranunculaceae	*Ranunculus sp*	A	yellow	perennial	actinomorphic	exposed	no	many	NA	NA
Rosaceae	*Comarum palustre*	A	red	perennial	actinomorphic	exposed	no	many	fso	30
Rosaceae	*Filipendula ulmaria*	C	white	perennial	actinomorphic	exposed	no	many	fso	100
Rosaceae	*Fragaria ananássa*	A	white	perennial	actinomorphic	exposed	no	many	fso	22.5
Rosaceae	*Fragaria vesca*	A	white	perennial	actinomorphic	exposed	no	many	vår	12.5
Rosaceae	*Geum rivale*	A	red-brown	perennial	actinomorphic	exposed	no	many	vår	30
Rosaceae	*Geum urbanum*	A	yellow	perennial	actinomorphic	exposed	no	many	fso	50
Rosaceae	*Potentilla erecta*	A	yellow	perennial	actinomorphic	exposed	no	many	fso	20

Rubiaceae	*Galium boreale*	B	white	perennial	actinomorphic	exposed	no	few	mso	27.5
Rubiaceae	*Galium palustre*	B	white	perennial	actinomorphic	exposed	no	few	fso	25
Rubiaceae	*Galium uliginosum*	B	white	perennial	actinomorphic	exposed	no	few	fso	22.5
Rubiaceae	*Galium verum*	B	yellow	perennial	actinomorphic	exposed	short	few	fso	40
Saxifragaceae	*Chrysosplenium alternifolium*	B	yellow-green	perennial	actinomorphic	exposed	no	many	vår	12.5
Scrophulariaceae	*Scrophularia nodosa*	B	brown-red	perennial	zygomorphic	concealed	short	few	mso	70
Solanaceae	*Solanum dulcamara*	B	violet	perennial	actinomorphic	exposed	no	many	fso	110
Urticaceae	*Urtica dioica*	B	green	perennial	actinomorphic	exposed	no	few	fso	65
Urticaceae	*Urtica sp*	B	green	perennial	actinomorphic	exposed	no	few	NA	NA
Violaceae	*Viola canina*	A	blue	perennial	zygomorphic	exposed	short	few	fso	12.5
Violaceae	*Viola mirabilis*	A	lilac	perennial	zygomorphic	exposed	short	few	vår	20
Violaceae	*Viola palustris*	A	lilac	perennial	zygomorphic	exposed	short	few	vår	6.5
Violaceae	*Viola tricolor*	A	violet-yellow-white	perennial	zygomorphic	exposed	short	few	vår	17.5
Violaceae	*Viola riviniana*	A	blue-violet	perennial	zygomorphic	exposed	short	few	vår	15
Violaceae	*Viola sp*	A	violet	perennial	zygomorphic	exposed	short	few	NA	NA

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*Artsdatabanken. 2015. Artsnavnebasen. Norsk taksonomisk database., http://www2.artsdatabanken.no/artsnavn/Contentpages/Hjem.aspx

** Lid, J., and D. Lid. 2005. Norsk flora. 7 edition by R. Elven. Det Norske Samlaget, Oslo, Norway.

Table A4: Likelihood ratio tests of final models attained by backwards elimination of variables from the full models. Response variables were species richness, rarefied richness, abundance, proportions of below-ground nesters, FDis and CWM of the intertegular distance (ITD) (Body size), and FDis of tongue length. For variables in the final models we used p-values <0.05 as selection criterion. Analyses were performed in R, package lme4. Species richness was fitted using GLMM with poisson-distributed errors and a log-link function, the models for abundance, FDis ITD, CWM ITD and FDis tongue length were fitted using Gaussian distributed errors and identity link, with Site as a random effect. The models for Proportion of below ground nesters were fitted using a GLMM with a binomial distribution. Significance codes: <0.001 '***' <0.01 '**' <0.05 '*'< 0.1 '.'

Response	**Explanatory terms**	**LRT**	**df**	***P***
Species richness (raw)	Year	24.629	2	<0.001 ***
	Elevation	10.568	1	0.001 **
	Treatment x Richness forbs	15.375	2	<0.001 ***
Rarefied richness q0 (log)				
	Year	48.341	2	<0.001 ***
	Elevation	5.989	1	0.01 *
	Treatment x Richness forbs	26.949	2	<0.001 ***
Abundance rarefied (log)	Elevation	7.868	1	0.005 **
	Year x Treatment x Richness forbs	11.962	4	0.018 *
FDis body size (log)	Year	18.299	2	<0.001 ***
	Treatment	12.637	2	0.002 **
	Elevation	13.58	1	<0.001 ***
CWM body size	Dead wood	4.541	1	0.033 *
	Treatment x FDis forbs	8.897	2	0.012 *
	Year x Treatment x Elevation	11.558	4	0.02 *
FDis Tongue length (log)	Elevation	9.030	1	0.003 **
	Treatment x Source habitat	9.861	2	0.007 **
	Year x Treatment x Dead wood	17.376	4	0.002 **
Prop. below-ground nesters	Treatment x Richness forbs	20.156	2	<0.001 ***
	Treatment x Dead wood	6.093	2	0.048 *
	Year x Treatment x FDis forbs	16.830	4	0.002 **
Turnover (Beta$_{JTU}$)	Forb species richness	11.223	1	<0.001 ***
	Year	5.477	2	0.065 .
Beta diversity (Beta$_{JAC}$)	Forb species richness	6.682	1	0.01 **
	Year	7.775	2	0.02 *

Table A5: The observed mean and standard deviation (mean ± SD) of species richness and rarefied abundance of solitary bees in the three treatments in 2013, 2014 and 2015.

	2013		**2014**		**2015**	
	Richness	**Abundance**	**Richness**	**Abundance**	**Richness**	**Abundance**
Uncut	3.4± 2.4	5.3±6.0	4.1 ± 3.5	5.5±5.4	5.9 ± 3.7	9.8±8.4
Cut	5.6 ± 3.9	7.3±6.3	6.5 ± 4.5	11.5±10.8	7.5 ± 3.9	14.0±10.0
Cut-remove	5.8 ± 5.3	10.5±16.4	7.7 ± 6.6	14.4±17.8	9.4 ± 7.8	24.8±30.1

Table A6: The effects of year, treatment (cut-remove, cut, and uncut) and environmental context on species richness and abundance (log(y+1)) of solitary bees in power-line clearings. Final model summary outputs from GLMMs, generalized linear mixed-effect models, and LMMs, linear mixed-effect models. Variables: year (2013 = reference level, 2014, 2015), treatment (cut-remove= reference level, cut, and uncut), richness forbs and elevation. SD, standard deviation; SE, standard error.

Species richness (raw) (GLMM)	**β**	**SE**	**z-value**	**P**
Intercept (2013, cut-remove)	1.509	0.138	10.919	<0.001
Year 2014	0.177	0.080	2.208	0.03
Year 2015	0.380	0.077	4.905	<0.001
Treatment uncut	-0.397	0.087	-4.558	<0.001
Treatment cut	-0.047	0.082	-0.576	0.56
Richness forbs	0.260	0.066	3.923	<0.001
Elevation	-0.449	0.126	-3.564	<0.001
Treatment uncut x Richness forbs	-0.299	0.080	-3.733	<0.001
Treatment cut x Richness forbs	-0.189	0.072	-2.619	0.009
Random effects:	**σ**	**SD**	**Obs.**	**Sites**
Site identity	0.246	0.496	171	19
Rarefied richness (q0) (LMM)	**β**	**SE**	**t-value**	**P**
Intercept (2013, cut-remove)	0.668	0.070	9.540	<0.001
Year 2014	0.100	0.043	2.309	0.022
Year 2015	0.314	0.043	7.254	<0.001
Treatment uncut	-0.273	0.045	-6.141	<0.001
Treatment cut	-0.041	0.044	-0.933	0.352
Richness forbs	0.205	0.041	4.981	<0.001
Elevation	-0.151	0.061	-2.472	0.024
Treatment uncut x Richness forbs	-0.241	0.046	-5.283	<0.001
Treatment cut x Richness forbs	-0.107	0.047	-2.288	0.024
Random effects:	**σ**	**SD**	**Obs.**	**Sites**
Site identity	0.637	0.252	171	19

Log abundance (rarefied) (LMM)	β	SE	t-value	P
Intercept (Year 2013, cut-remove)	1.900	0.176	10.811	<0.001
Year 2014	0.315	0.156	2.025	0.04
Year 2015	0.586	0.156	3.745	<0.001
Treatment uncut	-0.425	0.157	-2.704	0.01
Treatment cut	-0.042	0.157	-0.269	0.79
Richness forbs	-0.418	0.143	-2.916	0.01
Elevation	0.268	0.138	1.940	0.05
Treatment uncut× Richness forbs	-0.384	0.165	-2.330	0.02
Treatment cut × Richness forbs	-0.320	0.185	-1.734	0.09
Year 2014 ×Treatment uncut	-0.293	0.223	-1.312	0.19
Year 2015 × Treatment uncut	0.032	0.223	0.143	0.89
Year 2014 × Treatment cut	-0.110	0.222	-0.494	0.62
Year 2015 × Treatment cut	0.052	0.223	0.232	0.82
Year 2014 × Richness forbs	-0.021	0.163	-0.127	0.90
Year 2015 × Richness forbs	0.237	0.159	1.492	0.14
Year 2014 × Treatment uncut × Richness forbs	0.042	0.222	0.188	0.85
Year 2015 × Treatment uncut × Richness forbs	0.131	0.222	0.592	0.55
Year 2014 × Treatment cut × Richness forbs	0.366	0.238	1.538	0.13
Year 2015 × Treatment cut × Richness forbs	-0.226	0.239	-0.945	0.35
Random effects:	**σ**	**SD**	**Obs**	**Site**
Site identity	0.357	0.597	171	19

Table A7: The effects of year, treatment (cut-remove, cut, and uncut) and environmental context on functional dispersion (FDis) of body size (intertegular distance, ITD) (log(y+1)), community weighted mean (CWM) of body size (ITD), the FDis of tongue length (log (y+1)), the community weighted mean of tongue length and the proportions of below-ground nesters of solitary bees in power-line clearings. Final model summary outputs from LMMs, linear mixed-effect models, and GLMMs, generalized linear mixed-effect models. Variables: year (2013 = reference level, 2014, 2015), treatment (cut-remove= reference level, cut, and uncut), richness forbs, elevation, functional dispersion (FDis) of forbs, dead wood and source habitat (150-300-500m r2). SD, standard deviation; SE, standard error.

Prop. below-ground nesters (GLMM)	β	SE	z-value	P
Intercept (2013, cut-remove)	1.077	0.227	4.736	< 0.001
Year 2014	-0.121	0.274	-0.441	0.66
Year 2015	-0.153	0.24	-0.638	0.52
Treatment cut	-0.141	0.306	-0.462	0.64
Treatment uncut	1.083	0.467	2.322	0.02
Richness forbs	-0.483	0.133	-3.631	< 0.001
FDis forbs	0.055	0.203	0.27	0.79
Dead wood	-0.374	0.174	-2.153	0.03
Treatment cut × Richness forbs	0.496	0.156	3.178	0.001
Treatment uncut × Richness forbs	0.873	0.224	3.895	< 0.001
Year 2014 × Treatment cut	-0.052	0.412	-0.127	0.9
Year 2015 × Treatment cut	0.453	0.374	1.213	0.23
Year 2014 × Treatment uncut	-0.496	0.597	-0.831	0.41

Year 2015 × Treatment uncut	-0.463	0.524	-0.882	0.38
Year 2014 × FDis forbs	0.085	0.24	0.356	0.72
Year 2015 × FDis forbs	0.459	0.225	2.039	0.04
Treatment cut × FDis forbs	0.319	0.317	1.006	0.31
Treatment uncut × FDis forbs	0.221	0.416	0.531	0.6
Treatment cut × Dead wood	0.384	0.189	2.032	0.04
Treatment uncut × Dead wood	-0.146	0.232	-0.63	0.53
Year 2014 × Treatment cut × FDis forbs	-0.711	0.413	-1.721	0.09
Year 2015 × Treatment cut × FDis forbs	-1.374	0.421	-3.263	0.001
Year 2014 × Treatment uncut × FDis forbs	-0.055	0.5	-0.11	0.91
Year 2015 × Treatment uncut × FDis forbs	-1.119	0.484	-2.313	0.02
Random effects:	**σ**	**SD**	**Obs**	**Site**
Site identity	0.16	0.4	171	19

Functional dispersion body size (LMM)	**β**	**SE**	**t-value**	**P**
Intercept (2013, cut-remove)	0.408	0.047	8.598	<0.001
Year 2014	0.09	0.044	2.032	0.04
Year 2015	0.192	0.044	4.348	<0.001
Treatment cut	-0.027	0.044	-0.613	0.541
Treatment uncut	-0.149	0.044	-3.363	0.001
Elevation	-0.13	0.031	-4.212	<0.001
Treatment cut	0.098	0.126	0.776	0.44
Random effects:	**σ**	**SD**	**Obs**	**Site**
Site identity	0.007	0.086	171	19

Community weighted mean body size (LMM)	**β**	**SE**	**t-value**	**P**
Intercept (2013, cut-remove)	1.928	0.128	15.059	<0.001
Treatment cut	-0.135	0.146	-0.927	0.36
Treatment uncut	0.186	0.152	1.223	0.22
FDis forbs	-0.074	0.064	-1.149	0.25
Dead wood	-0.155	0.074	-2.081	0.05
Year 2014	0.218	0.147	1.48	0.14
Year 2015	0.209	0.147	1.419	0.16
Elevation	0.09	0.138	0.652	0.52
Treatment cut × FDis forbs	-0.059	0.107	-0.558	0.58
Treatment uncut × FDis forbs	0.215	0.089	2.411	0.02
Treatment cut × Year 2014	-0.022	0.205	-0.107	0.91
Treatment uncut × Year 2014	-0.212	0.211	-1.005	0.32
Treatment cut × Year 2015	0.105	0.203	0.519	0.61
Treatment uncut × Year 2015	-0.355	0.209	-1.698	0.09
Year 2014 × Elevation	-0.232	0.156	-1.487	0.14
Year 2015 × Elevation	0.016	0.155	0.106	0.92
Treatment cut × Elevation	0.103	0.151	0.686	0.49
Treatment uncut × Elevation	-0.007	0.17	-0.042	0.97

Treatment cut × Year 2014 × Elevation	0.024	0.208	0.113	0.91
Treatment uncut × Year 2014 × Elevation	0.416	0.228	1.823	0.07
Treatment cut × Year 2015 × Elevation	-0.119	0.199	-0.595	0.55
Treatment uncut × Year 2015 × Elevation	-0.262	0.226	-1.162	0.25
Random effects:	**σ**	**SD**	**Obs**	**Site**
Site identity	0.088	0.297	157	19
Functional dispersion tongue length (LMM)	**β**	**SE**	**t-value**	**P**
Intercept (2013, cut-remove)	0.377	0.053	7.051	< 0.001
Treatment cut	0.059	0.068	0.865	0.39
Treatment uncut	-0.084	0.068	-1.234	0.22
Source habitat	0.04	0.042	0.962	0.35
Year2014	0.163	0.068	2.41	0.02
Year2015	0.145	0.068	2.137	0.03
Dead wood	-0.04	0.054	-0.737	0.47
Elevation	-0.106	0.035	-3.021	0.01
Treatment cut × Source habitat	-0.085	0.039	-2.162	0.03
Treatment uncut × Source habitat	0.028	0.039	0.717	0.47
Treatment cut × Year 2014	-0.18	0.096	-1.882	0.06
Treatment uncut × Year 2014	-0.134	0.096	-1.393	0.17
Treatment cut × Year 2015	-0.112	0.096	-1.168	0.24
Treatment uncut × Year 2015	-0.071	0.096	-0.739	0.46
Year2014 × Dead wood	0.2	0.068	2.935	0
Year2015 × Dead wood	0.158	0.068	2.317	0.02
Treatment cut × Dead wood	0.158	0.068	2.322	0.02
Treatment uncut × Dead wood	0.082	0.068	1.201	0.23
Year2014 × Treatment cut × Dead wood	-0.365	0.096	-3.792	< 0.001
Year2014 × Treatment uncut × Dead wood	-0.184	0.096	-1.913	0.058
Year2015 × Treatment cut × Dead wood	-0.244	0.096	-2.534	0.01
Year2015 × Treatment uncut × Dead wood	-0.205	0.096	-2.133	0.03
Random effects:	**σ**	**SD**	**Obs**	**Site**
Site identity	0.096	0.31	171	19

Table A8: The effects of treatment (uncut = reference level, cut, and cut-remove) and environmental context on community composition, partitioned into turnover Beta$_{JTU}$ and overall beta diversity Beta$_{JAC}$, in power-line clearings. Final model summary outputs from LMMs, linear mixed-effect models. Variables: year (2013 = reference level, 2014, 2015), treatment (cut-remove = reference level, cut, and cut), richness forbs. SD, standard deviation; SE, standard error.

Turnover Beta$_{JTU}$ (LMM)	**β**	**SE**	**t-value**	**P**
Intercept (2013)	0.453	0.024	18.996	< 0.001
Year 2014	-0.019	0.028	-0.699	0.486
Year 2015	-0.063	0.0274	-2.288	0.24
Richness forbs	-0.056	0.015	-3.735	< 0.001
Random effects:	**σ**	**SD**	**Obs**	**Site**
Site identity	0.057	0.140	157	19
Beta diversity Beta$_{JAC}$ (LMM)	**β**	**SE**	**t-value**	**P**
Intercept (2013)	0.534	0.015	34.974	< 0.001
Year 2014	-2.885	0.02	-0.641	0.52
Year 2015	-1.206	0.02	-2.679	0.008
Richness forbs	-0.027	0.009	-2.942	0.004
Random effects:	**σ**	**SD**	**Obs**	**Site**
Site identity	0.0006	0.025	157	19

Figures

Figure A1: Photo of a flight interception trap in one of the sites in 2015. Photo: Mari Steinert.

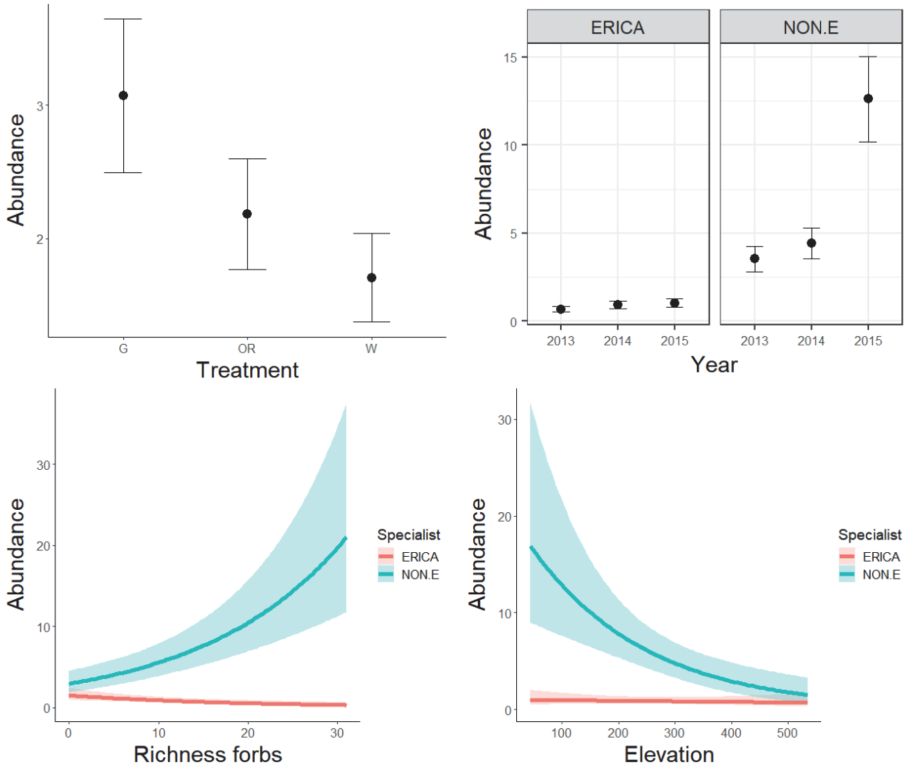

Figure A2: The final model of ericaceous (ERICA) vs non-ericaceous (NON.E) specialists: Showing how the rarefied abundance of ericaceous affiliated species diverge from the other bees in response to year, forb species richness and elevation. The black dots are the predicted values and the whiskers and the shaded green and red areas are the 95% CI limits.

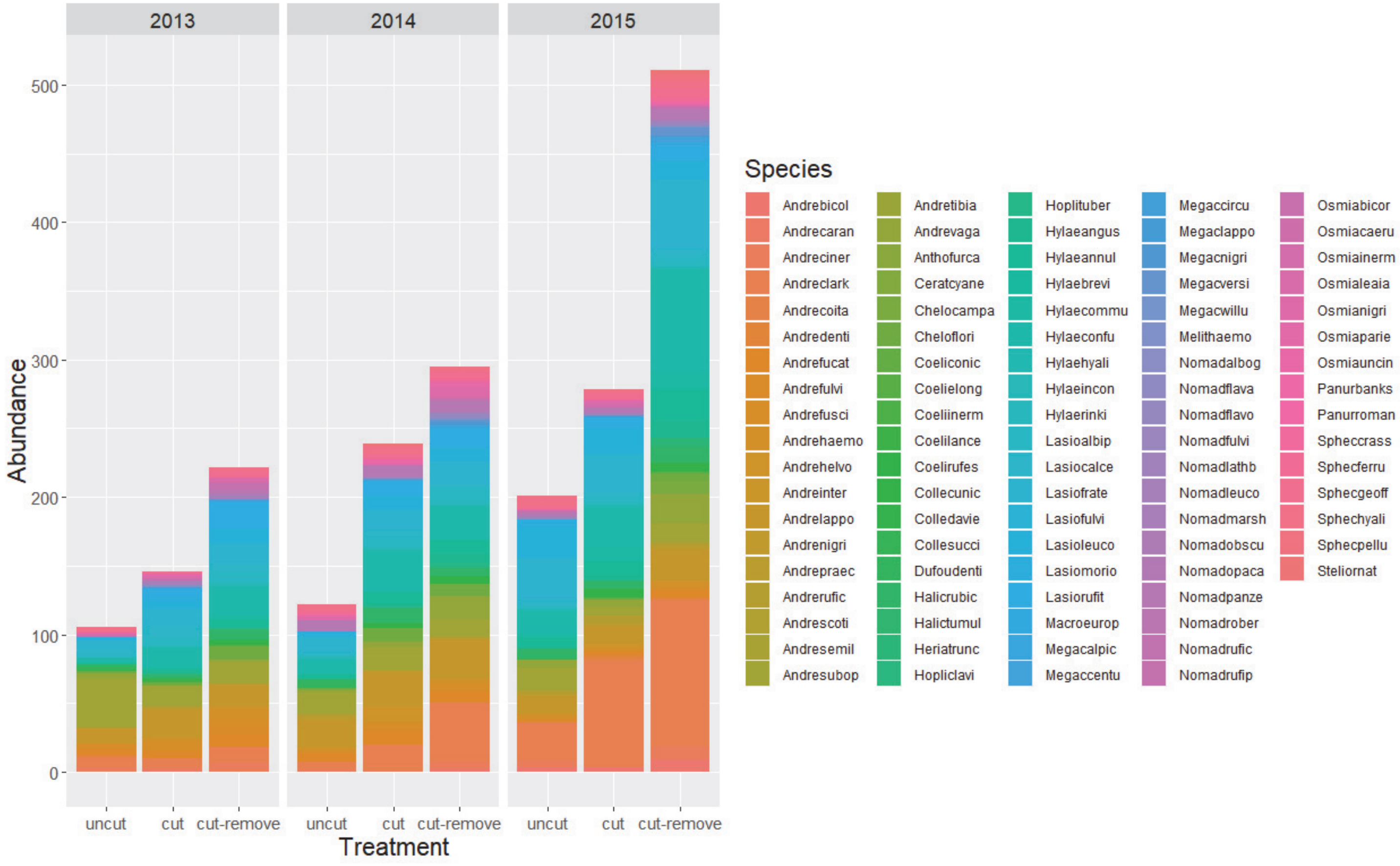

Figure A3: The rarefied abundance of each species, including cleptoparasites, in treatment plots in each year after maintenance clearing. See table A1 to get the full species names.

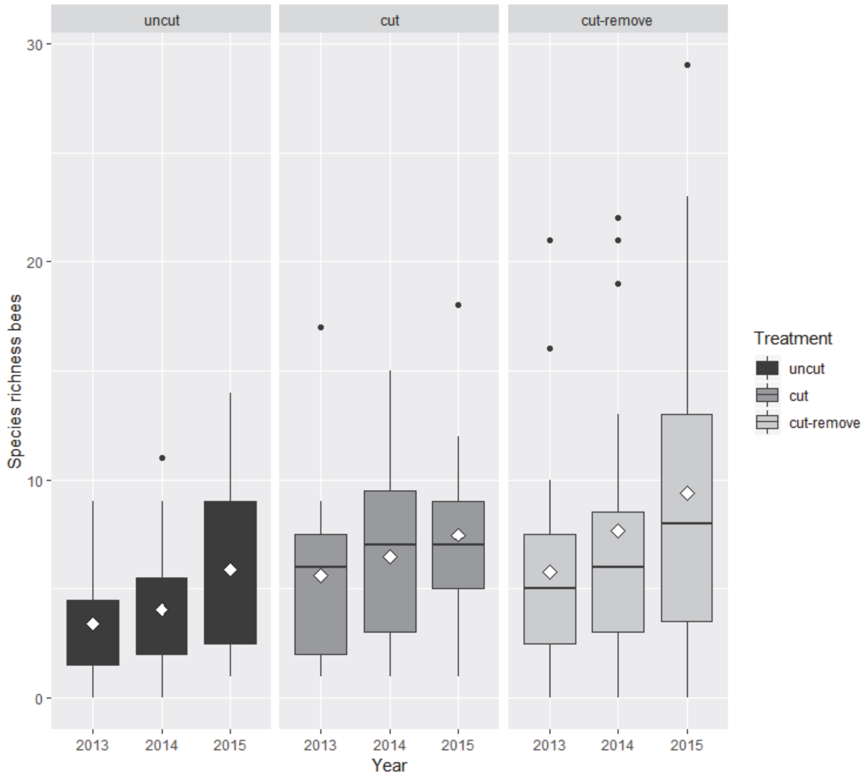

Figure A4: Boxplot of the raw species richness of bees in each treatment plot level (uncut, cut, cut-remove) in the three years. With mean (diamond) and median (mid-line).

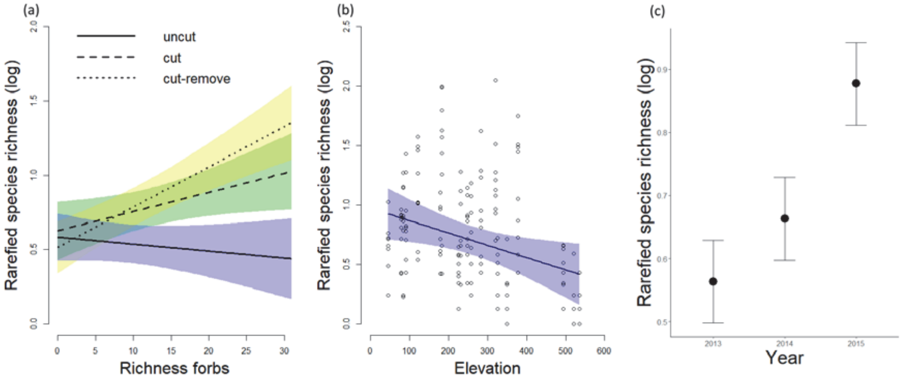

Figure A5: Rarefied species richness (log) in response to (a) treatment (uncut, cut and cut-remove) and forb species richness, (b) to elevation and (c) year. The shaded areas are 95% confidence intervals (CIs). Uncut (solid lines) has blue CIs, cut (dashed line) has green CIs, and cut-remove (dotted line) has yellow CIs.

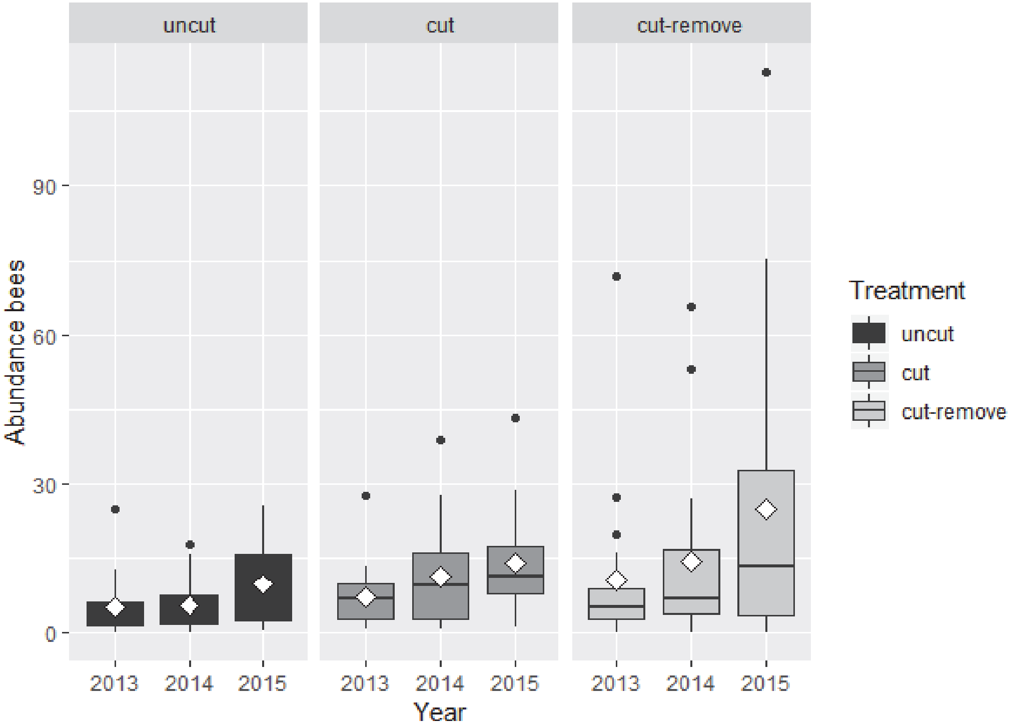

Figure A5: Boxplot of the abundance of bees in each treatment plot level (uncut, cut, cut-remove), in each year. With mean (diamond) and median (mid-line).

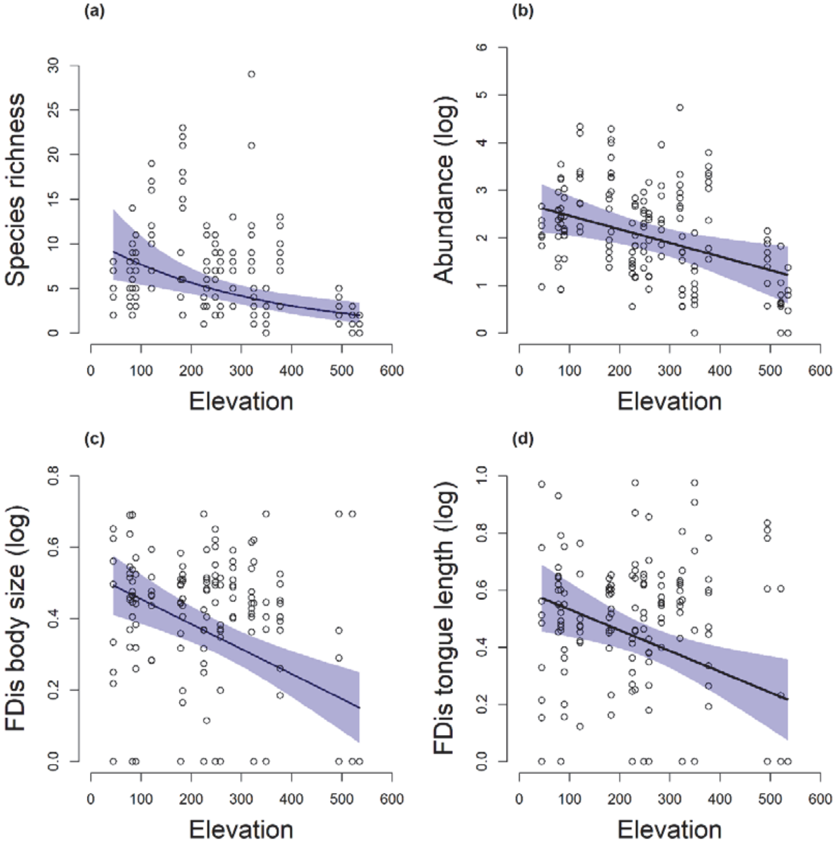

Figure A7: Species richness, Abundance (log), FDis body size (log) and FDis tongue length (log) in response to elevation. The shaded areas are 95% confidence intervals (CIs).

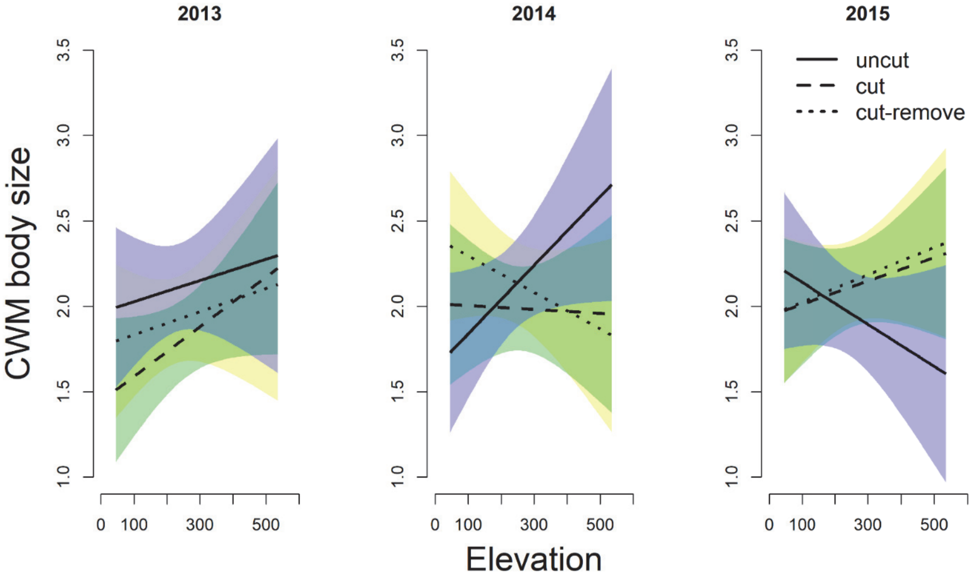

Figure A8: The community weighted mean (CWM) of body size in response to treatment (uncut, cut and cut-remove) and elevation. The shaded areas are 95% confidence intervals (CIs). Uncut (solid lines) has blue CIs, cut (dashed line) has green CIs, and cut-remove (dotted line) has yellow CIs.

Paper III

Bumble bee communities in power-line clearings: Effects of experimental management practices

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Abstract

Bumble bees fill an important function in temperate, boreal and alpine ecosystems as pollinators of wild plants and cultivated crops. Global declines in population sizes of many bumble bee species call for knowledge about how habitats influenced by human land use can be managed to accommodate diverse bumble bee communities. We carried out a field experiment to study effects on bumble bee communities in power-lines clearings in response to different vegetation clearing practices: (i) cutting, (ii) cutting and removing, and (iii) not cutting the woody vegetation, while at the same time assessing the modifying influence of environmental conditions. Cutting the woody vegetation improved habitat quality for bumble bees, whereas removal of the woody debris had little effect. The treatment effect depended on local forb species richness. Forb species richness and cover of forb species with nectar tube were positively related to species-based measures of bee diversity and abundance of generalist bees. The more specialized long-tongued and late emerging bumble bees– which are of special conservation interest – increased in response to the cut and cut-remove treatments and increased with functional variation of forb species. Most bumble bees seemed to thrive in the cleared treatment plots even three years after cutting, but the abundance of long-tongued species was substantially reduced three years post-clearing. Management to improve habitat conditions for bumble bees in power-line clearings does not require costly removal of woody debris after cutting, but more frequent cutting can benefit specialized bumble bee species of particular conservation interest.

Keywords: Habitat management; pollinator community; bumble bee conservation; boreal forest; functional diversity; flower resources

Introduction

Bumble bees have an important function in natural and human-dominated ecosystems as pollinators of wild plants and agricultural crops (Biesmeijer et al. 2006; Klein et al. 2007; Ollerton et al. 2011). Bumble bees are widely distributed in regions with cool climates, but populations of several species are declining in many parts of their natural range (Arbetman et al. 2017; Cameron et al. 2011; Goulson et al. 2008; 2015; Potts et al. 2010). The declines are driven by multiple, and potentially interacting threats of climate change, pesticides, pests and pathogens in addition to habitat loss and fragmentation due to human-induced modifications of the landscape (Potts et al. 2010; Winfree et al. 2009). Yet, not all land use change is entirely bad, and if properly managed, habitats strongly influenced by human activities may improve habitat quality for pollinating insects (Villemey et al. 2018). For instance, infrastructure corridors and human-made ecological boundaries may provide important pollinator habitats, e.g. road-verges (Hopwood 2008; Noordijk et al. 2009), railway lines (Moroń et al. 2014), hedgerows (Hanley & Wilkins 2015), field margins (Carvell et al. 2004) and power-line clearings (Berg et al. 2013; 2016; Hill & Bartomeus 2016; Russell et al. 2005; 2018; Steinert et al. 2018; 2020; Sydenham et al. 2016; Wagner et al. 2014; 2019). Furthermore, routine management practices in human-modified habitats may promote conservation of endangered species (Hanula et al. 2016). But more studies are needed to understand how different management practices influence pollinator communities, and to provide evidence-based guidelines for pollinator-friendly practices.

Power-line clearings are human-modified habitats, creating extensive networks of habitats potentially mimicking semi-natural grasslands, which may act as novel alternative habitats for bumble bee species (Hill & Bartomeus 2016). In boreal landscapes, semi-natural grasslands are an endangered nature type, which has suffered large declines over the last 55 years (Aune et al. 2018). In forested landscapes, the main aim for the vegetation management is to prevent trees from reaching the aerial lines. Consequently, the vegetation in power-line clearings typically comprise early to mid-successional phases of forest, often dominated by grasses, forb species, followed by shrubs and young deciduous trees. There is a substantial variation in the routine vegetation clearing practices within and among countries. Practices range from herbicide application or frequent mechanical mowing of all vegetation to less intensive disturbances such as manual clearing of the woody vegetation every 5–12 years, depending on productivity (e.g., Russell et al. 2018). Maintenance clearing creates open habitats facilitating insect-pollinated plants (Steinert et al. 2018), and plants associated with semi-natural landscapes (Eldegard et al. 2017). This provides potential foraging resources and nesting substrate for bumble bees (Goulson et al. 2008). Previous observational studies of bumble bees in power-line clearings found a similar abundance and diversity of bees in the clearings, compared to adjacent semi-natural habitats (Hill & Bartomeus 2016), and a higher abundance and diversity compared to adjacent forest (Wagner et al. 2019). Other studies have found that logging in clear-cuts, or forest fire events, can have a positive effect on bumble bees (Cartar 2005; Moretti et al. 2009; Pengelly & Cartar 2010; Williams et al. 2010). To further enhance the habitat quality for flower-visiting insects after logging it has been suggested that the logging residue should be removed (Korpela et al. 2015). To our knowledge, no previous studies have assessed the potential habitat enhancement effect of experimentally removing the woody debris in power-line clearings on bumble bee communities.

Conservation of pollinators should aim towards preserving a high functional diversity, in order to sustain a wide array of complementary pollination services (Albrecht et al. 2012; Hoehn et al. 2008). Management practices that promote species-based diversity, may not necessarily maintain trait diversity (Forrest et al. 2015). Bumble bee species are usually floral generalists and have a widespread geographic distribution. Most species are eusocial and colonial, nesting below ground in abandoned rodent holes, whereas some nests under rocks, or above ground in tree cavities or in twig or litter piles (Osborne et al. 2008b). Some species are social parasites on the social species (Fisher 1987). Yet, some species traits are associated with greater susceptibility to decline and extinction (Colla et al. 2012) and are thus of special conservation concern. This includes the more vulnerable groups of long-tongued bumble bee species and the species with late phenology (Goulson et al. 2005; 2008; Williams et al. 2009), which have showed consistent historical declines (Colla et al. 2012; Dupont et al. 2011). Long-tongued bumble bee species have more narrow diets and are associated with flower species with long nectar tubes (corollas) and high pollen quality (e.g. Fabaceae) (Goulson et al. 2005), a flower resource which also have experienced sharp declines during the last century (Carvell et al. 2006; 2011). Moreover, the decline in late emerging queens are related to the vulnerability to scarcity of late flower resources and competition for nesting sites (Carvell et al. 2011; Goulson et al. 2008).

The effects of habitat management may be dependent on the environmental context (Carvell et al. 2011; Sydenham et al. 2016), thus the management practices should be assessed under different abiotic and biotic environmental conditions to better inform bumble bee conservation. Species richness and abundance of plant species are important for pollinator community structure and diversity (Potts et al. 2003; 2005). An enhanced plant species richness may ensure the availability of species-specific pollen and nectar resource requirements in space and time for bumble bees (Potts et al. 2003). In general, bumble bees are large-bodied species that are able to fly long distances to forage (Greenleaf et al. 2007; Osborne et al. 2008a), which makes them efficient at collecting food resources in the landscape. Thus, availability of floral resources is required at a landscape scale (Carvell et al. 2011). The amount of source habitats in the landscape have been found to have a positive effect on species richness and abundance of bumble bees (Öckinger & Smith 2007). On the other hand, landscape fragmentation may be a limiting factor. Bumble bees are central-place foragers, and a fragmented landscape may potentially impede vital resources at an appropriate scale (Carrié et al. 2017; Winfree et al. 2009).

In this study, we carried out a large-scale field experiment to compare the effects on species and functional diversity of bumble bees in response to different maintenance clearing practices: (i) cutting the woody vegetation (current management practice), (ii) cutting and removing, and (iii) not cutting the woody vegetation. We also assessed whether environmental context modified the effects of management practices on the bumble bee responses; i.e. the potential influence of floral resources (i.e. richness of forbs, functional dispersion (FDis) of forbs, cover of Ericeae species, cover of forb species with a nectar tube, cover of Salix species, FDis of inflorescence, FDis of flower phenology), as well as influence of time after clearing (year), elevation, precipitation, light availability, source habitat, and landscape fragmentation. Specifically, we asked: (1) Does the effect on species-based diversity of bumble bees (species richness, abundance, diversity) differ between management practices, and is the effect modified by environmental context? (2) Does the effect on the functional trait groups of bumble bees; abundance of long vs. short tongued bumble bees; phenology of queen bumble bees (i.e. abundance of early or late emerging bees); and abundance of cuckoo bumble bees (*Psithyrus spp.*), differ between management practices, and is the effect modified by environmental context? Finally, we discuss the management implications of our findings, so that they can be used to inform pollinator-friendly management practices.

Methods

Study sites and experimental design

The study was conducted in southeast Norway (59.33°–61.12°N, 08.95°–11.36°E) at 45–535 masl (Fig. 1). The experimental design included 19 study sites within the main power-line grid, where there was a stretch of at least 200 meters with substantial regrowth of trees. Sites were located in boreal forests comprising mixed stands of Norway spruce (*Picea abies)*, Scots pine (*Pinus sylvestris)* and birch (*Betula spp.).* Each site had been subjected to the same management regime: manual cutting of all woody vegetation every 5 to 10 years (dependent on site productivity) without use of chemicals and without disturbing the field layer.

The vegetation in the clearings was in an early successional phase. Substantial regrowth of deciduous trees, together with shrubs and forbs dominated productive sites, while ericaceous dwarf shrubs dominated in sites with low productivity. After routine maintenance clearing the biomass (fine woody debris <10 cm in diameter) is left to decay on the ground. The experiment was conducted autumn 2012 [n = 16] and early spring 2013 [n = 3]. Within each site, we established three treatment plots of 30 m × ca. 60 m [corridor width], with an average distance of 120 m [min=50, max=345] between neighboring plots. The relatively short distances between treatment plots ensured low site-specific variation between treatments. Bumble bees may have large foraging distances, up to 10 km from their nests (Rao & Strange 2012), although foraging usually occurs within 500 m from their colony (Osborne et al. 1999; Osborne et al. 2008a). Consequently, differences in abundance of bumble bees in among different treatments should be interpreted as differences in habitat preference rather than differences in local population size. Yet, we assume that differences in habitat preferences is a good proxy for habitat quality (i.e. food and nesting locations), which may in turn influence local abundances. Each treatment plot was randomly assigned to one of three treatment practices: (1) cut: all trees cut and left to decay in the clearing; (2) cut-remove: all trees cut and woody debris removed from the plot and (3) uncut (4-9 years of regrowth) (Fig. 1). The woody debris in the cut-remove treatment was gathered in a pile on one side of the treatment plot.

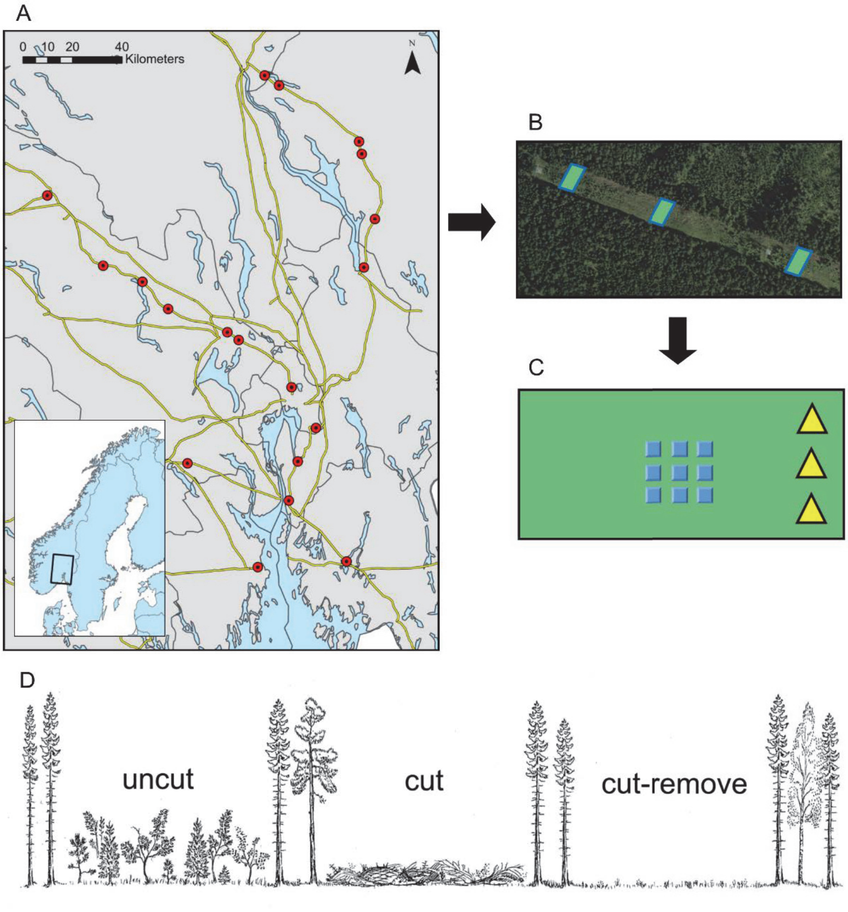

Fig. 1. *(A) Geographic distribution of the 19 study sites located along the main power-line grid in southeastern Norway. (B) Aerial photo of one site with three treatment plots. Distance between plots were averagely 120m. (C) Arrangement within one treatment plot with three flight-interception traps placed along the northern side of each treatment plot. Plant surveys were conducted from nine 1 m^2 subplots within each treatment plot. (D) Illustration of the three experimental treatment plots at each site, (i) with woody vegetation uncut; (ii) all trees cut and woody debris left to decay in the clearing; and (iii) all trees cut and woody debris removed.*

Sampling of bees and floral resources

We sampled the bumble bee communities in the power-line clearings using flight interception traps (window traps). Three traps were deployed within each treatment plot (19 sites, 3 treatments) and placed along the northernmost end of the treatment plot, to maximize sun exposure (Fig. 1). The traps had two transparent Plexiglas screens (370 mm x 210 mm), that formed a cross, with a funnel and container attached to it (Fig. A1). The container was filled with 50:50 mixture of water and green propylene glycol and a drop of detergent.

Traps were deployed immediately after snowmelt (April/May) and removed in early autumn (September). We emptied the containers at each trap − and brought the collected insect material to the laboratory for identification − four times in 2013 and five times in 2015, due to an earlier onset of snowmelt in spring 2015. The sampling procedure enabled a continuous and consistent sampling intensity throughout the main foraging activity season of bumble bees. The collected material was stored in 80% ethanol until identification. All bees were identified using regional identification keys (Bollingmo 2012, Løken 1985, Ødegaard et al. 2015). A verified identification of all individuals from the *Bombus lucorum sensu strictu* (*s.str.)* complex (i.e. *B. cryptarum, B. lucorum, B. magnus*, and *B. terrestris*), can only be achieved through genetic analyses (Williams et al. 2012). Therefore, we pooled these species into one operational taxonomic unit in the analyses. Voucher specimens are preserved at the Norwegian University of Life Sciences.

We collected data on forb species richness and the percentage cover of ericaceous dwarf shrubs and *Salix* species in each treatment plot. Plant surveys covered all the flowering plant species and were carried out in late June and early July in 2013 and 2015. Plant community surveys were timed to enable species identification of all insect-pollinated plant species, including species that flowered later in the season. Within the center of each treatment plot, we placed nine regularly spaced quadratic subplots of 1-m^2 within a 10 × 10 m quadrat (Fig. 1). In the nine subplots, we identified all vascular plants to species and visually estimated the abundances to the nearest 1% during each sampling visit. If a species was present in a subplot, but had <1% cover, it was recorded as 0.001%.

Data preparation

Total bumble bee species richness/abundance per treatment plot and year was calculated by pooling all bumble bee species/individuals sampled within one treatment plot in each year. We used treatment plot as sampling unit in the statistical analyses. We rarefied the responses to account for the variation in number of successful trapping sessions between treatment plots and years, which ranged from nine to 15. The sampling intensity was standardized by estimating the number of species and individuals expected to be sampled in a treatment plot given nine sampling sessions (Chao et al. 2014). The rarefied species richness measure (q0) (hereafter ‘species richness’) was calculated using the iNext package in R with sample size set to nine, and with 50 bootstrap replications (Hsieh et al. 2019). To calculate the rarefied abundance, we randomly sampled nine traps within a treatment plot to estimate total abundance of each bee species. We repeated the random sampling 1000 times and calculated mean abundance of each bee species within each treatment plot. The mean values were used as the rarefied abundance (hereafter ‘abundance’). The species richness summed from the rarefied abundance matrix was identical to the raw species richness (hereafter ‘raw richness’). We calculated a diversity index (Shannon diversity) from the rarefied abundance matrix for the bumble bees (Heip et al. 1998).

Functional traits

For all bumble bee species, we compiled information on life history and morphological traits, likely to be influenced by the treatments and environmental context. Trait attributes were obtained from regional field guides and assigned to each species (Bollingmo 2012, Ødegaard et al. 2015). We classified species according to their tongue lengths (i.e. long tongued vs short tongued bumble bees) because long-tongued species tend to be more specific in their floral preferences than short-tongued bumble bees, with preferences for flowers with deep corollas (Inouye 1980). The tongue length for each species was based on taxonomy, where the long-tongued species were represented by the subgenus’ *Thoracobombus* and *Megabombus* (Table A1). We also categorized all species according to their phenology (i.e. month of emergence for queens, ‘early’ (March, April) and ‘late’ (May, June)), and nesting strategy (eusocial vs social parasites (i.e. ‘cuckoo bumble bees’, *Psithyrus*)) (Table A1). The phenology for the queens were attained from regional field guides (Bollingmo 2012, Ødegaard et al. 2015). We used the abundance of individuals in each trait group as the functional trait responses in the analyses. To identify the influence of management practices on eusocial bumble bees, we excluded the cuckoo bumble bees from the analyses of the functional trait groups. The rationale for excluding cuckoo bees was the diverging biology from the eusocial species; they have a late phenology and produce a single generation towards the end of the summer season (Fisher 1987). The cuckoo bumble bees’ dependence on hosts – which may have different traits –could potentially mask effects of management practices on the trait groups of the eusocial bumble bee communities.

Floral resources

When calculating species richness and functional dispersion (FDis) of forbs, we used treatment plot as sample unit in the statistical analyses. We treated plant taxa that could only be identified to genus as morphospecies. We quantified floral resource diversity within the plant communities by assigning nine functional effect traits to each plant species (Table A1). The traits [extracted from Lid & Lid (2005)] were based on morphological characteristics of flowers, which are known to be important for pollinators (Table A2). We calculated different functional trait indices from the effect traits of forbs using the dbFD function of the FD package in R (Laliberté et al. 2014). We used the number of subplots in which a species occurred as a measure of abundance in the dbFD function. We used weighted abundances and the Cailliez correction for non-Euclidian distances when calculating the indices, because of the inclusion of categorical traits (Forrest et al. 2015; Laliberté et al. 2014). We calculated the functional dispersion of forbs (hereafter 'FDis forbs'), which is the mean distance between individual species and the community centroid in multidimensional trait space, and used it as a measure of the variation in trait values within a community (Laliberté & Legendre 2010). We also calculated the functional dispersion of the inflorescence of forbs (hereafter 'FDis inflorescence'), and the functional dispersion of flower phenology (hereafter 'FDis flower phenology'), and we summed the total % cover of forb species having a nectar tube, from the 9 subplots (hereafter 'Nectar tube species cover') (Tables A2, A3).

Landscape fragmentation and source habitat

We compiled information on landscape fragmentation and source habitat areas surrounding each site from ArcGIS (ESRI 2011) and Ar5 digital land use maps (Ahlstrøm et al. 2019), by extracting information about land use types at increasing radii around each site (150 m, 300 m, 500 m, 1000 m, 2000 m). As a measure of landscape fragmentation, we calculated the Shannon diversity (Heip et al. 1998), of the total number of polygons of different land use types (11 in total), from the different radii around each site. As a measure of available source habitat, we used the total area of non-forested landscape elements (i.e. semi-natural areas/pastures, open surfaces, road-verges, and other non-tilled arable land) that can function as potential source habitats for bumble bees in the power-line clearings. To account for collinearity among measures extracted from different radii around each site, measures from different scales (all radii) were combined into one single variable using a principal component analysis (PCA), where we extracted the first PCA axes, transformed on a scale of 0–1 (Dormann et al. 2013). Elevation was obtained from digital maps (Kartverket 2019) and site-level data on average monthly precipitation was provided by the Norwegian

Meteorological Institute (Table 1). We also recorded direction, slope and latitude in each treatment plot, to calculate the solar irradiation index (Oke 1987), hereafter 'irradiation index'. All calculations were computed in R (R Development Core Team 2017).

Statistical analyses

To test for treatment effects on bumble bee responses, we fitted linear mixed effect models (LMMs), with identity link, assuming a normal distribution of errors. This approach was used for all the bumble bee response variables; species richness, abundance, diversity, and abundance of; long-tongued bees, short-tongued bees, bees with early emerging queens, bees with late emerging queens, cuckoo bumble bees, and bees belonging to the *B. lucorum* group (Table 1). LMMs were used due to the rarefied responses consisting of non-integers. To achieve a normal distribution of the residuals we log+1 transformed overall abundance, and abundance of long-tongued bees, short-tongued bees, early emerging bees, late emerging bees, cuckoo bees, and bees belonging to the *B. lucorum* group. We carried out a preselection of candidate environmental co-variables (P-values ≤ 0.10); for each response variable, we tested each environmental variable separately and in a two-way interaction with the categorical variable 'treatment'. Candidate environmental co-variables were year, elevation, forb richness, forb FDis, Ericacea species cover, *Salix* species cover, nectar tube species cover, FDis flower phenology, FDis inflorescence, irradiation index, source habitat, and landscape fragmentation (Table 1). For each model, we scaled all numerical variables and included site identity as random effect to account for among-sites variation and repeated sampling (i.e. three treatment plots sampled once per year). We calculated the generalized variance inflation factor (GVIF) values for all explanatory variables in each candidate model (Fox & Monette 1992; Zuur et al. 2010) using the car package in R (Fox et al. 2019). We retained all variables with a GVIF value of <3 in the full model (Zuur et al. 2010). Final models were selected by stepwise backward elimination based on likelihood ratio tests (LRTs), until only significant variables remained ($P \leq 0.05$) (Table A4).

For all the final models, we visually assessed model fit by plotting residuals against the fitted values for all explanatory variables and assessed the distribution of residuals using QQ-plots and the DHARMa package in R (Hartig 2018). All models were fitted using the lme4 package in R (Bates et al. 2019), and all analyses were carried out in R version 3.2.5 (R Development Core Team 2017). Model estimates were extracted using the effects package (Fox 2003).

Table 1: *The variables in the analyses. Response variables and candidate explanatory variables in the analyses of full regression models. Measured values (range) of the bees, and the functional trait groups. Spatial scale and measured values (range/levels) of the environmental conditions, habitat characteristics and the plant community (floral resources). Variables in bold were included in the full (most complex) models after preselection. For description of the variables, see methods chapter under 'Data preparation'.*

Variables in analyses	Spatial scale	Range/levels (mean)
Responses		
Rarefied richness		**0 – 11 (5.9)**
(Species richness)		**0 – 14 (7.8)**
Abundance		**0 – 178.5 (43.2)**
Diversity		**0 – 2.2 (1.5)**
Long-tongued bumblebees		**0 – 80.6 (7.9)**
Short-tongued bumblebees		**0 – 159.5 (31.5)**
Early emergence queens		**0 – 157.2 (30.4)**
Late emergence queens		**0 – 96.3 (8.9)**
Cockoo bees		**0 – 27.3 (3.8)**
Bombus lucorum s.str.		**0 – 115.4 (17.4)**
Explanatory variables		
Year	**Site**	**2013, 2015**
Treatment	**Plot**	**uncut, cut, cut-remove**
Precipitation (mm)	**Site**	**45 – 86 (62.9)**
Elevation (m.a.s.l.)	**Site**	**45 – 535 (260)**
Irradiation index	Plot	-0.32 – 0.87 (0.39)
Source habitat area (PC1)	Site	0 – 1 (0.56)
Landscape fragmentation (Shannon diversity)	Site	1.6 – 3 (2.2)
Richness forbs	**Plot**	**0 – 31 (10.8)**
Ericacea dwarf shrub species (sum cover)	**Plot**	**0 – 58.8 (10.6)**
Salix species (sum cover)	Plot	0 – 6.7 (0.37)
Nectar species (sum cover)	**Plot**	**0 – 100 (17.16)**
FDis forbs	**Plot**	**0.20 – 0.41 (0.32)**
FDis flower phenology	Plot	0.01 – 0.41 (0.28)
FDis inflorenscence	Plot	0.0003 – 0.46 (0.3)

Results

We collected a total of 7266 individuals of bumble bees in 2013 (n= 3235) and 2015 (n=4031) (Fig. A2), comprising 22 species from 9 subgenera, of which 10 species were short-tongued, 6 were long-tongued, 7 were early emerging, and 9 were late emerging. Additionally, 6 species were cuckoo bees (668 individuals) (Table A3). A large proportion of the sampled individuals belonged to the *B. lucorum s.str.* group (2934 individuals) (Fig. 2).

We found that average richness and abundance of bumble bees was higher in the cut and cut-remove treatment plots, compared to the uncut plots (Table 2). We also found that the power-line clearings did not only support typical forest dwelling species such as, *Bombus jonellus*, *B. hypnorum* or *B. cingulatus*, but also several species associated with flower-rich natural or semi-natural grasslands, and other open habitats (e.g. *B. ruderarius*, *B. humilis*, *B. sylvarum*, *B. wurflenii*, and *B. sylvarum*) (Table A2).

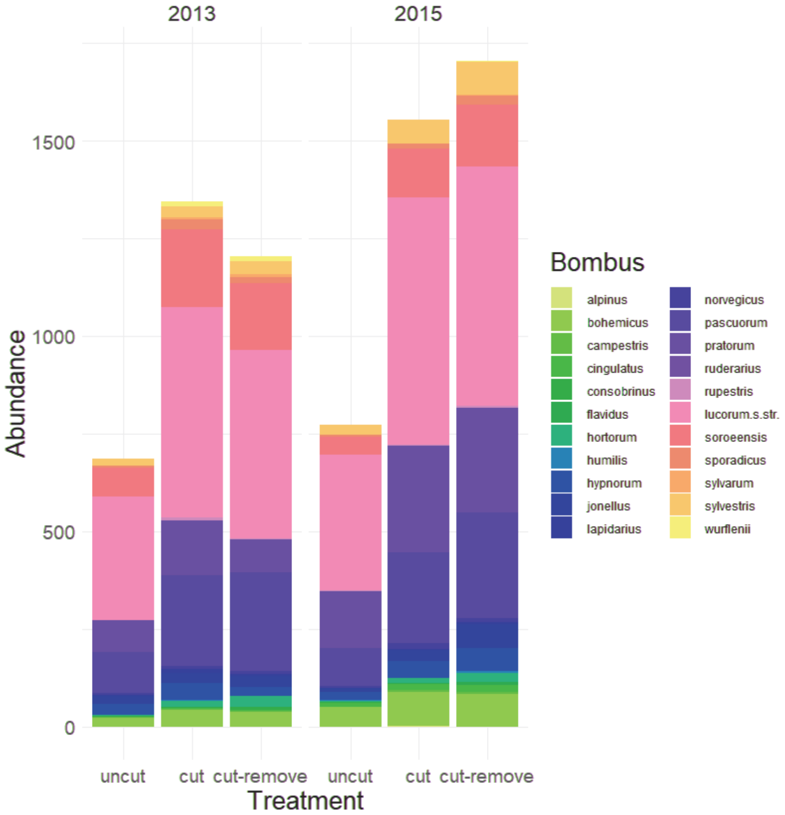

Fig. 2. *Bumble bees collected in the study. Abundance (raw) of bumble bees in each treatment (uncut, cut, cut-remove) in the two years (2013, 2015), with color-codes showing the abundance of each bumble bee species.*

Table 1: *The observed mean and standard deviation (mean ± SD) of richness and abundance of bumblebees in each treatment plot in the two years (2013 and 2015).*

	Richness		**Abundance**	
	2013	2015	2013	2015
uncut	5.8 ± 2.7	6.5 ± 2.2	27.4 ± 29.4	24.5 ± 24.4
cut	8.6 ± 2.9	8.8 ± 2.2	54.0 ± 40.6	49.9 ± 42.4
cut-remove	7.4 ± 2.9	9.6 ± 2.1	49.1 ± 46.0	54.1 ± 38.7

Species-based diversities

For all the species-based diversity measures, there was a positive effect of both the cut and the cut-remove treatments, compared to the uncut treatment, and the positive effect increased with forb species richness (Table 3, treatment × forb richness: bee species richness (Fig. 3a, LRT = 13.28, df = 2, P = 0.001), bee abundance (Fig. 3d, LRT = 8.14, df = 2, P = 0.017), and bee diversity (Fig. 3f, LRT = 12.23, df = 2, P = 0.002)). The estimated slopes of the relationship between species richness/abundance/diversity/raw richness and forb richness were not parallel for the cut and cut-remove treatments, but we did not find any statistically significant differences between the treatments (Figs. 3; A4, Tables 3; A5).

Species richness increased with 1.4 species from the first year to the third year after maintenance clearing (Fig. 4a, Table 3, LRT = 22.97, df = 1, $P \leq 0.001$). In addition, species richness showed an estimated increase from 5.2 to 9.4 species with increasing cover of forb species with nectar tube (Fig. 3b, Table 3, LRT = 12.46, df = 1, $P \leq 0.001$), and an estimated increase from 4.3 to 7 species along the FDis of forbs gradient (Fig. 3c, Table 3, LRT = 6.21, df = 1, P = 0.013). Bumble bee abundance increased from 23 to 101 individuals with increasing cover of forb species with nectar tube (Fig. 3e, Table 3, LRT = 10.62, df. = 1, P = 0.001). Diversity increased by 8% from the first to the last year (Fig. 4b, Table 3, LRT = 4.61, df = 1, P = 0.032) and declined 37% along the precipitation gradient (Fig. 3g, Table 3, LRT = 9.45, df = 1, P = 0.002).

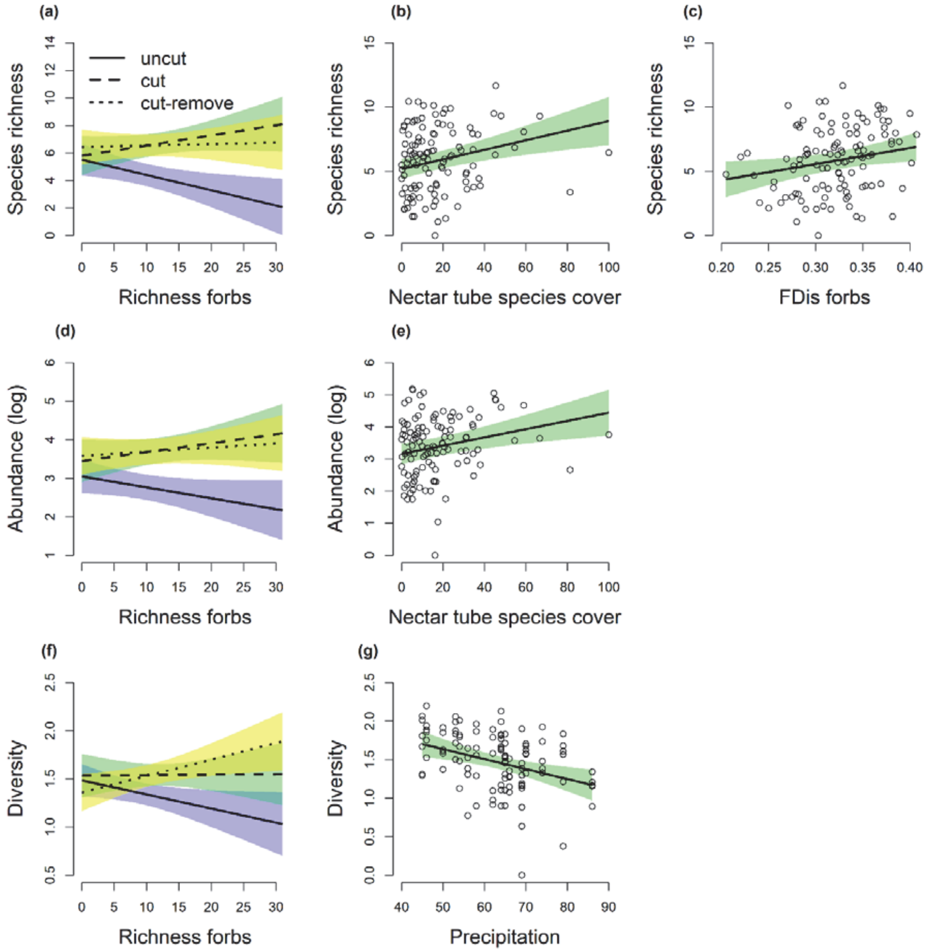

Fig. 3. *Effect of treatments and explanatory variables on species-based diversity of bumble bees: The treatment effect (treatments: uncut, cut, cut-remove) on (a) species richness in response to richness of forbs species, (b) species richness in response to cover of nectar tube species, and (c) species richness in response to functional dispersion (FDis) of forbs. The treatment effect on (d) abundance (log(y+1)) in response to richness of forbs, and (e) abundance (log(y+1)) in response to cover of forb species with a nectar tube. The treatment effect on (f) diversity with increasing species richness of forbs, and diversity in response to precipitation. The shaded areas are 95% confidence intervals (CIs). Uncut (solid lines) has blue CIs, cut (dashed line) has green CIs, and cut-remove (dotted line) has yellow CIs.*

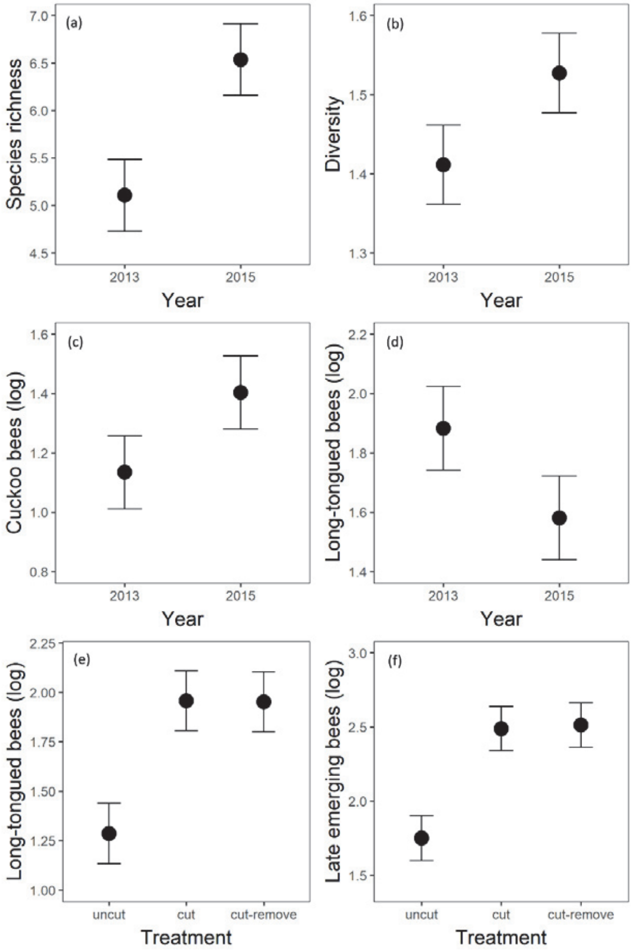

Fig. 4. *Effect of year and treatment on bumble bees: (a) Richness and (b) diversity in response to year (2013, 2015). (c) Abundance of cuckoo bees (log(y+1)) and (d) abundance of long-tongued bees (log(y+1)) in response to year. (e) Abundance of long-tongued species (log(y+1)) and (f) late emerging species (log(y+1)) in response to the three treatments (uncut, cut, cut-remove). Black dots and whiskers are estimated values and 95 % CI limits.*

Functional trait groups

Within the individual trait groups, the long-tongued and late emerging species – which are of special conservation interest –were positively associated with the cleared treatments (cut and cut-remove) (Figs. 4e, 4f) and increased with functional variation of forb species (Figs. 5b; 5c). Average abundance of long-tongued bumble bee species was 6 individuals in both the cut and cut-remove treatment, compared to 2.6 individuals in the uncut treatment (Fig. 4e, Table 3, LRT = 27.23, df = 2, P ≤0.001). Abundance of long-tongued species decreased by 1.7 individuals from 2013 to 2015 (Fig. 4d Table 3, LRT = 7.55, df = 1, P = 0.006), and was negatively related to elevation (Fig. 5a, Table 3, LRT = 5.69, df = 1, P = 0.017). In contrast, abundance of long-tongued species showed a strong positive relationship with functional dispersion of forbs, increasing from 1.8 to 8.5 individuals along the FDis of forbs gradient (Fig. 5b, Table 3, LRT = 11.11, df = 1, P ≤0.001). For the abundance of late emerging species there were 6 individuals more in both the cut and cut-remove treatments, than in the uncut treatment (Fig. 4f, Table 3, LRT = 32.87, df = 2, P ≤0.001). The late emerging species also showed a twofold increase along the FDis of forbs gradient (Fig. 5c, Table 3, LRT = 9.02, df = 1, P = 0.003).

For the generalist trait groups, we found the same main patterns as for the species-based diversities (Fig. 5, Table 3). Abundance of short-tongued species was positively related to richness of forbs in both the cleared treatments, in contrast to the uncut treatment (Fig 5g, Table 3, treatment × richness forbs: LRT = 7.06, df = 2, P = 0.029). As for the species-based bee diversity responses we found no significant differences between the cut and cut-remove practices (Fig. 5g, Table 3). Abundance of short-tongued species increased from 14 to 81 individuals along the ericaceous dwarf shrub gradient (Fig. 5d, Table 3, LRT = 16.19, df = 1, P ≤0.001). The treatment effect on the abundance of early emerging species depended on richness of forbs (treatment × richness forbs: LRT = 7.53, df = 2, P = 0.023), increasing from 20 to 45 individuals in the cut treatment, compared to a decrease from 25 to 23 individuals in cut-remove and from 14 to four individuals in the uncut treatment along the forbs richness gradient (Fig. 5c, Table 3). Abundance of early emerging species also increased from 14 to 89 individuals with increasing cover of forb species with nectar tube (Fig. 5d, Table 3, LRT = 12.63, df = 1, P ≤0.001).

The treatment effect on abundance of cuckoo bees depended on cover of forb species with nectar tube (treatment × nectar species cover: LRT = 11.66, df = 2, P = 0.004). With increasing cover of nectar species, abundance of cuckoo bumble bees went from two to 9 individuals in the cut treatment and increased from 1.6 to 57 individuals in the cut-remove treatment, compared to a reduction from two to one individual in treatment uncut (Fig. 5i, Table 3). Cuckoo bees increased from an average estimated abundance of two individuals the first year to three individuals the last year (Fig. 4c, Table 3, LRT = 8.65, df = 1, P = 0.014). The cuckoo bees also decreased 79% along the precipitation gradient (Fig. 5f, Table 3, LRT = 4.8, df = 1, P = 0.044).

The abundance of the *B. lucorum s.str.* group were strongly associated with treatments cut and cut-remove, with an estimated average of 2 individuals more in the cut than in cut-remove and 10 individuals more in cut than in treatment uncut (Fig. A3b, Table 3, LRT = 29.66, df = 2, P ≤0.001). Abundance of *B. lucorum* bees also increased more than four-fold along the observed gradient of Ericaceae cover (Fig. A3d, Table 3, LRT= 10.60, df=1, P= 0.001).

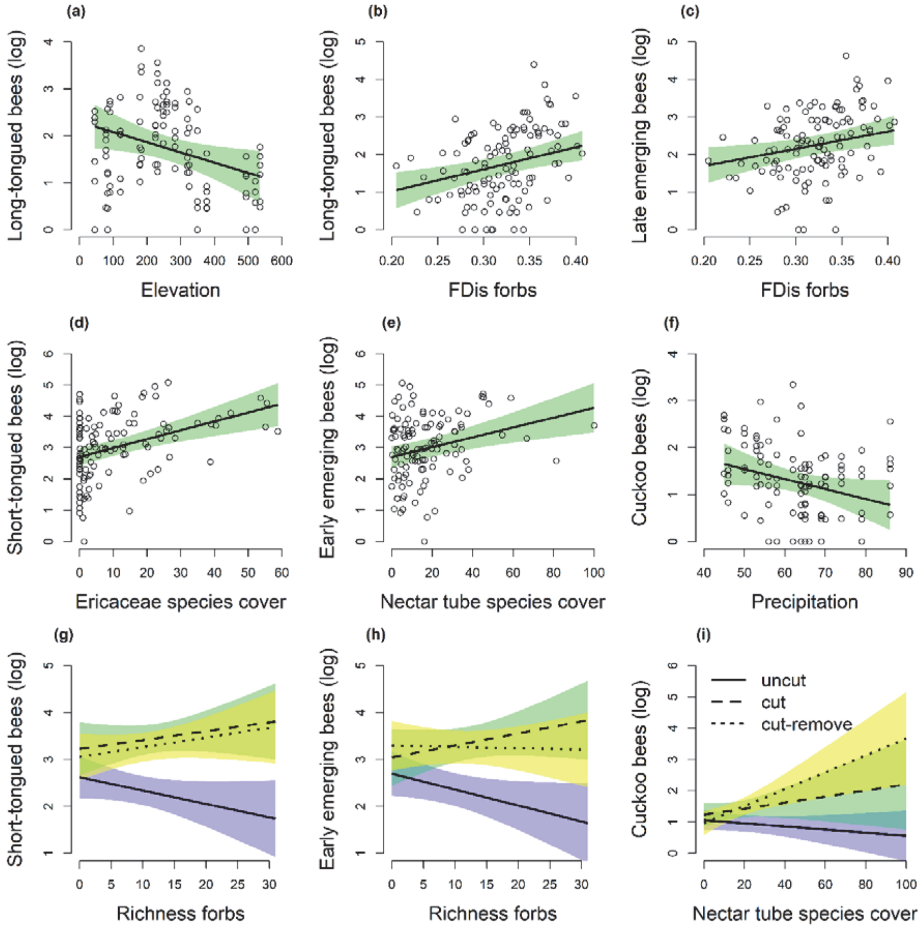

Fig. 5. *Effect of treatments and environmental factors on the abundance of functional trait groups of bumble bees: (a) Abundance of long-tongued species (log(y+1)) in response to elevation, and (b) to functional dispersion (FDis) of forbs. (c) Abundance of late emerging species (log(y+1)) in response to FDis of forbs. (d) Abundance of short-tongued species (log(y+1)) in response to cover of ericaceous dwarf shrubs. (e) abundance of early emerging bees (log(y+1)) in response to cover of forb species with nectar tube. (f) Abundance of cuckoo bees in response to precipitation. (g) Abundance of short-tongued bees (log(y+1)), and (h) abundance of early emerging bees in response to the three treatments (uncut, cut, cut-remove), and increasing species richness of forbs. (i) The treatment effect on abundance of cuckoo bees with increasing cover of forb species with nectar tube. The shaded areas are 95% confidence intervals (CIs). Uncut (solid lines) has blue CIs, cut (dashed line) has green CIs, and cut-remove (dotted line) has yellow CIs.*

Table 2: *Final model summary outputs from LMMs, linear mixed-effects models. The effects of treatment and environmental factors on species richness, abundance (log), and diversity of bumblebees, on abundance of cuckoo bumble bees (log), abundance of long-tongued bumble bees (log), short-tongued bumble bees (log), abundance of early emerging bumble bees (log), and late emerging bumble bees (log) in power-line clearings. Variables: year (2013 = reference level, and 2015), treatment (uncut = reference level, cut, and cut-remove), richness forbs, FDis forbs, elevation, precipitation, Nectar tube species cover, Ericaceae species cover. SE = standard error;* σ^2 *= variance;* τ_{00} *= variance of intercepts;* R^2m *= marginal* R^2*, represents the variance explained by fixed effects;* R^2c *= conditional* R^2*, represents variance explained by both fixed and random effects.*

	Species richness				**Abundance**			
Fixed effects	*β*	*SE*	*t*	*p*	*β*	*SE*	*t*	*p*
Intercept (Year 2013, Uncut)	3.61	0.44	8.2	<0.001	2.74	0.17	16.27	<0.001
Cut	2.27	0.38	5.92	<0.001	0.95	0.14	6.81	<0.001
Cut-remove	2.23	0.37	5.99	<0.001	0.95	0.14	7.02	<0.001
Year 2015	1.43	0.29	4.89	<0.001				
Richness forbs	-0.83	0.33	-2.52	0.012	-0.21	0.12	-1.76	0.079
Cut × Richness forbs	1.38	0.4	3.47	0.001	0.38	0.14	2.66	0.008
Cut-remove × Richness forbs	0.91	0.37	2.44	0.015	0.29	0.14	2.11	0.035
FDis forbs	0.51	0.21	2.43	0.015				
Nectar tube species cover	0.63	0.18	3.51	<0.001	0.22	0.07	3.23	0.001
Random Effects								
σ^2	2.38				0.33			
τ_{00}	1.89 $_{\text{Site}}$				0.36 $_{\text{Site}}$			
N	19 $_{\text{Site}}$				19 $_{\text{Site}}$			
Observations	114				114			
R^2m / R^2c	0.37 / 0.65				0.26 / 0.65			

	Diversity				**Cockoo bees**			
Fixed effects	*β*	*SE*	*t*	*p*	*β*	*SE*	*t*	*p*
Intercept (Year 2013, Uncut)	1.27	0.06	19.79	<0.001	0.84	0.15	5.71	<0.001
Cut	0.21	0.07	3.06	0.002	0.42	0.14	3.08	0.002
Cut-remove	0.21	0.07	3.15	0.002	0.46	0.14	3.34	0.001
Year 2015	0.12	0.05	2.12	0.034	0.27	0.11	2.42	0.016
Richness forbs	-0.11	0.05	-2.06	0.040				
Cut × Richness forbs	0.11	0.07	1.56	0.119				
Cut-remove × Richness forbs	0.24	0.07	3.47	0.001				
Precipitation	-0.14	0.04	-3.24	0.001	-0.22	0.11	-2	0.046
Nectar species cover					-0.09	0.08	-1.05	0.295
Cut × Nectar tube species cover					0.25	0.16	1.56	0.119
Cut-remove × Nectar tube species cover					0.54	0.17	3.24	0.001
Random Effects								
σ^2	0.08				0.35			
τ_{00}	0.02 $_{\text{Site}}$				0.17 $_{\text{Site}}$			
N	19 $_{\text{Site}}$				19 $_{\text{Site}}$			
Observations	114				114			
R^2m / R^2c	0.33 / 0.42				0.23 / 0.49			

	Long-tongued				**Short-tongued**			
Fixed effects	*β*	*SE*	*t*	*p*	*β*	*SE*	*t*	*p*
Intercept (Year 2013, Uncut)	1.44	0.16	8.8	<0.001	2.32	0.16	14.7	<0.001
Cut	0.67	0.14	4.86	<0.001	1.11	0.16	6.85	<0.001
Cut-remove	0.67	0.14	4.84	<0.001	0.96	0.16	6.19	<0.001
Year 2015	-0.3	0.11	-2.74	0.006				
Elevation	-0.32	0.13	-2.43	0.015				
FDis forbs	0.24	0.07	3.33	0.001				
Ericacea species cover					0.39	0.09	4.22	<0.001
Richness forbs					-0.21	0.13	-1.62	0.105
Cut-remove × Richness forbs					0.37	0.16	2.36	0.018
Cut × Richness forbs					0.35	0.16	2.14	0.032
Cut-remove × Richness forbs					0.37	0.16	2.36	0.018
Random Effects								
σ^2	0.34				0.43			
τ_{00}	0.26_{Site}				0.23_{Site}			
N	19_{Site}				19_{Site}			
Observations	114				114			
R^2m / R^2c	0.33 / 0.62				0.38 / 0.62			

	Early emerging				**Late emerging**			
Fixed effects	β	*SE*	*t*	*p*	*β*	*SE*	*t*	*p*
Intercept (Year 2013, Uncut)	2.33	0.18	13.09	<0.001	1.75	0.15	11.61	<0.001
Cut	0.99	0.16	6.28	<0.001	0.74	0.14	5.39	<0.001
Cut-remove	0.93	0.15	6.1	<0.001	0.76	0.14	5.59	<0.001
Richness forbs	-0.25	0.13	-1.9	0.057				
Cut × Richness forbs	0.44	0.16	2.74	0.006				
Cut-remove × Richness forbs	0.23	0.15	1.5	0.135				
FDis forbs					0.19	0.07	2.65	0.008
Nectar tube species cover	0.27	0.08	3.54	<0.001				
Random Effects								
σ^2	0.41				0.34			
τ_{00}	0.38_{Site}				0.26_{Site}			
N	19_{Site}				19_{Site}			
Observations	114				114			
R^2m / R^2c	0.21 / 0.64				0.25 / 0.56			

4.0 Discussion

Experimental clearing of the vegetation in power-line clearings enhanced the habitat quality for bumble bees, irrespective of woody debris retention or removal. Our study clearly demonstrates the positive effects of maintenance clearing on bumble bees the first years after cutting. The treatment effects on bumble bee species richness, abundance and diversity were dependent on forb species richness. Particularly, the cover of forb species with nectar tube was positively associated with bumble bee species richness and abundance. Functional groups of special conservation concern, such as the long-tongued specialists and the late emerging species, also seemed to prefer the early successional habitats in the cleared treatment plots and increased in abundance in habitats with a larger variation of functional traits of forbs. Bumble bee richness and diversity increased over time, but the long-tongued species were more abundant in the first year after clearing.

The large difference between the two types of cleared plots and the uncut treatment plots showed that the effect of maintaining the vegetation in an early successional phase has a pronounced positive effect on bumble bees. This effect was further amplified by increased levels of floral resources. These results are in accordance with previous studies showing how flower rich early successional stands within clear-cuts in boreal forest landscapes are especially important for wild bee species (Cartar 2005; Rubene et al. 2015). Furthermore, the early successional vegetation enhanced the habitat quality through increased forbs richness, which agrees with previous studies documenting a higher bumble bee richness and abundance where there is an elevated species richness or cover of flowers (Carvell et al. 2004; Pywell et al. 2005; Pywell et al. 2006; Rubene et al. 2015). Our results also show that bumble bees are attracted to sites containing flowers with nectar tube, which was expected since bumble bees are well known for their preference for plants with high nectar content (Pywell et al. 2006; Goulson et al. 2005).

Bumble bee species richness and diversity increased in all treatments from the first to the third year, showing how bumble bees were attracted to the power-line clearings at least during the first three years after cutting. This finding suggests that the less intensively managed habitats in power-line clearings – with early successional vegetation left undisturbed over several years – may be of great importance as alternative natural or semi natural grassland habitats for bumble bees. According to Taki et al. (2013), the positive effects of early successional forest openings increased richness and abundance of social bees as the successional stages progressed over decades in natural regenerating forest, without leveling off. In our study, based on the results in our uncut treatment plots, the regrowth of trees after e.g. five or more years after cutting (dependent on site-productivity) was negatively correlated with bumble bee diversity. Thus, our results indicate that a more frequent cutting would benefit bumble bee communities. Our opposing result to Taki et al. (2013), could be that their study was based on few bumble bee species, which likely do not mirror larger bumble bee communities. To further improve the conservation efforts for bumble bees in power-line clearings, it would be essential for future studies to find the optimal timing of cutting, similar to what has been done for butterflies (e.g. Komonen et al. 2013).

Woody debris removal did not seem to increase bumble bee habitat quality compared with the plots where cut woody debris was left to decay. This result was somewhat surprising and contradicts previous findings where woody debris removal had an added positive effect on solitary bees in power-line clearings (Steinert et al. 2020; Sydenham et al. 2016). The lack of a clear preference for either of the cleared treatments may be due to the modest differences in floral resources between the two cleared treatments (Steinert et al. 2018), thus bumble bees will forage over the entire site. Additionally, bumble bees are robust dispersers, and may not be limited by vegetation height when searching for food. Clearing and leaving the woody debris to decay may also provide other important resources for bumble bees, such as nesting and overwintering sites. Persson et al. (2015), found that bumble bees nesting above-ground are suffering relatively more from loss of nesting habitats. Leaving the woody debris to decay on the ground may be beneficial for both below and above-ground nesters of bumble bees, because bumble bees prefer nest entrances concealed by dense vegetation or different types of debris (Lanterman et al. 2019). In addition, open habitats may also be favourable for small mammals (Michał & Rafał 2014) that create nest sites for many bumblebees. Compared to more intensively managed habitats, such as meadows or road verges, power-line clearings may provide periods of undisturbed nesting habitat, which may be a limiting factor in most other open areas undergoing more frequent management regimes. However, the similar diversity in both types of cleared treatment plots can also be ascribed the bumble bees' ability to forage over large areas (Osborne et al. 2008a), indicating that habitats with flower resources are likely to be visited, irrespective of distances between the treatment plots.

In addition to identifying management practices, which increase the species-based diversity, we also wanted to understand to what degree these practices retain the functional diversity of bumble bee communities, to ensure the provision of complementary pollination services (Albrecht et al. 2012; Hoehn et al. 2008). By taking functional trait groups into account we were able to identify the effects on the vulnerable long-tongued and late emergence species. The long-tongued species preferred the cleared habitats the first year after cutting, when vegetation was short, which accords with typical grassland habitats where floral resources for the more specialized species can be found (Goulson et al. 2008).

Additionally, the abundance of long-tongued species was positively correlated with a high functional diversity of floral traits, likely related to the ability to find preferred food plants throughout the season. Among the long-tongued species, belonging to the Thoracobombus and Megabombus, all species except *B. pascuorum* and *B. hortorum* had low abundances. However, the most abundant, *B. pascuorum*, was relatively stable in both years, thus the other less common long-tongued species must have driven the response of favoring the early succession in the clearings first year after cutting. We also found that the abundance of long-tongued species was higher at lower elevations, which corresponds to the more productive sites associated with more heterogenous landscapes within our study area. Late emerging species were markedly more abundant in the two cleared treatment plots and in areas with a high functional diversity of floral traits, which is likely related to the availability of important floral resources (Persson et al. 2015). A larger variety of flower types increases bumble bee niche differentiation and reduces interspecific competition from *Bombus* species for the late-emerging species (Goulson et al. 2008). Variation in traits of both plants and bee species may be advantageous, allowing for different colonies to forage on separate parts of a rich flora (Persson et al. 2015).

The short-tongued bees and the early emerging species included some of the more abundant and common species and showed similar responses to the species-based diversities, with a higher abundance related to forbs species richness in both the cleared treatments. The short-tongued species were also positively responding to increased cover of ericaceous species. This response was likely driven by the more common *B. jonellus* and *B. hypnorum*, in addition to the *B. lucorum* group, which were more abundant in the Ericaceae dominated sites. We may expect species where the queens have an early spring emergence (e.g. *Bombus lucorum s.str., B. lapidarius, B. hypnorum, B. pratorum, B. hypnorum*) to be vulnerable to resource availability at the onset of the season. Contrary to our expectations we found no effect of the cover of *Salix* species on the abundance of early emergence species. Possibly because willow or *Salix* species can be found outside the power-line clearings and would only be present in the treatment plots the third year after cutting. In addition, the flowering of some *Salix* species may have occurred before we installed the traps in late April/May. We also tested the abundant *B. lucorum* group and found that they increased substantially with the cover of ericaceous species. However, these species may be found in a wide variety of habitats from the coast to forests and mountains (Ødegaard et al. 2015). Accordingly, the abundance of this group was also high in sites with intermediate and low levels of Ericacea species cover (i.e. low productive sites) (Fig. A2).

The cuckoo bees preferred the treatments where woody debris was removed in areas with increasing cover of forb species with nectar tubes. We expected cuckoo bees to be more abundant in plots with high host abundance. The most abundant cuckoo bees were *B. bohemicus* and *B. sylvestris*, which are social parasites on *B. lucorum* (within the *B. lucorum* group) and *B. pratorum*, respectively, some of the most common *Bombus* species in Norway (Ødegaard et al. 2015). Particularly, the abundance of these two cuckoo bee species increased over time corresponding to the temporal increase of their hosts, supporting the theory that cuckoo bees may be indicators of an improved habitat quality, through their host dependency (Sheffield et al. 2013). Given the dependency on declining host species (Lhomme & Hines 2018), some of the cuckoo bees are relatively rare and at risk of extinction (Suhonen et al. 2016), underlining the importance of the early successional habitats in the clearings for conservation of species rich bumble bee communities.

Social bee species have been found to be positively correlated with the proportion of semi-natural habitats in the landscape (Williams et al. 2010), and therefore we expected the amount of source habitat areas in the surroundings to influence our measured bumble bee responses. However, we found no effect of available source habitat area or landscape fragmentation on any of the responses. Possibly the lack of relationships is because our proxies for amount of source habitat and landscape fragmentation did not capture habitat elements on a scale that is relevant for bumble bees, since some bumble bees are able to forage over larger distances than two kilometers (Osborne et al. 2008a). However, foraging ranges are often reported to be below 1 kilometer (Knight et al. 2005; Osborne et al. 2008a). Therefore, another explanation may be that the bumble bees were not limited by source habitats within flight distances at our sites.

Conclusions and management implications

Early successional habitats have become increasingly patchy in modern landscapes, which makes the knowledge of managing the extensive areas of human modified habitats for conservation purposes a promising way forward. Our research demonstrates the importance of early successional habitats for species diversity and functional trait groups of bumble bees, and the woody debris in the field layer and the regrowth during three years post cutting does not seem to matter as long as there are sufficient flower resources available. Conservation efforts for bumble bees in power-line clearings should aim at promoting habitat heterogeneity and stability of floral and nesting resources (Russell et al. 2018). But this is not necessarily achieved by implementation of a large-scale woody debris removal as an addition to standard management protocol in boreal regions. However, woody debris removal may increase the functional diversity of floral resources (Steinert et al. 2018), which may benefit the more vulnerable long-tongued and late emergence species. This is in accordance with conservation recommendations for solitary bees in power-line clearings, because solitary bees are found to benefit from early successional habitats where the ground is exposed (Steinert et al. 2020). Recommendations for overall wild bee conservation would thus be to implement a mosaic of woody debris retention and removal in power-line clearings, to support diverse wild bee communities.

Power-line clearings proves to be valuable alternative habitats for bumble bees in forests, likely providing nest sites and enhanced foraging resources, with the potential to preserve the important ecosystem functions and services bumble bees provide. Conservation measures at a local scale could contribute to increase the resource availability at a landscape scale, which is important for regional bumble bee populations (Knight et al. 2005). When habitats in the power-line clearings are kept in early succession, this may generate local increases of pollinators, potentially acting as source habitats for native bee populations (Russel et al. 2018). This has the potential of redistributing pollinators in the landscape, which may lead to new stable and persistent pollinator populations (M'Gonigle et al. 2015). Our results suggest that most bumble bees thrive in less intensively disturbed early successional habitats, whereas the more vulnerable and extinction prone species seem to also benefit from increasing the frequency of cutting, i.e. preventing the regrowth from outcompeting floral resources. To promote bumble bees, we suggest that a more frequent cutting of the vegetation than the standard long intervals of up to 10-12 years, has the potential to sustain the floral vegetation in time and space for bumble bees.

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Author contribution

MS performed the analyses, wrote the first draft of the manuscript and led the writing of the manuscript. KE and SRM designed and initiated the experiment. MS and MAKS identified the bumble bees. All authors discussed the results and contributed to previous drafts and the final manuscript.

Conflict of Interest

The authors declare that they have no conflict of interest.

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Appendix

Appendix: Supplementary material

Title: **“Bumble bee communities in power-line clearings: effects of experimental management practices”**

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Table A1 Functional traits of forbs**.** Description of the functional traits and the value per trait.

No.	Trait	Value/No. categories	Description
1.	Inflorescence	3	A: singular flowers B: singular flowers in a group C: multi flowers/pseudanthium
2.	Flower colors	16	color variations
3.	Exposed nectar/pollen	2	exposed / not exposed
4.	Nectar tube	3	nectar tube / no nectar tube
5.	Pollen per flower	2	few: less than 4 anthers per flower many: more than 4 anthers per flower
6.	Flowering period	4	vår = spring fso = early summer mso = mid summer sso = late summer
7.	Height	6.5 – 125	average potential height (cm)
8.	Floral symmetry	2	Actinomorphic / zygomorphic
9.	Lifenastrategy	3	Annual / biennial / perennial

Table A2 List of forb species and the corresponding functional traits; 9 functional traits that were used to calculate the functional diversity indices (i.e. functional dispersion). Nomenclature follows Artsdatabanken (2015)*. Traits are retained from Lid and Lid (2005)**

Family	**Species**	**Functional traits**								
		Inflore-scence	**Flower colors**	**Life-strategy**	**Symmetry**	**nectar/ pollen**	**Nectar tube**	**Pollen per flower**	**First flowering**	**Average height (cm)**
Apiaceae	*Angelica sylvestris*	C	white	perennial	actinomorphic	exposed	no	few	mso	125
Apiaceae	*Anthriscus sylvestris*	C	white	perennial	actinomorphic	exposed	no	many	fso	100
Apiaceae	*Peucedanum palustre*	C	white	biennial	actinomorphic	exposed	no	many	mso	80
Apiaceae	*Pimpinella saxifraga*	C	white	perennial	actinomorphic	exposed	no	many	fso	35
Asparagaceae	*Convallaria majalis*	B	white	perennial	actinomorphic	concealed	no	few	vår	20
Asteraceae	*Achillea millefolium*	C	white-pink	perennial	actinomorphic	exposed	no	few	mso	35
Asteraceae	*Antennaria dioica*	C	white-pink	perennial	actinomorphic	exposed	no	few	fso	15
Asteraceae	*Carduus vulgare*	C	purple	biennial	actinomorphic	exposed	short	few	mso	95
Asteraceae	*Cirsium arvense*	C	purple	perennial	actinomorphic	exposed	short	few	mso	80
Asteraceae	*Cirsium heterophyllum*	C	purple	perennial	actinomorphic	exposed	short	few	mso	100
Asteraceae	*Cirsium palustre*	C	purple	biennial	actinomorphic	exposed	short	few	mso	125
Asteraceae	*Gnaphalium sp*	C	brown	perennial	actinomorphic	exposed	short	few	mso	27.5
Asteraceae	*Hieracium lactucella*	C	yellow	perennial	actinomorphic	exposed	long	few	fso	20
Asteraceae	*Hieracium pilosella sp*	C	yellow	perennial	actinomorphic	exposed	long	few	fso	17.5
Asteraceae	*Hieracium sp*	C	yellow	perennial	actinomorphic	exposed	long	few	NA	NA
Asteraceae	*Hieracium Sylvatica sp*	C	yellow	perennial	actinomorphic	exposed	long	few	fso	37.5
Asteraceae	*Hierarcium umbellatum*	C	yellow	perennial	actinomorphic	exposed	long	few	mso	42.5
Asteraceae	*Hierarcium vulgatum*	C	yellow	perennial	actinomorphic	exposed	long	few	fso	50
Asteraceae	*Hypochaeris maculata*	C	yellow	perennial	actinomorphic	exposed	long	many	fso	40
Asteraceae	*Lapsana communis*	C	yellow	perennial	actinomorphic	exposed	long	few	mso	75
Asteraceae	*Leontodon autumnale*	C	yellow	perennial	actinomorphic	exposed	long	few	mso	22.5
Asteraceae	*Leucanthemum vulgare*	C	white-yellow	perennial	actinomorphic	exposed	short	few	fso	45
Asteraceae	*Omaloteca sylvatica*	C	brown	perennial	actinomorphic	exposed	long	few	mso	27.5
Asteraceae	*Solidago canadensis*	C	yellow	perennial	actinomorphic	exposed	long	many	sso	100
Asteraceae	*Solidago virgaurea*	C	yellow	perennial	actinomorphic	exposed	long	many	mso	52.5

Asteraceae	*Tussilago farfara*	C	yellow	perennial	actinomorphic	exposed	long	few	vår	12.5
Asteraceae	*Tanacetum vulgaris*	C	yellow	perennial	actinomorphic	exposed	short	few	mso	95
Asteraceae	*Taraxacum sp*	C	yellow	perennial	actinomorphic	exposed	long	many	NA	22.5
Balsaminaceae	*Impatiens noli-tangere*	A	yellow	annual	zygomorphic	concealed	long	few	mso	55
Brassicaceae	*Cardamine amara*	B	white	perennial	actinomorphic	exposed	short	few	vår	27.5
Brassicaceae	*Cardamine dentata*	B	white-lilac	perennial	actinomorphic	exposed	short	few	fso	30
Brassicaceae	*Cardamine pratensis*	B	white-lilac	perennial	actinomorphic	exposed	short	few	vår	35
Brassicaceae	*Thlaspi caerulescens*	C	white-pink	perennial	actinomorphic	exposed	Short	many	vår	20
Campanulaceae	*Campanula persicifolia*	A	blue	perennial	actinomorphic	exposed	no	few	mso	55
Campanulaceae	*Campanula rotundifólia*	A	blue	perennial	actinomorphic	exposed	no	few	fso	30
Caprifoliaceae	*Succisa pratensis*	C	blue-violet-lilac	perennial	actinomorphic	exposed	long	few	sso	40
Caprifoliaceae	*Valeriana sambucifolia*	C	white-pink	perennial	zygomorphic	exposed	long	few	fso	110
Carophyllaceae	*Carophyllaceae sp*	A	white	perennial	actinomorphic	exposed	no	many	NA	NA
Carophyllaceae	*Cerastium arvénse*	A	white	perennial	actinomorphic	exposed	no	many	fso	20
Carophyllaceae	*Cerastium fontanum*	A	white	perennial	actinomorphic	exposed	no	many	fso	25
Carophyllaceae	*Moehringia trinervia*	A	white	annual	actinomorphic	exposed	no	many	fso	12.5
Carophyllaceae	*Silene dioica*	A	pink	perennial	actinomorphic	exposed	long	many	fso	40
Carophyllaceae	*Silene rupestris*	A	white	annual	actinomorphic	exposed	short	many	mso	12.5
Carophyllaceae	*Stellaria graminea*	A	white	perennial	actinomorphic	exposed	no	many	fso	25
Carophyllaceae	*Stellaria longifolia*	A	white	perennial	actinomorphic	exposed	no	many	fso	22.5
Carophyllaceae	*Stellaria media*	A	white	annual/ biennial	actinomorphic	exposed	no	many	vår	22
Carophyllaceae	*Stellaria nemorum*	A	white	perennial	actinomorphic	exposed	no	many	fso	30
Cichoriaceae	*Mycelis muralis*	A	yellow	perennial	actinomorphic	exposed	long	few	mso	70
Clusiaceae	*Hypericum maculatum*	B	yellow	perennial	actinomorphic	exposed	no	many	mso	85
Clusiaceae	*Hypericum perforatum*	B	yellow	perennial	actinomorphic	exposed	no	many	mso	50
Convallariaceae	*Maianthemum bifolium*	B	white	perennial	actinomorphic	exposed	no	few	vår	12.5
Cornaceae	*Chamaepericlymenum suecicum*	A	white	perennial	actinomorphic	exposed	no	many	fso	12.5
Crassulaceae	*Sedum telephium*	C	white-green	perennial	actinomorphic	exposed	no	many	mso	35
Dipsacaceae	*Knautia arvensis*	C	pink	perennial	actinomorphic	exposed	long	few	mso	55

Ericaceae	*Pyrola rotundifolia*	B	white-pink	perennial	actinomorphic	concealed	no	many	fso	20
Ericaceae	*Pyrola media*	B	white-pink	perennial	actinomorphic	concealed	no	many	fso	20
Fabaceae	*Lathyrus linifolius*	A	purple-blue	perennial	zygomorphic	concealed	long	few	vår	20
Fabaceae	*Lathyrus pratensis*	B	yellow	perennial	zygomorphic	concealed	long	few	fso	40
Fabaceae	*Lathyrus vernus*	B	purple	perennial	zygomorphic	concealed	long	few	vår	30
Fabaceae	*Trifolium medium*	C	pink	perennial	zygomorphic	concealed	long	few	fso	35
Fabaceae	*Trifolium pratense*	C	pink	perennial	zygomorphic	concealed	long	few	fso	32.5
Fabaceae	*Trifolium repens*	C	white-pink	perennial	zygomorphic	concealed	long	few	fso	25
Fabaceae	*Vicia cracca*	B	blue-violet	perennial	zygomorphic	concealed	long	few	fso	50
Fabaceae	*Vicia sepium*	B	purple	perennial	zygomorphic	concealed	long	few	fso	45
Fabaceae	*Vicia sp*	B	pink-purple-blue	perennial	zygomorphic	concealed	long	few	NA	NA
Geraniaceae	*Geranium sylvaticum*	A	purple	perennial	actinomorphic	exposed	short	many	fso	50
Lamiaceae	*Ajuga pyramidalis*	B	blue-violet	perennial	zygomorphic	exposed	long	few	vår	15
Lamiaceae	*Clinopodium vulgare*	A	pink	perennial	zygomorphic	exposed	long	few	mso	40
Lamiaceae	*Galeopsis sp*	B	purple-pink-white	annual	zygomorphic	concealed	long	few	mso	NA
Lamiaceae	*Glechoma hederacea*	A	blue-violet	perennial	zygomorphic	concealed	long	few	vår	17.5
Lamiaceae	*Lamium purpureum*	A	pink	annual	zygomorphic	concealed	long	few	vår	17.5
Lamiaceae	*Lamium sp*	A	purple-pink	annual	zygomorphic	concealed	long	few	vår	22.5
Lamiaceae	*Prunella vulgaris*	B	blue-violet	perennial	zygomorphic	concealed	long	few	mso	15
Lamiaceae	*Scutellaria gallericulata*	A	blue-violet	perennial	zygomorphic	concealed	long	few	mso	22.5
Lamiaceae	*Stachys palustris*	B	pink	perennial	zygomorphic	concealed	long	few	mso	60
Lamiaceae	*Stachys sylvatica*	B	red-violet	perennial	zygomorphic	concealed	long	few	mso	75
Melanthiaceae	*Paris quadrifolia*	A	yellow-green	perennial	actinomorphic	exposed	no	many	vår	25
Onagraceae	*Chamerion angustifolium*	B	purple	perennial	actinomorphic	exposed	short	many	mso	125
Onagraceae	*Circaea alpina*	B	white	perennial	zygomorphic	exposed	short	few	fso	12.5
Onagraceae	*Epilobium montanum*	A	pink	perennial	actinomorphic	exposed	short	few	mso	60
Onagraceae	*Epilobium sp*	A	pink	perennial	actinomorphic	exposed	short	few	NA	NA
Orchidaceae	*Dactylorhiza maculata*	B	white-purple	perennial	zygomorphic	concealed	long	few	fso	25
Orchidaceae	*Epipactis atrorubens*	B	red-violet	perennial	zygomorphic	exposed	long	few	mso	35
Orchidaceae	*Listera ovata*	B	green	perennial	zygomorphic	exposed	long	few	fso	40

Orchidaceae	*Platanthera bifolia*	B	white	perennial	zygomorphic	concealed	long	few	fso	32.5
Orobanchaceae	*Euphrasia sp*	A	white-lilac	annual	zygomorphic	exposed	long	few	NA	NA
Orobanchaceae	*Euphrasia stricta*	A	white-lilac	annual	zygomorphic	exposed	long	few	mso	15
Orobanchaceae	*Melampyrum pratense*	A	yellow	annual	zygomorphic	exposed	long	few	fso	25
Orobanchaceae	*Melampyrum sp*	A	yellow	annual	zygomorphic	exposed	long	few	NA	NA
Orobanchaceae	*Melampyrum sylvaticum*	A	yellow	annual	zygomorphic	concealed	long	few	fso	25
Oxalidaceae	*Oxalis acetosella*	A	white-lilac	perennial	actinomorphic	exposed	no	many	vår	7.5
Plantaginaceae	*Linaria vulgaris*	B	yellow	perennial	zygomorphic	concealed	long	few	mso	42.5
Plantaginaceae	*Plantago lanceolata*	C	brown	perennial	actinomorphic	exposed	short	few	fso	30
Plantaginaceae	*Veronica beccabunga*	A	blue	perennial	actinomorphic	exposed	no	few	fso	25
Plantaginaceae	*Veronica chamaedrys*	A	blue	perennial	actinomorphic	exposed	no	few	vår	17.5
Plantaginaceae	*Veronica officinalis*	B	blue	perennial	actinomorphic	exposed	no	few	fso	20
Plantaginaceae	*Veronica scutellata*	A	white-lilac	perennial	actinomorphic	exposed	no	few	fso	17.5
Polygalaceae	*Polygala sp*	B	blue-violet	perennial	zygomorphic	concealed	long	few	NA	17.5
Polygalaceae	*Polygala vulgaris*	B	blue-violet	perennial	zygomorphic	concealed	long	few	fso	20
Polygonaceae	*Bistorta vivipara*	B	white	perennial	actinomorphic	exposed	no	few	fso	17.5
Polygonaceae	*Rumex acetosa*	B	red	perennial	actinomorphic	exposed	no	few	fso	50
Polygonaceae	*Rumex acetosella*	B	red	perennial	actinomorphic	exposed	no	few	fso	17.5
Primulaceae	*Lysimachia vulgaris*	B	yellow	perennial	actinomorphic	exposed	no	few	mso	100
Primulaceae	*Trientalis europaea*	A	white	perennial	actinomorphic	exposed	no	many	fso	12.5
Ranunculaceae	*Actaea spicata*	B	white	perennial	actinomorphic	exposed	no	many	fso	50
Ranunculaceae	*Anemone nemorosa*	A	white	perennial	actinomorphic	exposed	short	many	vår	20
Ranunculaceae	*Caltha palustris*	A	yellow	perennial	actinomorphic	exposed	no	many	vår	22.5
Ranunculaceae	*Hepatica nobilis*	A	blue	perennial	actinomorphic	exposed	no	many	vår	12.5
Ranunculaceae	*Ranunculus acris*	A	yellow	perennial	actinomorphic	exposed	no	many	fso	47.5
Ranunculaceae	*Ranunculus auricomus*	A	yellow	perennial	actinomorphic	exposed	no	many	vår	15
Ranunculaceae	*Ranunculus repens*	A	yellow	perennial	actinomorphic	exposed	no	many	fso	27.5
Ranunculaceae	*Ranunculus sp*	A	yellow	perennial	actinomorphic	exposed	no	many	NA	NA
Rosaceae	*Comarum palustre*	A	red	perennial	actinomorphic	exposed	no	many	fso	30
Rosaceae	*Filipendula ulmaria*	C	white	perennial	actinomorphic	exposed	no	many	fso	100

Rosaceae	*Fragaria ananássa*	A	white	perennial	actinomorphic	exposed	no	many	fso	22.5
Rosaceae	*Fragaria vesca*	A	white	perennial	actinomorphic	exposed	no	many	vår	12.5
Rosaceae	*Geum rivale*	A	red-brown	perennial	actinomorphic	exposed	no	many	vår	30
Rosaceae	*Geum urbanum*	A	yellow	perennial	actinomorphic	exposed	no	many	fso	50
Rosaceae	*Potentilla erecta*	A	yellow	perennial	actinomorphic	exposed	no	many	fso	20
Rubiaceae	*Galium boreale*	B	white	perennial	actinomorphic	exposed	no	few	mso	27.5
Rubiaceae	*Galium palustre*	B	white	perennial	actinomorphic	exposed	no	few	fso	25
Rubiaceae	*Galium uliginosum*	B	white	perennial	actinomorphic	exposed	no	few	fso	22.5
Rubiaceae	*Galium verum*	B	yellow	perennial	actinomorphic	exposed	short	few	fso	40
Saxifragaceae	*Chrysosplenium alternifolium*	B	yellow-green	perennial	actinomorphic	exposed	no	many	vår	12.5
Scrophulariaceae	*Scrophularia nodosa*	B	brown-red	perennial	zygomorphic	concealed	short	few	mso	70
Solanaceae	*Solanum dulcamara*	B	violet	perennial	actinomorphic	exposed	no	many	fso	110
Urticaceae	*Urtica dioica*	B	green	perennial	actinomorphic	exposed	no	few	fso	65
Urticaceae	*Urtica sp*	B	green	perennial	actinomorphic	exposed	no	few	NA	NA
Violaceae	*Viola canina*	A	blue	perennial	zygomorphic	exposed	short	few	fso	12.5
Violaceae	*Viola mirabilis*	A	lilac	perennial	zygomorphic	exposed	short	few	vår	20
Violaceae	*Viola palustris*	A	lilac	perennial	zygomorphic	exposed	short	few	vår	6.5
Violaceae	*Viola tricolor*	A	violet-yellow-white	perennial	zygomorphic	exposed	short	few	vår	17.5
Violaceae	*Viola riviniana*	A	blue-violet	perennial	zygomorphic	exposed	short	few	vår	15
Violaceae	*Viola sp*	A	violet	perennial	zygomorphic	exposed	short	few	NA	NA

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*Artsdatabanken. 2015. Artsnavnebasen. Norsk taksonomisk database., http://www2.artsdatabanken.no/artsnavn/Contentpages/Hjem.aspx

** Lid, J., and D. Lid. 2005. Norsk flora. 7 edition by R. Elven. Det Norske Samlaget, Oslo, Norway.

Table A3 List of bumblebees, subgenus, and the corresponding functional traits; tongue-length (long-tongued >8 mm/short-tongued<8 mm), phenology of the queens (early emergence (March, April)/late emergence (May, June)); Sociality (eusocial/cuckoo bumblebees). Phenology based on data from Bollingmo 2012* and Ødegaard et al. 2015**

Nr.	Species	Subgenus	Tongue-length	Phenology	Sociality
1	*Bombus alpinus*	Alpinobombus	short	May	eusocial
2	*Bombus bohemicus*	Psithyrus	short	April	cuckoo
3	*Bombus campestris*	Psithyrus	short	June	cuckoo
4	*Bombus cingulatus*	Pyrobombus	short	May	eusocial
5	*Bombus consobrinus*	Megabombus	long	June	eusocial
6	*Bombus flavidus*	Psithyrus	short	June	cuckoo
7	*Bombus hortorum*	Megabombus	long	May	eusocial
8	*Bombus humilis*	Thoracobombus	long	May	eusocial
9	*Bombus hypnorum*	Pyrobombus	short	March	eusocial
10	*Bombus jonellus*	Pyrobombus	short	April	eusocial
11	*Bombus lapidarius*	Melanobombus	short	April	eusocial
12	*Bombus norvegicus*	Psithyrus	short	May	cuckoo
13	*Bombus pascuorum*	Thoracobombus	long	May	eusocial
14	*Bombus pratorum*	Pyrobombus	short	March	eusocial
15	*Bombus ruderarius*	Thoracobombus	long	May	eusocial
16	*Bombus rupestris*	Psithyrus	short	June	cuckoo
17	*Bombus lucorum s.str.*	Bombus s.str.	short	March	eusocial
18	*Bombus soroeensis*	Kallobombus	short	April	eusocial
19	*Bombus sporadicus*	Bombus s str.	short	May	eusocial
20	*Bombus sylvarum*	Thoracobombus	long	April	eusocial
21	*Bombus sylvestris*	Psithyrus	short	May	cuckoo
22	*Bombus wurflenii*	Alpigenobombus	short	May	eusocial

*Bollingmo, T. 2012. Norges humler med Humleskolen. – BRAINS Media, Trondheim [Norwegian]

**Ødegaard, F., Staverløkk, A., Gjershaug, J. O., Bengtson, R., & Mjelde, A. (2015). Humler i Norge. Kjennetegn, Utbredelse og Levesett. Norsk institutt for naturforskning, Trondheim [Norwegian]

Table A4 Likelihood ratio tests of final models attained by backwards elimination of variables from the full models. Response variables were species richness (rarefied), raw richness, abundance, diversity, abundance of long tongued (specialists), short tongued (generalists), abundance of species of early emergence and late emergence, abundance of cuckoo bees, and abundance of *B. lucorum* group. For variables in the final models we used p-values <0.05 as selection criterion. Analyses were performed in R, package lme4. All models were fitted using Gaussian distributed errors and identity link, with Site as a random effect. R^2m is the marginal coefficient and R^2c is the conditional coefficient of determination. Significance codes: <0.001 '***' <0.01 '**' <0.05 '*'< 0.1 '.'

Variables	Df	LRT	P		R^2m	R^2c
Rarefied richness (LMM)						
Year	1	22.97	< 0.001	***	0.37	0.65
FDis forbs	1	6.21	0.013	*		
Nectar species cover	1	12.46	< 0.001	***		
Treatment x Richness forbs	2	13.28	0.001	**		
Raw richness (LMM)						
Year	1	6.21	0.012	*	0.26	0.51
Treatment x Richness forbs	2	14.01	< 0.001	***		
Abundance (LMM) log(y+1)						
Nectar species cover	1	10.62	0.001	**	0.26	0.65
Treatment x Richness forbs	2	8.14	0.017	*		
Diversity (LMM)						
Year	1	4.61	0.032	*	0.33	0.42
Precipitation	1	9.45	0.002	**		
Treatment x Richness forbs	2	12.233	0.002	**		
Long tongued (LMM) log(y+1)						
Treatment	2	27.23	< 0.001	***	0.33	0.62
Year	1	7.55	0.006	**		
Elevation	1	5.69	0.017	*		
Fdis forbs	1	11.11	< 0.001	***		
Short tongued (LMM) log(y+1)						
Ericacea species cover	1	16.19	< 0.001	***	0.38	0.62
Treatment x Richness forbs	2	7.06	0.029	*		
Early emergence (LMM) log(y+1)						
Nectar species cover	1	12.63	< 0.001	***	0.21	0.64
Treatment x Richness forbs	2	7.53	0.023	*		
Late emergence (LMM) log(y+1)						
Treatment	2	32.87	< 0.001	***	0.25	0.56
Fdis forbs	1	9.02	0.003	**		

Jordhumler (LMM) log(y+1)						
Treatment	2	29.66	< 0.001	***	0.23	0.46
Ericacea species cover	1	10.60	0.001	**		
Cuckoo bees (LMM) log(y+1)						
Year	1	8.65	0.014	*	0.23	0.49
Precipitation	1	4.80	0.044	*		
Treatment x Nectar species cover	2	11.66	0.004	**		

Table A5 Summary output from LMMs (linear mixed effects models) for raw species richness and abundance of *B. lucorum s.str*. group (log). Fixed effects: Treatment (uncut (intercept), cut and cut-remove), year (2013 and 2015), richness forbs and cover of ericaceous dwarf shrubs. SE = standard error; σ^2 = variance; τ_{00} = variance of intercepts; R^2m = marginal R^2, represents the variance explained by fixed effects; R^2c = conditional R^2, represents variance explained by both fixed and random effects.

	Raw richness				**B. lucorum s. str.**			
Predictors	β	*SE*	*t-value*	*p*	*β*	*SE*	*t-value*	*P*
Intercept (Year 2013, Uncut)	5.51	0.51	10.91	<0.001	1.76	0.17	10.09	<0.001
Cut	2.71	0.48	5.66	<0.001	0.99	0.19	5.28	<0.001
Cut-remove	2.46	0.47	5.28	<0.001	0.85	0.18	4.65	<0.001
Year 2015	0.92	0.37	2.46	0.014				
Richness forbs	-0.81	0.39	-2.06	0.039				
Cut × Richness forbs	0.97	0.5	1.94	0.052				
Cut-remove × Richness forbs	1.76	0.47	3.74	<0.001				
Ericacea species cover					0.37	0.1	3.55	<0.001
Random Effects								
σ^2	3.97				0.62			
τ_{00}	2.04 $_{\text{Site}}$				0.26 $_{\text{Site}}$			
N	19 $_{\text{Site}}$				19 $_{\text{Site}}$			
Observations	114				114			
R^2m / R^2c	0.26/0.51				0.23/0.46			

Figures

Fig. A1 Photo of a flight-interception trap installed in 2015 (early spring). Photo: Mari Steinert.

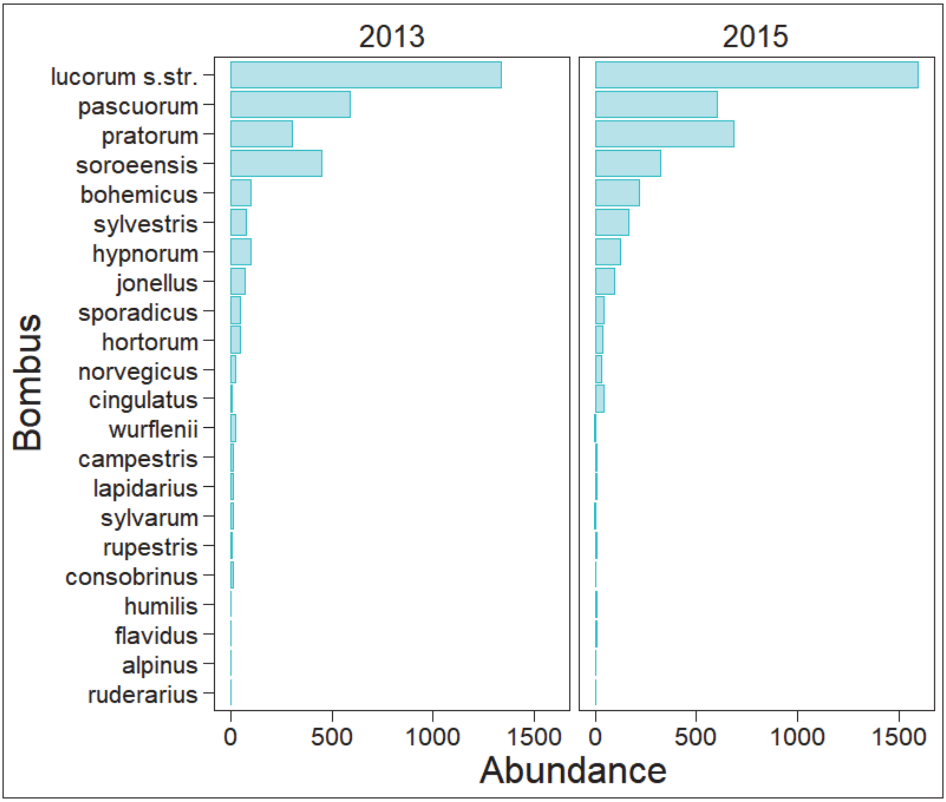

Fig. A2 Species relative abundance in each year. There were 22 species in the study, of which 6 were cuckoo bumble bees (i.e. *B. bohemicus, B. sylvestris, B. norvegicus, B. campestris, B. rupstris, B. flavidus*).

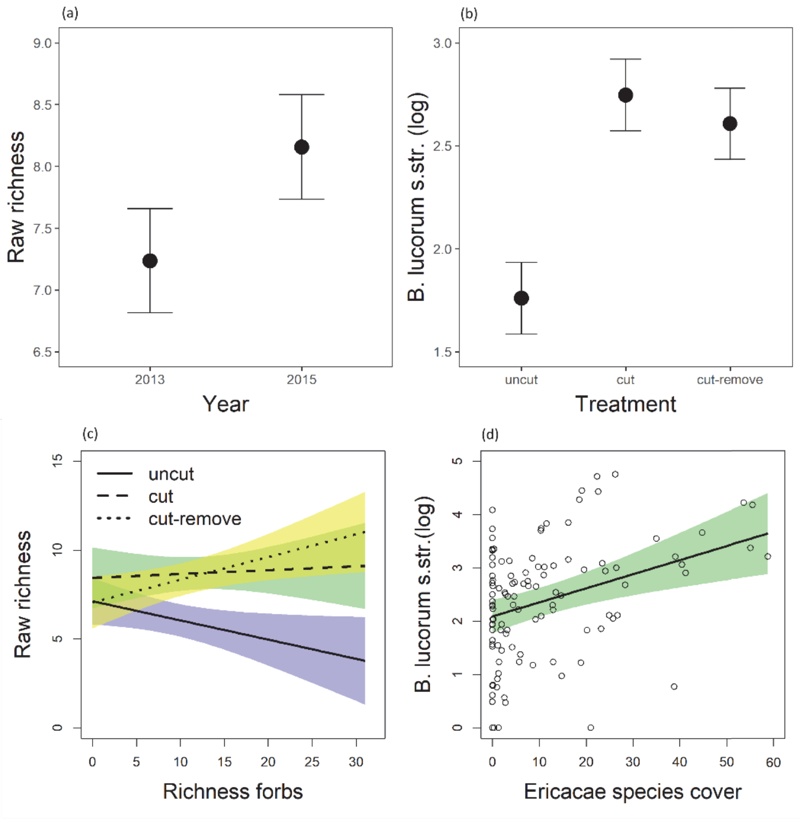

Fig. A3 (a) Raw richness of bumble bees in response to year and (b) abundance of the *Bombus lucorum* group in response to treatments (uncut, cut, cut-remove). Treatment effect on (c) raw richness with increasing richness of forbs. (d) *B. lucorum* group in response to cover of Ericaceae species

Paper IV

Power-line clearings provide important late-season foraging resources for bumble bees in boreal production forests

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Abstract. Homogenous and dense forests with reduced understory diversity threaten the provision of flower resources for wild bees throughout their foraging season. Bumble bees are key pollinators of native plants in boreal forest landscapes, but reforestation and intensification of forest management have led to a reduction in essential bumble bee habitats. Therefore, in forest landscapes, human modified habitats such as power-line clearings may provide valuable alternative habitats mimicking natural forest openings. This study assessed the use of power-line clearings and forest habitats throughout the foraging season of bumble bees. We sampled bumble bees within power-line clearings and 100 m into the adjacent forest at 20 sites located in forested landscapes in South Eastern Norway. We tested if the spatial and temporal variation in species richness and abundance of bumble bees differed between habitat types (clearing vs forest) and assessed how the habitat use was affected by flower resources, light availability, tree cover density. We found that power-line clearings are valuable habitats for both forest dwelling bumble bees as well as bumble bee species related to semi-natural grasslands. In spring when bilberry (*Vaccinium myrtillus*) was flowering, the richness and abundance of bumble bees were similar in the power-line clearing and the forest habitats. However, as the summer progressed the difference between the habitats increased. Bumble bee richness and abundance peaked in the power-line clearings in late summer, coinciding with the peak flowering period of heather (*Calluna vulgaris*), which indicates the importance of heather as a late-season flower resource for bumble bees. Heather is a light-tolerant species, associated with open habitats and open forest stands, which highlights the value of power-line clearings and confirms that reduced stand density can have positive effects on the biodiversity and pollination functions in the understory of managed forests. We also found that bumble bee richness increased with richness of forb species and abundance of bumble bees decreased in open habitats but increased in forest habitats with richness of dwarf shrubs. Within landscapes dominated by production forests, efforts should be made to preserve open canopy habitats particularly with a high richness of forbs and abundance of heather as this is where bumble bee diversity is seemingly greatest.

Keywords: Boreal forest; open habitats; understory vegetation; Bombus; pollination; ericaceous dwarf shrubs; tree cover density

1. Introduction

Bumble bees are key pollinators of native plant populations throughout the northern hemisphere (Corbet et al. 1991, Goulson 2003), providing essential pollination functions to many plants in the boreal forest understory. In recent years, pollinator declines in many parts of the world have led to increased attention towards wild bee conservation (Potts et al. 2016, Goulson et al. 2015). One of the main drivers of pollinator decline is habitat loss through human land use intensification (Potts et al. 2010). Native bumble bee species are associated with open habitats and are dependent on heterogenous environments where they can find flower resources during their entire life span. However, pollinator friendly habitats have become scarce, especially in boreal forest landscapes.

Over the last century, management practices in modern forestry have altered the structure and dynamics of the Scandinavian boreal forests (Östlund et al. 1997). The heterogeneous and dynamic stand structures in natural forests have been replaced by production forests of even-aged stands (Kuuluvainen 2009). The production forests lack structural and successional variability due to absence of natural disturbances (Brumelis et al. 2011). In recent years the forest stands have also become denser which have been found to have a negative impact on the vegetation in the forest understory and their pollinators (Hedwall et al. 2013, Petersson et al. 2019). Moreover, from 1960 until 2015, the amount of semi-natural grasslands has been reduced by one-half (Aune et al. 2018), mainly caused by agricultural intensification and farmland abandonment followed by reforestation (Norderhaug and Johansen 2011). Thus, the major declines of semi-natural grasslands (Aune et al. 2018), in addition to the homogenisation of forest landscapes (Brumelis et al. 2011) have led to a reduction in essential bumble bee habitats.

Loss of open areas and denser forests potentially increase the value of man-made open forest habitats, like clear-cuts and power-line corridors, for bumble bees. Indeed, there has been an increased interest in human modified landscapes, and the value of extensive networks of linear infrastructure for biodiversity conservation (Wojcik and Buchmann 2012, Hanula 2016). For example, there is a growing body of research identifying the positive effects of power-line clearings for wild bees when power-lines transect forest landscapes (Hill and Bartomeus 2016, Steinert et al. 2020, Wagner et al. 2014, 2019).

In Norway, the vegetation below power-lines is repeatedly cut every 5 to 12 years, to prevent trees from reaching the aerial lines. The power-line clearings resemble clear-cuts or gaps from intermediate natural disturbances but differ by being maintained at an early successional stage and by being linear (Eldegard et al. 2015). Early successional vegetation in open canopy habitats may support diverse and abundant bumble bee communities (Taki et al. 2013, Roberts et al. 2018), and potentially provide alternative habitats to semi-natural grasslands for bumble bees (Hill and Bartomeus 2016). Some studies have also documented wild bee communities in power-line clearings and adjacent forest habitats (Wagner et al. 2019, Russel et al. 2018). But to our knowledge, spatio-temporal patterns in bumble bee richness and abundance in the power-line clearings/forest habitats, and whether such patterns depend on flower resources in the power-line clearings/forest understory, remains unknown.

In boreal forested landscapes, bumble bees provide essential pollination functions to ericaceous dwarf shrubs, because most ericaceous species are dependent on buzz-pollination (Buchmann 1983). Most bumble bee species are floral generalists, with large demands for pollen and nectar to feed their colony over a long foraging season from snowmelt in early spring until early autumn (Goulson 2003). The forest understory is often dominated by ericaceous dwarf shrubs, such as bilberry, *Vaccinium myrtillus*, lingonberry, *V. vitis-idaea,* crowberry, *V. uliginosum,* and heather, *Calluna vulgaris*. Several of these ericaceous dwarf shrubs provide abundant and important food resources for bumble bees in limited periods throughout the foraging season (Moquet et al. 2017a, 2017b). Bumble bees foraging on abundant or dominant pollen and nectar resources, may increase the foraging efficiency by reducing search and handling time (Spiesman et al. 2017). Flowering plants in the forest understory may not provide sufficient pollen and nectar supplies over the entire foraging season, and such temporal or spatial gaps in flower resource availability could threaten colony survival. In contrast, open early successional habitats in the power-line clearings may offer a continuous provision of forb species throughout the entire flight-activity period of bumble bees (Eldegard et al. 2017). In addition, canopy gaps in managed forests reduce the tree cover density, which has been found to be positive for ericaceous dwarf shrub vegetation, while at the same time benefit pollinators (Romey et al. 2007). Stand density and light availability is particularly important for understory vegetation in conifer forests (Petersson et al. 2019). Bilberry is more likely to be found in shaded habitats, as the optimal light conditions for bilberry are intermediate shading from the forest canopy (Eldegard et al. 2019). More open habitats with lower stand densities benefit the drought and light-tolerant species like heather, due to increased irradiance (Parlane et al 2006) and changes in microclimate (Pohlman et al. 2009).

The main aim of this study was to assess the importance of power-line clearing habitats compared to forest habitats for bumble bees in landscapes dominated by production forests. We tested this by monitoring variation in bumble bee communities in the clearings and forest habitats throughout the foraging season. We expected that the power-line clearings and forest habitats would have different bumble bee communities, because among the bumble bees, some species are more typically forest dwelling and others are more commonly associated with semi-natural grasslands. However, within forested landscapes bumble bees move in space and time, in search of a continuous supply of resources throughout their flight-activity period. In the forest habitats in spring– during the flowering season of bilberry – we expected to find a higher richness and abundance of bumble bees since the dominant ericaceous dwarf shrub bilberry benefit from shaded habitats (Moquet et al. 2017b). Since bumble bees forage on several species of dwarf shrubs, we expected a higher richness of dwarf shrubs to attract a higher abundance of bumble bees especially into the forest habitats. In the power-line clearings we expected to find a higher richness and abundance of bumble bees during the flowering season of heather in late summer, which is a dominant dwarf shrub in open habitats (Moquet et al. 2017b). And we expected the richness and abundance of bumble bees to increase in power-line clearings with a high forb species richness (Steinert et al. 2020). Tree cover density and light availability was expected to influence habitat preference and was included to capture the variation in regrowth in the open habitats and in the tree layer density in the forest habitats, and to account for habitats with warmer microclimatic conditions, beneficial for efficient foraging (Corbet et al. 1993). We hypothesized that:

1. The spatial and temporal variation in bumble bee richness and abundance in power-line clearings and forest habitats would be related to flower resource availability, tree cover density and light availability.
2. There would be a higher abundance of bumble bees in the forest habitats in spring, during the flowering period of bilberry, or in sites with a high richness of dwarf shrubs.
3. Power-line clearings would be especially important for bumble bees during the flowering period of heather, or in sites with a high richness of forbs, resulting in an increased species richness and abundance of bees within power line clearings

4. Both power-line clearings and forest habitats with a low tree cover density and high light availability would provide more stable floral resources for bumble bees throughout the foraging season.

2. Methods

2.1 Study area

The study was conducted in boreal forests in South-Eastern Norway. The boreal forest is dominated by the coniferous tree species Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*. The most common deciduous trees are birch, *Betula spp.,* rowan *Sorbus aucuparia*, *Salix spp.* and European aspen *Populus tremula*, but usually these constitute a small proportion of managed forest stands. Understory vegetation typically include herbaceous species, grasses and dwarf shrubs in the field layer, and bryophytes and lichens in the bottom layer (Nilsson and Wardle 2005). Power-line clearings transecting forested areas in Norway are subject to a routine management regime of manual cutting of all woody vegetation every 5-12 years, without chemical use. In sites with high productivity, selective cutting of tall trees was done every five years. Power-line clearings are characterized as early successional open canopy habitats with altered microclimate due to increased exposure to sunlight, temperature fluctuations, wind velocity, lower levels of relative humidity and moisture in the ground layer (litter and soil) (Swanson et al. 2010). And the clearings typically comprise native early successional graminoids, forbs, dwarf shrubs and shrubs, before slowly accumulating regrowth dominated by deciduous trees.

2.2 Sampling design

We carried out a large-scale field study in 20 sites, distributed across the main power-line grid in southeastern Norway (58°–61°N, 8–11°E), at 25–610 m.a.s.l. (Fig. 1). The sites were selected by first arbitrarily selecting 84 candidate sites on a map along the main power-line grid in South-Eastern Norway. Of the 84 sites, 51 sites were selected by drawing lots from the 84 sites. The 51 sites where used for an extensive data collection of plants and invertebrates (Eldegard et al. 2015). Out of the 51 sites, we selected 20 sites to collect bumble bees. Criteria’s for choosing these 20 sites were accessibility in spring, minimization of transportation costs, permit to deploy traps from land-owners, and that the site was not going to be subjected to maintenance clearing in near future. In addition, the 20 sites had to have

200 m of forest perpendicular to the power-line clearings on both sides. If the criteria of forest cover were not fulfilled, the site was moved to the nearest location with forest along the clearing. At each site, we placed four plots (4 m × 5 m) in the clearing center and a parallel set of plots 100 m into the adjacent forest interior, from the forest edge in the power-line clearing. The plots were placed 50 m apart. Within each plot, we placed five 1-m^2 subplots along the centerline of each plot (Fig.1).

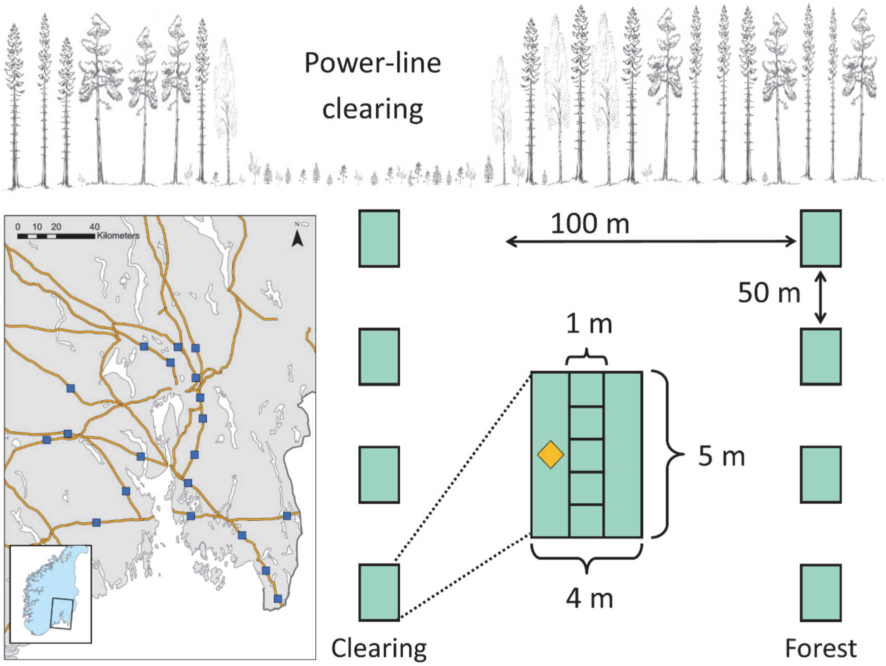

Figure 1: *Geographical location of the 20 study sites (A), located in the main power-line grid in South-Eastern Norway. Sites were situated in boreal production forests. Illustration of the study design (B), with four plots (4 × 5 m), 50 m apart, in the center of the power-line clearing and four plots located in parallel, 100 m from the forest edge into adjacent forest. Bumble bees were sampled in one flight-interception trap (diamond) within each plot (10 traps each site), and flower resources were surveyed within five subplots (1m2) along the center of each plot (5 m2 x 10 plots).*

2.3 Data collection

We collected bumble bee using flight interception traps (window traps). Ten of the sites were sampled in 2010 and 10 of the sites were sampled in 2011. At each site, in each of the four plots within the two habitats, i.e. power-line clearing (Clearing) and forest habitat (Forest), we placed one trap. The traps consisted of two transparent Plexiglas screens (370 mm × 210 mm), forming a cross, with a funnel and a container attached to the bottom. The container was filled with 50:50 mixture of water and green propylene glycol and a drop of detergent. The traps were installed in spring in late April or early May and removed in early autumn in September (May 1st – September 19th in 2010, and April 26th – September 30th in 2011). Each container was emptied once a month, during the main activity period of bumble bees: in spring/early summer (May/June); early/mid-summer (June/July); late summer (July/August); and late summer/autumn (August/September) (Table A1). The traps were deployed after snowmelt; thus, the dates were slightly different for the two years. The collected material was stored in 80% ethanol and brought back to the lab for identification. All bees were identified using a regional identification key (Løken 1985). A verified identification of the *Bombus lucorum sensu strictu* (*s.str.)* complex can only be achieved through genetic analyses (Williams et al. 2012). Therefore, all individuals from the *B. lucorum s.str.* group (i.e. *B. cryptarum, B. lucorum, B. magnus*, and *B. terrestris*), were pooled into one operational taxonomic unit in the analyses.

We collected data on understory vegetation and habitat characteristics at 12 sites in 2009 (July 6th–Aug 5th) and 8 sites in 2010 (June 29th–Aug 5th). We visually estimated total cover and richness of all vascular plant species in the five 1-m^2 subplots within each of the 8 plots at every site (Fig. 1). If a species was present in a subplot, but had <1% cover, it was recorded as 1%. We also recorded aspect, slope and latitude for each plot.

2.4 Data preparation

We calculated richness and abundance by summing the species and individuals in each sampling period and used sampling period from each trap as our unit in the statistical analyses. Our dataset consisted of many missing values, from samples that were accidentally damaged during transport. To account for the incomplete dataset, we chose to use the smallest sampling unit (sampling period) and selected a nested random effects structure in the statistical modelling. The random effect structure accounted for within-sites variation and repeated sampling in each trap (i.e. eight plots sampled four times).

Plant data from the five 1-m^2 subplots within each 4 m × 5 m plot were used to calculate species richness of forbs and dwarf shrubs and cover of *Calluna vulgaris* (heather) and *Vaccinium myrtillus* (bilberry) per plot. We chose to use richness of forb species as a measure of flower resources related to the early successional habitats in the power-line clearings (Eldegard et al. 2017), and richness of dwarf shrubs as a measure to identify the sites with a more diverse forest understory, because bumble bees may forage on a number of dwarfs shrub species (Moquet et al. 2017a; 2017b). Additionally, a high richness of forbs or dwarf shrubs, likely represents plants with different phenology, which may signify more food resources available throughout the foraging season. In the understory of boreal forest, bilberry or heather often dominate; they may overlap spatially but vary substantially in their relative abundance. The percent cover of bilberry is higher at intermediate irradiance, whereas cover of heather increase with increasing irradiance (Parlane et al. 2006). Thus, the increased irradiance in the open power-line clearing habitats may benefit drought and light tolerant species, such as heather, while relatively shade adapted species, such as bilberry, have a competitive advantage in the forest.

To estimate the tree cover density (TCD) within each habitat, we extracted measurements derived from remotely sensed images. Tree cover density (%) was obtained from digital raster maps using coordinates from each plot within each site, and downloaded from Copernicus, Land monitoring service, with 2012 as the reference year (Copernicus Land Monitoring Service 2012). From the recorded aspect, slope and latitude we calculated the solar irradiation index (Oke 1987), hereafter ‘irradiation index’, as a measure of light availability. Elevation was recorded at site level from digital maps (Kartverket 2019). All data analyses were done in R (R Development Core Team 2017).

2.5 Statistical analyses

To visualize the difference in bumble bees between the two habitats, we performed a Nonmetric Multidimensional Scaling ordination (NMDS) (Oksanen et al. 2013), using the metaMDS function, with 999 permutations, and k=3 dimensions. We aggregated the abundance of bumble bees to Site-level and used Bray-Curtis distance and square root-transformations. The stress value was 0.12, and Shepard’s plot indicated an acceptable fit.

Table 1. *Variables included in the analyses. Measured values (range) of the response variables and candidate explanatory variables in the full regression models. Spatial scale and measured values (range/levels) of the environmental conditions, habitat characteristics and the plant community (floral resources). For description of the variables, see methods chapter, under 'Data preparation'.*

Variables in analyses	Spatial scale	Range/levels (mean)
Response variables		
Species richness	Plot (Trap)	1 – 7 (2.03) species
Abundance	Plot (Trap)	1 – 91 (7.61) individuals
Explanatory variables		
Habitat	Site	clearing, forest
Sampling period	Plot	May/June (T1), June/July (T2), July/August (T3), August/September (T4)
Richness forbs	Plot	0 – 21 (2.71) species
Richness dwarf shrubs	Plot	0 – 7 (2.87) species
Cover heather	Plot	0 – 55 (8.12) %
Cover bilberry	Plot	0 – 45 (6.70) %
Irradiation index	Plot	0.00 – 0.82 (0.47)
Tree cover density	Plot	0 – 85 (24.27) %
Elevation	Site	25 – 610 (228.2) m.a.s.l

After testing different random effect structures and generalized linear models (GLMMs) for our count data, we fitted linear mixed effects models (LMMs), with Gaussian-distributed errors and identity link, with the random structure of plots nested in site (1|site) + (1|site:plot). Different random structures were tested using Anova. To account for collinearity between explanatory variables, we only included variables with a correlation coefficient below 0.6 (Table A2). We also calculated the variance inflation factor (VIF) values for all explanatory variables in each candidate model (Fox and Monette 1992; Zuur et al. 2010) using the car package in R (Fox et al. 2019). All variables had a VIF value below 2 in the full model (Zuur et al. 2010). We tested the two responses, richness and abundance of bumble bees (per trap and sampling session) with the different environmental variables in two and three-way interactions with habitat and sampling period. We log transformed abundance to achieve a normal distribution of the residuals and for each model, we scaled all numerical variables. We carried out a preselection of candidate environmental co-variables (P-values ≤ 0.10); for each response variable, we tested each environmental variable separately and in a two and three-way interaction with the categorical variables; 'habitat' and 'sampling period'. Candidate environmental co-variables were richness of forbs, richness of dwarf shrubs, cover of *V. myrtillus*, cover of *C. vulgaris*, tree cover density, irradiation index, and elevation (Table 1). We included the tree cover density in interaction with habitat to account for among-sites variation in tree regrowth in the power-line clearings and variation in tree cover in adjacent forest plots. Final models were selected by stepwise backward elimination based on likelihood ratio tests (LRTs), until only significant (P ≤ 0.05) variables remained.

To validate the model fit, we used the DHARMa package in R (Hartig, 2018) to produce residual plots, and visually assessed the plotted residuals against the fitted values for all explanatory variables and assessed the distribution of residuals. Model estimates were extracted using the effects package (Fox 2003). Final output for the abundance was back transformed before plotted. All models were fitted using the lme4 package in R (Bates et al. 2019), and all analyses were carried out in R version 3.2.5 (R Development Core Team 2017).

Table 2. *Bumble bee individuals per species sampled in the two habitats.*

Species	**Power-line clearing**	**Forest**
Bombus lucorum s.str	1169	42
Bombus pratorum	441	60
Bombus pascuorum	382	26
Bombus hypnorum	74	1
Bombus jonellus	37	3
Bombus bohemicus	29	0
Bombus sylvestris	23	7
Bombus norvegicus	15	4
Bombus soroeensis	4	1
Bombus hortorum	4	0
Bombus ruderarius	2	0
Bombus sylvarum	2	0
Bombus campestris	1	0
Sum total	**2183**	**144**

3. Results

We recorded a total of 2327 bumble bee individuals, comprising 13 *Bombus* species, of which four species were cuckoo bumble bees. All the 13 species were present in the power-line clearings, whereas only eight species were found in the forest (Table 2, Fig. A1). Within each plot, we found an average (±SE) of 2.3 ± 0.09 species and 9.7 ± 1.05 individuals in the power-line clearings and 1.3 ± 0.07 species and 1.78 ± 0.13 individuals in the forest habitats. We found significantly higher cover of bilberry and tree cover density in the forest compared to the power-line clearings, and significantly higher cover of heather and richness of forbs in the power-line clearings compared to the forest (Fig. 2). There were no significant differences in richness of dwarf shrubs or irradiance index between the two habitats (Fig. 2).

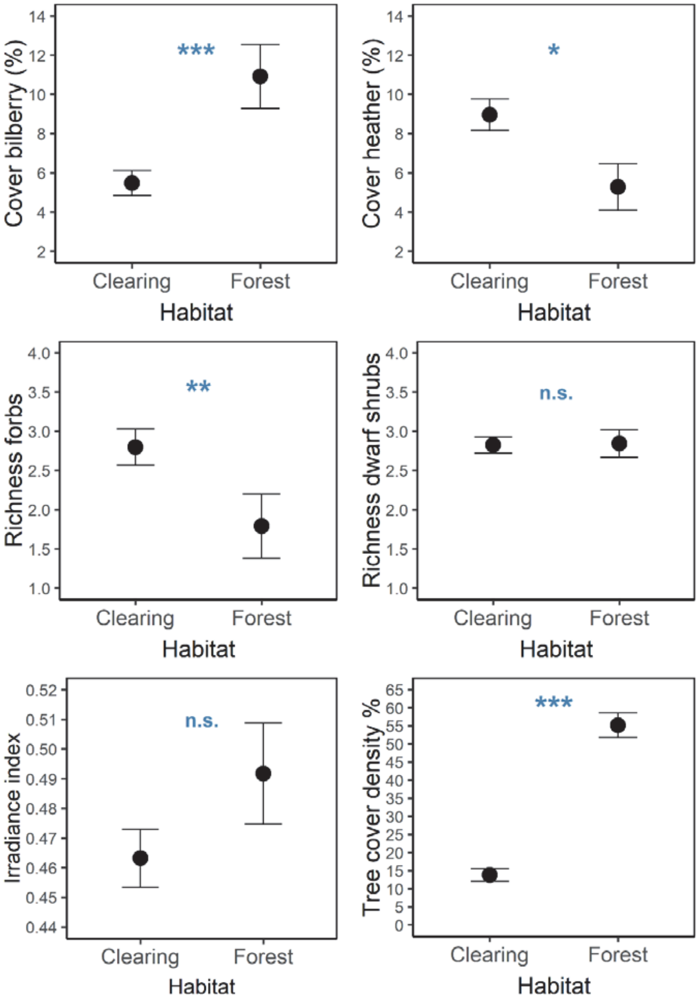

Figure 2:** Observed means (± SE) of the explanatory variables in the two habitats; cover of bilberry (%), cover of heather (%), richness of forb species, richness of dwarf species, irradiance index, and tree cover density (%) in power-line clearings (Clearings) and adjacent production forest (Forest) habitats. Asterisks represent significance levels (P < 0.001 ** P < 0.01, * P < 0.05) for pairwise comparisons of habitat means. n.s. = no significance.*

The NMDS ordination of the bumble bee abundance showed that there was a difference between bumble bee communities in the clearings and adjacent forest habitats at each site, with some overlap (Fig. 3). Centroids of the two habitats can be viewed as the average position of observations in ordination space. In the power-line clearings, site scores were more clustered around the centroid, signifying more similar species composition in this habitat. In the forest habitats site scores were more dispersed around the centroid, signifying larger variation in bumble bee composition in the forest (Fig. 3).

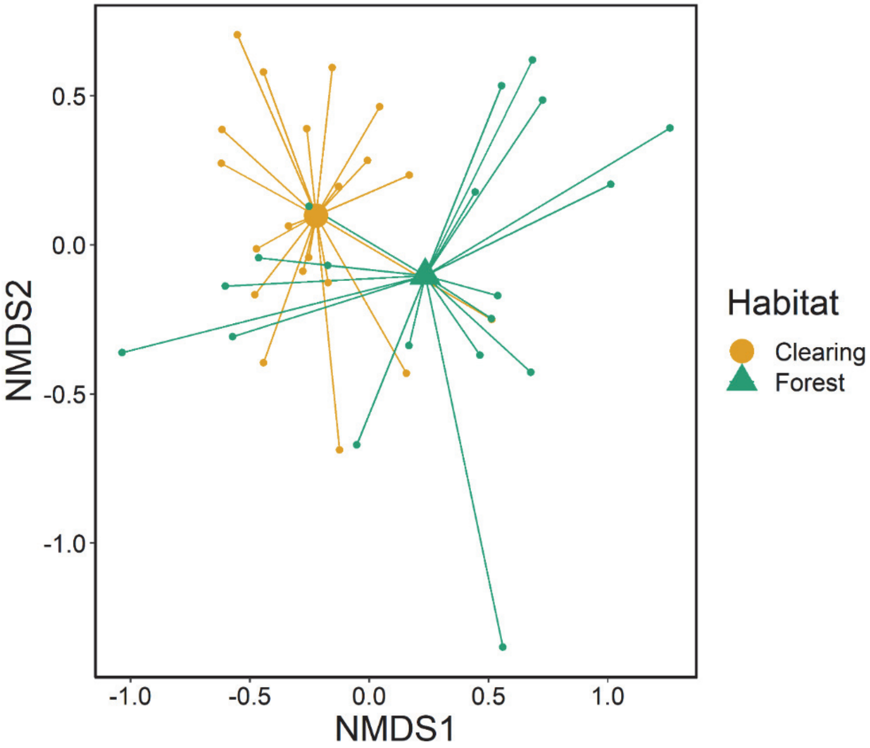

Figure 3: *Difference between and variation within bumble bee communities in power line clearings and adjacent boreal production forests. Two-dimensional presentation of Nonmetric Multidimensional Scaling (NMDS) of bumble bee community composition in the open clearings and forest habitats, with species abundance matrix aggregated at site level. Spider plot showing the dispersion of species composition from the centroids, where the centroids represent the mean species composition within each habitat.*

In the power-line clearings, the estimated richness and abundance of bumble (per trap and sampling session) varied substantially through the sampling season (Table 3, A3), with significantly higher richness and abundance in July/August. Richness and abundance of bumble bees were relatively stable in the forest habitat, without a temporal pattern. Richness and abundance were not significantly different between clearings and forest habitats in May/June (Fig. 4). In the clearings, species richness increased from 1.6 species in May/June to 2 species in June/July, to 2.8 species in July/August, and then decreased to 2 species in August/September. Species richness slightly increased from 1.3 in May/June to 1.5 in August/September in the forest (Fig. 4, Table 3, A3). Abundance increased from 1.7 individuals in May/June to 3.3 individuals in June/July, to 7.2 individuals in July/August, and then decreased to 4 individuals in August/September. In the forest habitats abundance was 1.5 individuals in May/June and August/September, compared to 1.2 and 1.4 individuals in June/July and July/August, respectively (Fig. 4, Table 3, A3).

Table 3. *Likelihood ratio tests of final models attained by backward elimination of variables from the full models. Response variables were species richness and abundance. For variables in the final models we used p-values ≤ 0.05 as selection criterion. Analyses were performed in R, package lme4. Both responses were fitted using LMMs with Gaussian distributed errors and identity link, with site and plot as nested random effects.*

Response	**Explanatory terms**	***LRT***	***Df***	***P***
Richness	Richness forbs	3.785	1	0.052
	Cover heather	5.487	1	0.019
	Elevation	5.072	1	0.024
	Habitat × Sampling period	10.795	3	0.013
Abundance (log)	Elevation	7.089	1	0.008
	Habitat × Sampling period	23.089	3	< 0.001
	Habitat × Richness dwarf shrubs	6.887	1	0.009
	Sampling period × Cover heather	9.424	3	0.024

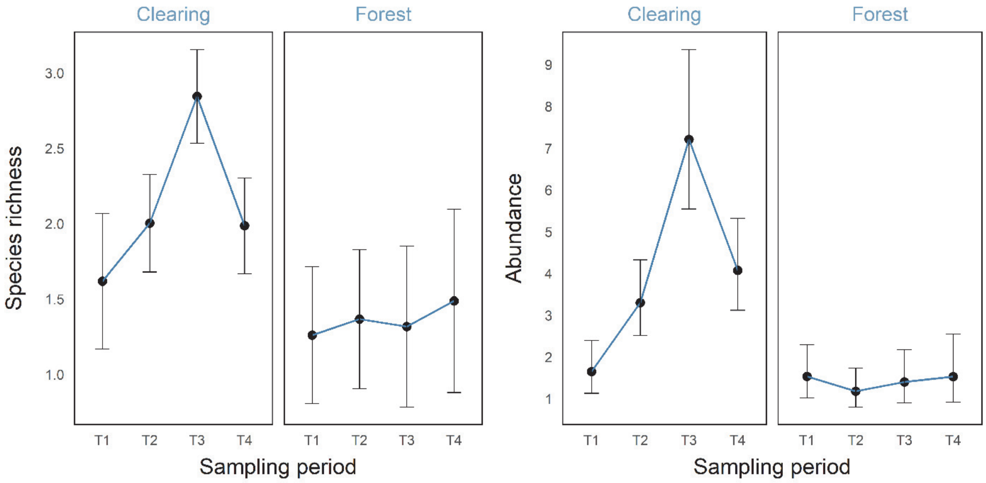

Figure 4: *Mean (± 95% CI) species richness and abundance of bumble bees in power line clearings (Clearing) and production forest habitats (Forest) over the four sampling periods during the main foraging season, where T1 is sampling period May/June, T2 is sampling period in June/July, T3 is sampling period in July/August, and T4 is sampling period in August/September.*

Bumble bee species richness increased from 1.8 to 2.7 species with richness of forbs species (Fig. 5a, Table 3, A3) and increased from 1.8 to 2.7 species with cover of heather (Fig. 5b, Table 3, A3). Abundance of bumblebees decreased from 5.9 to 2.11 with richness of dwarf shrubs in the power-line clearings, while abundance increased from 1.2 to 1.7 individuals with richness of dwarf shrub species in the forest (Fig. 5c, Table 3, A3). Abundance increased with cover of heather in the two sampling periods towards the end of the foraging season, although not significantly different from the two early sampling periods: Abundance decreased from 1.7 to 1.3 individuals at the beginning of the season in May/June, and from 2.6 to 2.1 in June/July with increasing cover of heather. Before an increase from 3.9 to 14.9 individuals in July/August, and from 2.7 to 8.2 in August/September with increasing cover of heather (Fig. 5d, Table 3, A3). Bumble bee richness and abundance decreased from 2.4 to 1.2 species, and from 4.7 to 1.3 individuals along the elevation gradient (25 - 620 m.a.s.l.) (Figure A2, Table 3, A3). Tree cover density, irradiance index and bilberry cover were not statistically significant in any of the final models.

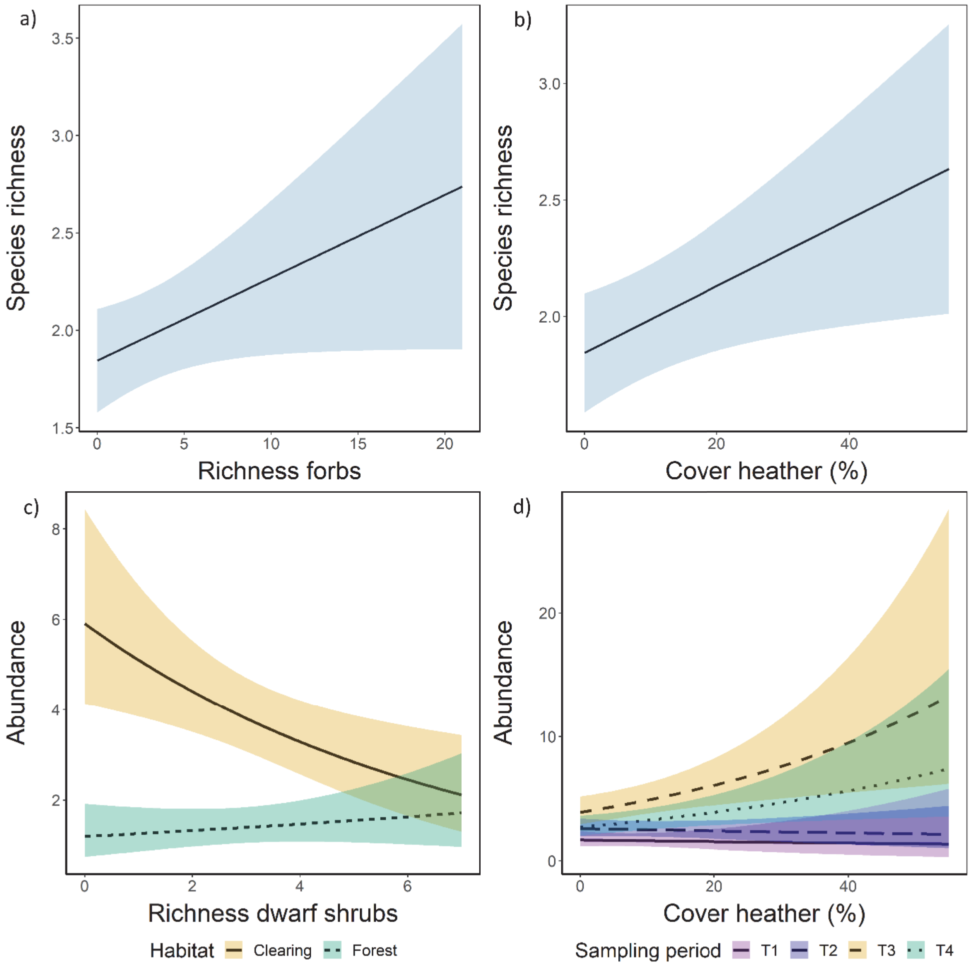

Figure 5: *Relationships between species richness or abundance of bumble bees and floral resources. (a) Species richness of forbs and species richness of bumble bees, irrespective of habitat. (b) Percent cover of heather (C. vulgaris) and species richness of bumble bees, irrespective of habitat. (c) Richness of dwarf shrubs and abundance of bumble bee in the two habitats. Yellow confidence interval (CI) and solid line shows estimated relationships or power line clearing habitats (Clearings), whereas green CI and dotted line are production forest habitats (Forest). (d) Temporal patterns in the influence of cover of heather on abundance of bumble bees; estimated relationships for the four sampling periods: Pink CI and solid line are the first sampling period in spring (May/June); violet CI and long dashed line are the second sampling period in early summer (June/July); yellow CI and dashed line are the third sampling period in late summer (July/August); green CI and dotted line are the fourth sampling period in late summer/early autumn (August/September).*

4. Discussion

Our results demonstrate the importance of open habitats, such as power-line clearings, for bumble bees in boreal production forests. We found substantially more species and individuals in the power-lien clearings, but there was a higher variation in species composition in the forest habitats compared to the open habitats. The species we found in the forest habitats were also found in the power-line clearing habitats, which mainly comprised the three most abundant and common bumble bee species in our study, i.e. *Bombus lucorum s.str., B. pascuorum,* and *B. pratorum*. In the power-line clearings, we also found species more typically associated with semi-natural grasslands, i.e. *B. hortorum, B. ruderarius* and B. sylvarum, in addition to the majority of the cuckoo bumble bees.

We found temporal and spatial variation in bumble bee richness and abundance throughout the foraging season. Temporal variation in richness and abundance of bumble bees can be due to temporal variation in availability of flower resources. We found that bumble bees used both open and forest habitats to the same degree in spring and early summer, but towards the end of the summer we found more bumble bees in the power-line clearings than in the forest habitats. This temporal pattern likely reflects a spatial shift in habitat use from forest into the power-line clearings towards the end of the summer season. For example, because bumble bee species, foraging in the forest understory, search for flower resources in the power-line clearings towards the end of the season.

The increase in richness and abundance in July/August, before a decrease in August/September in the open habitats fits well with the anticipated increase in bumble bee population sizes towards the end of the foraging season, as the colonies are continuously growing larger. The largest increase coincided with the peak in bumble bee colony-sizes in late summer, when males and new queens, in addition to broods of cuckoo bumble bees will have emerged. The decrease in early autumn corresponds with the end of bumble bee colony life-time. We found no temporal patterns in abundance and richness of bumble bees in the forest habitats.

The bumble bee communities were influenced by floral resource availability in both habitats, but only cover of heather had a significant temporal variation in the influence on bumble bee abundance, and only the influence of richness of dwarf shrubs differed significantly between clearings and forest habitats. Interestingly, cover of bilberry was not an important explanatory variable in any of the models, despite the previously documented importance of bilberry as a vital pollen and nectar resource in the nest-founding phase (Moquet et al. 2017b). The similar richness and abundance of bumble bees in the open and forest habitats at the beginning of the foraging season, may indicate that both habitats are equally important in spring/early summer, corresponding to the peak flowering season of bilberry.

The cover of heather was the only variable which had a temporal variation in the influence on abundance of bumble bees, and the peak in richness and abundance coincided with the flowering period of heather. Heather is an abundant ericaceous dwarf shrub, typically associated with open habitats or less dense forest stands with a higher light irradiance (Parlane et al. 2006). Heather attracts generalist pollinators and are mostly visited for the nectar (Mouquet et al. 2017b). The abundant occurrences of heather are comparable to mass-flowering crops (Westphal et al. 2003, Holzschuh et al. 2013), and provide an important late summer food resource for many bumble bee species, particularly males and new queens (Moquet et al. 2017b). Our results accord with Spiesman et al. (2017), who found that floral dominance was more important than abundance and richness of floral resources for bumble bee colony growth and reproduction. Additionally, other studies in agricultural landscapes have demonstrated the value of late-season mass-flowering of red-clover for bumble bees (Rundlöf et al. 2014), and how native bee species benefit from foraging in a mix of mass-flowering agricultural crops and semi-natural habitats (Holzschuh et al. 2013). Comparable to mass-flowering crops, the heather resource is important for a limited period in the forest landscape, and our results suggest that heather is an essential contribution to the continuous provision of flower resources for bumble bees during the season.

Species richness of bumble bees increased with forb species. Power line clearings have a higher richness and diversity of forb species compared to the adjacent production forest (Eldegard et al. 2017), suggesting that availability of forb species explain why bumble bees were attracted to the power-line clearings. Previous studies of wild bees have shown that bee species in forested landscapes are generally associated with early successional forest openings (Roberts et al. 2017, Korpela et al. 2015). Wagner et al. (2019), found substantial differences in wild bees between power-line clearings and adjacent closed canopy forests, and concluded that many of the species found in the forest also depended on nearby open habitats. Although not formally tested in their study, their data also show the largest contrast between the forest sites and power-line clearings late in summer when floral resources in the forest were scarce (Wagner et al. 2019). Our findings support previous studies emphasizing how power-line clearings may provide opportunities for conserving early successional plants and the invertebrates that depend on them, especially in forested regions (Eldegard et al. 2017, Hanula et al. 2016, Hill and Bartomeus 2016, Russel et al. 2005; 2018, Steinert et al. 2018; 2020, Wagner et al. 2014; 2019).

The ordination plot showed that the variation in bumble bee composition seemed to be more similar among sites in the clearing habitats than in the forest habitats. Likely this is because the plant communities in the forest understory are less diverse or that there is larger variation in plant cover, which may cause a high among-site variation in bumble bee visitation. The only floral resource that had different habitat effect on the bumble bee abundance was richness of dwarf shrubs. An increased richness of dwarf shrubs attracted more bumble bee individuals in the forest habitats, but the effect size was small. Bumble bees may forage on several different ericaceous dwarf shrub species over the season (Moquet et al. 2017a; 2017b), and sites with a higher richness of dwarf shrubs would offer more continuous flower resources throughout the season. By contrast we found that the power-line clearings with a high richness of dwarf shrubs had fewer bumble bees, which could be because a higher richness of dwarf shrubs species are associated with low productivity (Eldegard et al. 2017). A higher richness of forb species is generally associated with productive sites (Eldegard et al. 2017), and in open habitats it was expected that more productive sites, with a high forb species richness would attract more bumble bee individuals (Steinert et al. 2020).

The stand density in managed forests affects the plant communities in the understory. An observed decrease in the field layer cover of vascular plants, including cover of bilberry, has been related to increased forest density and reduced forest age in boreal forests in Sweden (Hedwall et al. 2013). Thus, in dense forests with reduced field layer vegetation, open habitats in power-line clearings become even more important. Interestingly we did not find an influence of irradiation index or tree cover density on the bumble bee communities. Tree cover density was correlated with habitat type and the explained variation in tree cover density was likely captured by the differences between open and forest habitat. Nevertheless, even if our results did not show direct effects of tree cover density, our results strongly suggest that the production forest understory is not providing enough resources throughout the season. Maintaining early successional habitats in forested ecosystems may also contribute to preserving mutually beneficial plant-pollinator interactions as plants in canopy gaps receive more pollinator visits than those in closed forests (Proctor et al. (2012). Thus, it is likely that an increased forest density, with the absence of forest openings, would be disadvantageous for sustaining native plant populations, their pollinators, and associated ecosystem services.

Modern forest management has not only increased stand density but also initiated a shift from even-aged stands of Scots pine (*Pinus sylvestris*) to even-aged stands of Norway spruce (*Picea abies*) with shorter rotation periods (Felton et al. 2019, Petersson et al. 2019). Such a trend may be detrimental to sustain high biodiversity in the forest understory. A high cover of bilberry and heather together with a high richness of dwarf shrubs are more often found in mature Scots pine stands (Petersson et al. 2019), associated with well drained and nutrient poor soils (Engelmark and Hytteborn 1999). In comparison, spruce stands are often associated with more nutrient rich soils, which also coincide with a higher richness of forbs (Petersson et al. 2019). However, understory vegetation is dependent on age and tree layer density of the Norway spruce stands (Petersson et al. 2019). Negative effects of too dense and homogenous forests could be mitigated through integrating pollinator friendly conservation practices in forestry management. Open canopy habitats should be promoted within largely forested areas of homogenous dense stands, either by thinning (Taki et al. 2010, Romey et al. 2007), or careful rotation planning of clear-cuts combined with less dense old-growth stands. Dependent on the landscape matrix, conservation efforts in forestry should be implemented on a landscape scale, preferably near other existing early successional habitats (e.g. power-line clearings) to ensure connectivity between the habitats.

5. Conclusion

Our results demonstrate that, in a production forest landscape, power-line clearings are valuable habitats for both forest dwelling bumble bees as well as bumble bee species related to semi-natural grasslands. Forest-dwelling bumble bee species, foraging on mass flowering ericaceous species, use open habitats towards the end of the season. The open canopy habitats in power-line clearings ensure a continuous supply of floral resources throughout the foraging season for bumble bee species, which may be essential for bumble bee reproduction and survival. Heather was identified as an important late-season flower resource for bumble bees. Heather is a light-tolerant species, associated with open habitats or open forest stands, and our results support how an increased stand density may have detrimental effects on the biodiversity and pollination functions in the understory of managed forests. Thus, forest management supporting more open stand structures, through e.g. more spacious plantings or thinning practices, is recommended to ensure survival of bumble bees. Our study also emphasizes the importance of implementing the growing body of knowledge of pollinator management in human modified landscapes in forest management planning. More heterogenous forests with open habitats and less dense stands, have the potential to enhance understory diversity of insect pollinated plants and their pollinators, together with the associated multiple ecosystem services they provide.

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Author contribution

MS performed the analyses, wrote the first draft of the manuscript and led the writing of the manuscript. KE and SRM designed and initiated the experiment. All authors discussed the results and contributed to previous drafts and the final manuscript.

Conflict of Interest

The authors declare that they have no conflict of interest.

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Appendix

Appendix – Supplementary material

Title: **“Power-line clearings provide important late-season foraging resources for bumble bees in boreal production forests”**

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Tables:

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Table A1. Time periods for each of the four sampling events in 2010 and 2011. Ten traps were operated in 2010 and 10 traps were operated in 2011. Each trap was active for approximately 1 month each period.

Sampling period	Year	Date from	Date to
T1	2010	1-24/5	15-17/6
T2	2010	15-17/6	15-19/7
T3	2010	15-19/7	14-18/8
T4	2010	14-18/8	15-19/9
T1	2011	26/4-3/5	25-29/5
T2	2011	25-29/5	26-30/6
T3	2011	26-30/6	26/7-1/8
T4	2011	26/7-1/8	2-30/9

Table A2. Pearson correlation coefficients for variables tested in the analyses.

	Richness	Abundance	Habitat	Sampling period	Richness forbs	Richness dwarf shrubs
Richness	1	0.732	-0.343	0.177	0.151	-0.069
Abundance	0.732	1	-0.259	0.196	0.096	-0.103
Habitat	-0.343	-0.259	1	-0.263	-0.128	0.005
Toem	0.177	0.196	-0.263	1	0.024	0.039
N0_forb	0.151	0.096	-0.128	0.024	1	-0.456
N0_dwarfshrub	-0.069	-0.103	0.005	0.039	-0.456	1
C_VaccMyrt	-0.017	-0.044	0.216	-0.077	-0.189	0.044
C_CallVulg	0.122	0.092	-0.141	0.113	-0.259	0.252
RI	0.016	-0.001	0.087	-0.078	0.075	0.013
Elevation_map	-0.134	-0.165	-0.019	0.027	0.102	0.060
TCD	-0.192	-0.074	0.568	-0.192	-0.009	-0.184

	Cover bilberry	Cover heather	RI	Elevation	TCD
RichnessB	-0.017	0.122	0.016	-0.134	-0.192
AbundanceB	-0.044	0.092	-0.001	-0.165	-0.074
fHabitat	0.216	-0.141	0.087	-0.019	0.568
fToem	-0.077	0.113	-0.078	0.027	-0.192
N0_forb	-0.189	-0.259	0.075	0.102	-0.009
N0_dwarfshrub	0.044	0.252	0.013	0.060	-0.184
C_VaccMyrt	1	-0.235	-0.132	-0.192	0.146
C_CallVulg	-0.235	1	0.078	0.201	-0.292
RI	-0.132	0.078	1	0.215	0.042
Elevation_map	-0.192	0.201	0.215	1	-0.103
TCD	0.146	-0.292	0.042	-0.103	1

Table A3. Summary output from the linear mixed effects models (LMMs). The effects of the two habitats, power-line clearings (Clearings) and forest habitats (Forest); sampling periods through the foraging season (T1= May/June; T2= June/July; T3= July/August, T4= August/September); floral resources; (comprising cover of bilberry *V. myrtillus* (%); heather *C. vulgaris* (%); richness of dwarf shrubs and richness of forbs); elevation; tree cover density (%); and light availability (irradiance index) on richness and abundance of bumble bees in boreal production forests. SE = standard error; σ^2 = variance; τ_{00} = variance of intercepts; R^2m = marginal R^2, represents the variance explained by fixed effects; R^2c = conditional R^2, represents variance explained by both fixed and random effects.

	Richness				
Fixed effects	β	*SE*	*CI*	*t*	*p*
Intercept (Sampling period T1, Clearing habitat)	1.62	0.23	1.17 – 2.07	7.07	**<0.001**
Forest habitat	-0.36	0.29	-0.93 – 0.21	-1.23	0.218
Sampling period T2	0.38	0.24	-0.08 – 0.85	1.61	0.107
Sampling period T3	1.23	0.23	0.77 – 1.69	5.23	**<0.001**
Sampling period T4	0.37	0.24	-0.09 – 0.83	1.56	0.119
Richness forbs	0.16	0.08	-0.00 – 0.32	1.9	0.057
Cover heather	0.18	0.08	0.03 – 0.32	2.31	**0.021**
Elevation	-0.27	0.12	-0.51 – -0.03	-2.24	**0.025**
Forest habitat × Sampling period T2	-0.28	0.37	-1.00 – 0.45	-0.75	0.451
Forest habitat × Sampling period T3	-1.17	0.39	-1.94 – -0.40	-2.97	**0.003**
Forest habitat × Sampling period T4	-0.14	0.42	-0.97 – 0.69	-0.33	0.739
Random effects					
σ^2	0.96				
τ_{00}	0.09 $_{\text{Plot:Site}}$				
	0.20 $_{\text{Site}}$				
N	8 $_{\text{Plot}}$				
	20 $_{\text{Site}}$				
Observations	306				
Marginal R^2 / Conditional R^2	0.246 / 0.420				

	Abundance (log)				
Fixed effects	*β*	*SE*	*CI*	*t*	*p*
Intercept (Sampling period T1, Clearing habitat)	0.5	0.19	0.13 – 0.87	2.65	**0.008**
Forest habitat	-0.07	0.25	-0.55 – 0.41	-0.29	0.769
Sampling period T2	0.69	0.19	0.31 – 1.07	3.57	**<0.001**
Sampling period T3	1.47	0.19	1.10 – 1.85	7.73	**<0.001**
Sampling period T4	0.9	0.19	0.53 – 1.28	4.71	**<0.001**
Cover heather	-0.04	0.18	-0.40 – 0.31	-0.25	0.804

Elevation	-0.28	0.1	-0.48 – -0.08	-2.71	**0.007**
Forest habitat × Sampling period T2	-0.95	0.31	-1.56 – -0.35	-3.09	**0.002**
Forest habitat × Sampling period T3	-1.56	0.33	-2.20 – -0.92	-4.79	**<0.001**
Forest habitat × Sampling period T4	-0.91	0.36	-1.60 – -0.21	-2.55	**0.011**
Richness dwarf shrubs	-0.23	0.08	-0.39 – -0.07	-2.79	**0.005**
Sampling period T2 × Cover heather	0	0.19	-0.38 – 0.38	0.02	0.984
Sampling period T3 × Cover heather	0.32	0.2	-0.07 – 0.70	1.62	0.106
Sampling period T4 × Cover heather	0.27	0.19	-0.11 – 0.65	1.38	0.168
Forest habitat × Richness dwarf shrubs	0.31	0.12	0.07 – 0.54	2.59	**0.01**
Random effects					
σ^2	0.62				
τ_{00}	$0.08_{\text{Plot:Site}}$				
	0.15_{Site}				
N	8_{Plot}				
	20_{Site}				
Observations	306				
Marginal R^2 / Conditional R^2	0.381 / 0.547				

Figures

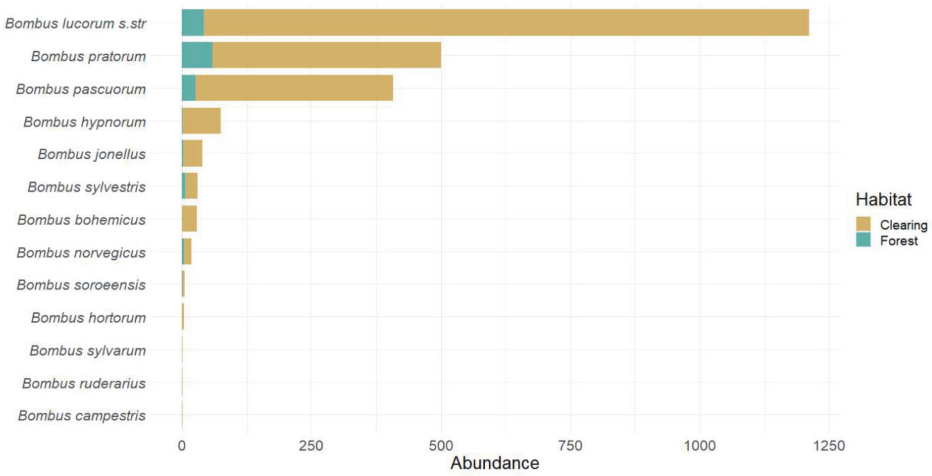

Fig. A1. Number of bumble bee individuals collected per species in power line clearings and in adjacent boreal production forests.

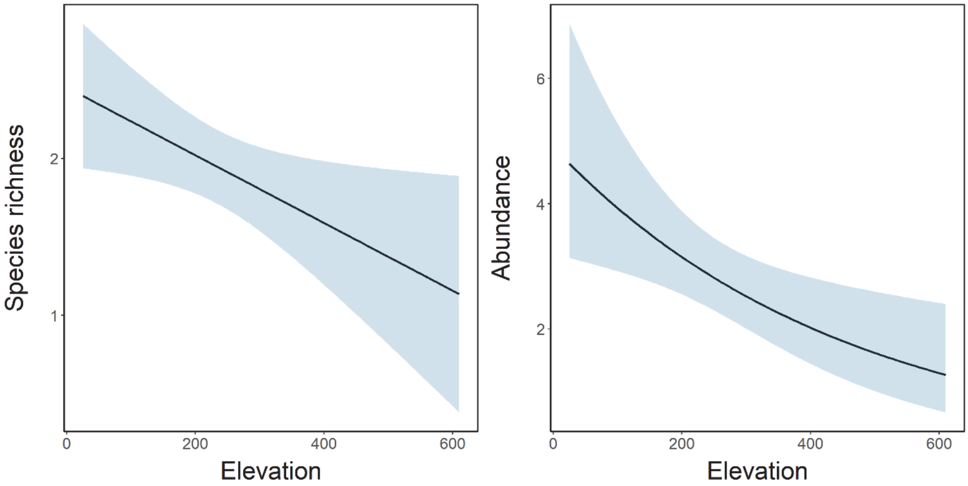

Fig. A2. Species richness and abundance of bumble bees in response to elevation from final models.

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