




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

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**Abstract.** 1. Bumble bees fill an important function in temperate, boreal and alpine ecosystems as pollinators of wild plants and cultivated crops. Global declines in population size 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.

2. We carried out a field experiment to study effects on bumble bee communities in power-line clearings in response to different vegetation clearing practices: (i) cutting, (ii) cutting and removing, and (iii) not cutting the woody vegetation, whilst simultaneously assessing the effect of environmental variables, both individually and in interaction with treatment.

3. Cutting the woody vegetation improved habitat quality for bumble bees relative to the uncut treatment, whereas removal of woody debris provided no additional benefit. The treatment effect on bee richness, diversity, abundance, and the abundance of generalist bees depended on local forb species richness. Increasing functional variation of forbs and cover of forbs with nectar tubes were positively related to species richness and abundance of bees, irrespective of treatment.

4. The abundance of specialized long-tongued and late emerging bumble bees – which are of special conservation interest – were higher in the cut and cut-remove treatments and increased with functional variation of forb species irrespective of treatments.

5. 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.

**Key words.** Boreal forest, bumble bee conservation, flower resources, functional diversity, habitat management, pollinator community.

## 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 (Goulson *et al.*, 2008, 2015; Potts *et al.*, 2010; Cameron *et al.*, 2011; Arbetman *et al.*, 2017). 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 (Winfree *et al.*, 2009; Potts *et al.*, 2010). Yet, not all effects of land use change are negative for pollinators, 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 (Morón *et al.*, 2014), hedgerows (Hanley & Wilkins, 2015), field margins (Carvell *et al.*, 2004) and power-line clearings (Russell *et al.*, 2005, 2018; Berg *et al.*, 2013, 2016; Wagner *et al.*, 2014, 2019; Hill & Bartomeus, 2016; Sydenham *et al.*, 2016; Steinert *et al.*, 2018, 2020). Furthermore, routine management practices in human-modified habitats may promote conservation of endangered

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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 of 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 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). Removing the woody debris in power-line clearings have been found to promote a sustained positive effect on solitary bee communities (Steinert *et al.*, 2020). And regrowth of trees and retention of woody debris on the ground likely inhibit the growth of flowering plant species or the availability of flowering plants for the pollinators (Steinert *et al.*, 2018, 2020). 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 (Hoehn *et al.*, 2008; Albrecht *et al.*, 2012). Management practices that promote taxonomic 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 nest under rocks, or above ground in tree cavities, or in twig or litter piles (Osborne *et al.*, 2008b). Some species are social parasites upon a 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. These include the more vulnerable groups of long-tongued bumble bee species and species with late phenology (Goulson *et al.*, 2005, 2008; Williams *et al.*, 2009), which have showed consistent historical declines (Dupont *et al.*, 2011; Colla *et al.*, 2012). 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 that has also experienced sharp declines during the last century in Europe (Carvell *et al.*, 2006, 2011). Moreover, the decline in late-emerging queens are related to the scarcity of late flower resources and competition for nesting sites (Goulson *et al.*, 2008; Carvell *et al.*, 2011).

The effects of habitat management may be dependent on environmental context (Carvell *et al.*, 2011; Sydenham *et al.*, 2016), thus management practices should be assessed under different abiotic and biotic environmental conditions to better inform bumble bee conservation. Plant species richness and abundance influence pollinator community structure and diversity (Potts *et al.*, 2003, 2005). Enhanced plant species richness may ensure the availability of species-specific pollen and nectar resource requirements for bumble bees over necessary spatial and temporal scales (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, bumble bees are able to respond to the availability of floral resources at a landscape scale (Carvell *et al.*, 2011). Areas with a higher number of grassland habitats (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 (Winfrey *et al.*, 2009; Carrié *et al.*, 2017).

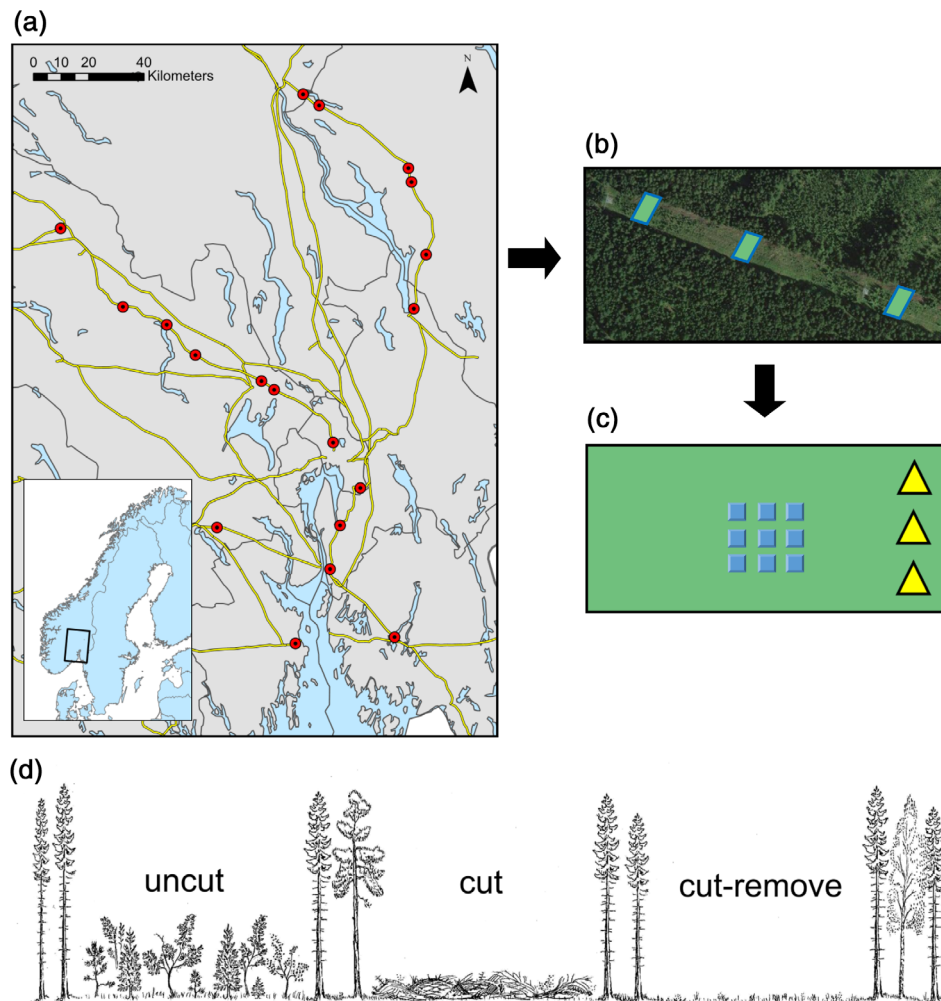
In this study, we carried out a large-scale field experiment to compare the effects on species and functional diversity of bumble bees in response to different maintenance clearing practices: (i) cutting the woody vegetation (current management practice), (ii) cutting and removing, and (iii) not cutting the woody vegetation. We also assessed whether environmental context modified the effects of management practices on the bumble bee responses or whether the environmental conditions influenced the bumble bee responses directly. We wanted to test the potential influence of abundance, taxonomic and functional diversity of forbs, as well as influence of time after clearing (year), elevation, precipitation, light availability, source habitat, and landscape fragmentation. Specifically, we asked: (i) Do bumble bee species richness, abundance and diversity differ among management practices? And (ii) Do functional trait groups of bumble bees [e.g., the abundance of long vs. short tongued bees, abundance of early vs. late-emerging bees, and abundance of cuckoo bees (*Psithyrus spp.*)] differ between management practices? We also assessed whether any effects of management on bumble bee responses were modified by the 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 m 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 5–10 years (dependent on site productivity) without use of chemicals and without disturbing the field layer (the herbs 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 experimental treatments were applied 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 neighbouring plots. The relatively short distances between treatment plots ensured low site-specific variation between treatments. Bumble bees have large foraging distances and may forage up to 10 km from their nests (Rao & Strange, 2012), although foraging usually occurs within 500 m from their colony (Osborne *et al.*, 1999;



**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 was on average 120 m. (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<sup>2</sup> subplots within the center of 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) cut-remove, all trees cut and woody debris removed. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Osborne *et al.*, 2008a). Consequently, differences in abundance of bumble bees 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: (i) cut: all trees cut and left to decay in the clearing; (ii) cut-remove: all trees cut and woody debris removed from the plot and (iii) 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.

#### Sampling of bees and floral resources

Bees and plants were sampled the first and third season after treatment applications. We sampled the bumble bee communities in the power-line clearings using flight interception traps (window traps) (Duelli *et al.*, 1999, Knuff *et al.*, 2019). Three traps were deployed within each treatment plot (19 sites, 3 treatments) and placed along the northernmost side of each treatment plot, to maximise sun exposure (Fig. 1) and to acquire similar trapping conditions. The traps had two transparent Plexiglas screens (370 mm × 210 mm), that formed a cross, with a funnel and container attached to it (Supporting Information Fig. SA1). 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 (Løken, 1985, Bollingmo, 2012, 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 (herbaceous plants that are not graminoids) and the percentage cover of ericaceous dwarf shrubs and *Salix* species in each treatment plot. The percentage cover was measured relative to all vascular plants in each plot. Plant surveys 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<sup>2</sup> within a 10 × 10 m quadrat (Fig. 1). In the nine subplots, we identified all vascular plants to species and visually estimated the cover 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 9 to 15. The sampling intensity was standardised 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 ( $q_0$ ) (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 raw species richness was summed from the raw abundance matrix (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 subgenera *Thoracobombus* and *Megabombus* (Supporting Information Table SA1). We also categorised 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*)] (Supporting Information Table SA1). The phenology for the queens were attained from regional field guides (Bollingmo, 2012, Ødegaard *et al.*, 2015). We used the rarefied 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 (Supporting Information Table SA1). The traits [extracted from Lid and Lid (2005)] were based on morphological characteristics of flowers, which are known to be important for pollinators (Supporting Information Table SA2). 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 (Laliberté *et al.*, 2014; Forrest *et al.*, 2015). 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 and 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 nine subplots (hereafter ‘Nectar tube species cover’) (Supporting Information Tables SA2 and SA3).

### 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 (m.a.s.l.) 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

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

Variables in bold were included in the full (most complex) models after preselection. For description of the variables, see methods under ‘Data preparation’.

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  $\leq 0.10$ ) (Bursac *et al.*, 2008); 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 generalised 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 ( $P \leq 0.05$ ) (Supporting Information Table SA4).

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, 2019). 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).

## Results

We collected 7266 bumble bees in 2013 ( $n = 3235$ ) and 2015 ( $n = 4031$ ) (Supporting Information Fig. SA2), 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, six species were cuckoo bees (668 individuals) (Supporting Information 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*) (Supporting Information Table A2).

### Species richness, abundance and diversity

For all the taxonomic indices, there was a positive effect of both the cut and the cut-remove treatments, compared to the uncut

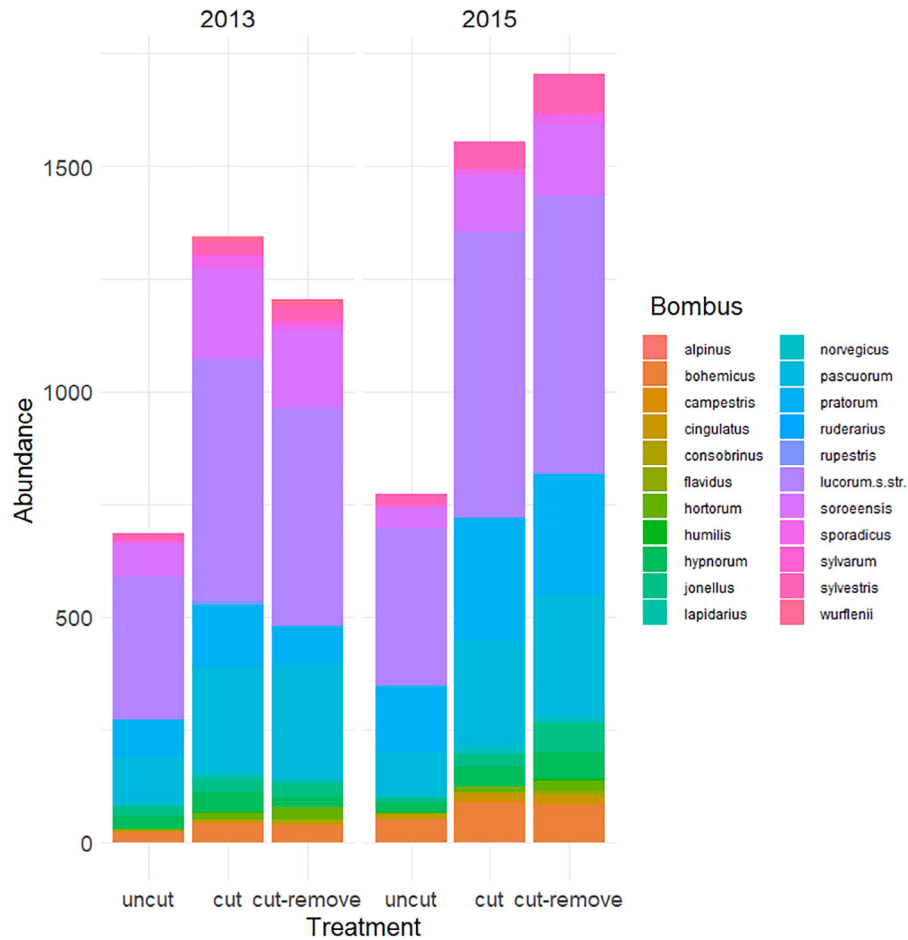
treatment, and the positive effect increased with forb species richness (Table 3). We found a significant treatment  $\times$  forb richness effect on bee species richness (Fig. 3a, LRT = 13.28,  $df = 2$ ,  $P = 0.001$ ), bee abundance (Fig. 3d, LRT = 8.14,  $df = 2$ ,  $P = 0.017$ ), and bee diversity (Fig. 3f, LRT = 12.23,  $df = 2$ ,  $P = 0.002$ ) in the cut and cut-remove treatments. However, there were no significant differences between the cut and cut-remove treatment in species richness/abundance/diversity/raw richness along the gradient of forb richness (Figs. 3; Supporting Information Fig. A3).

Species richness increased by 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 along the gradient of 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,  $df = 1$ ,  $P = 0.002$ ).

### 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) (Fig. 4e, f) and increased with functional variation of forb species (Fig. 5b, c). Average abundance of long-tongued bumble bee species was six 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,  $df = 2$ ,  $P \leq 0.001$ ). 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,  $df = 1$ ,  $P \leq 0.001$ ). For the abundance of late-emerging species, there were six more individuals in both the cut and cut-remove treatments, than in the uncut treatment (Fig. 4f, Table 3, LRT = 32.87,  $df = 2$ ,  $P \leq 0.001$ ). 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 taxonomic responses (Fig. 5, Table 3). Abundance of short-tongued species, showed a positive effect of both the cut and cut-remove treatments versus the uncut treatment (but no significant differences between the cut and cut-remove treatments), with the positive effect increasing with forb species richness (Fig. 5g, Table 3, treatment  $\times$  richness forbs: LRT = 7.06,  $df = 2$ ,  $P = 0.029$ ). We also found that short-tongued species increased from 14 to 81 individuals along the ericaceous



**Fig 2.** Bumble bees collected in the study. Abundance (raw) of bumble bees in each treatment (uncut, cut, cut-remove) in 2 years (2013, 2015), with colour-codes showing the abundance of each bumble bee species. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**Table 2.** The observed mean and standard deviation (mean  $\pm$  SD) of richness and abundance of bumble bees in each treatment plot in 2 years (2013 and 2015).

	Richness		Abundance	
	2013	2015	2013	2015
Uncut	5.8 $\pm$ 2.7	6.5 $\pm$ 2.2	27.4 $\pm$ 29.4	24.5 $\pm$ 24.4
Cut	8.6 $\pm$ 2.9	8.8 $\pm$ 2.2	54.0 $\pm$ 40.6	49.9 $\pm$ 42.4
Cut-remove	7.4 $\pm$ 2.9	9.6 $\pm$ 2.1	49.1 $\pm$ 46.0	54.1 $\pm$ 38.7

dwarf shrub gradient (Fig. 5d, Table 3, LRT = 16.19, df = 1,  $P \leq 0.001$ ). The treatment effect on the abundance of early emerging species depended on richness of forbs (treatment  $\times$  richness forbs: LRT = 7.53, df = 2,  $P = 0.023$ ). The early emerging species increased 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. 5h, Table 3). The early emerging species also increased from 14 to 89 individuals

with increasing cover of forb species with nectar tube (Fig. 5e, Table 3, LRT = 12.63, df = 1,  $P \leq 0.001$ ).

The treatment effect on abundance of cuckoo bees depended on cover of forb species with nectar tube (treatment  $\times$  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 nine 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 two individuals more in the cut than in cut-remove and 10 individuals more in cut than in treatment uncut (Supporting Information Fig. SA3b, Table 3, LRT = 29.66, df = 2,  $P \leq 0.001$ ). Abundance of *B. lucorum* bees also increased more than four-fold along the observed gradient of Ericaceae cover

**Table 3.** 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.

<i>Fixed effects</i>	Species richness				Abundance			
	$\beta$	<i>SE</i>	<i>t</i>	<i>p</i>	$\beta$	<i>SE</i>	<i>t</i>	<i>p</i>
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
<i>Random effects</i>								
$\sigma^2$	2.38				0.33			
$\tau_{00}$	1.89 <sub>Site</sub>				0.36 <sub>Site</sub>			
<i>N</i>	19 <sub>Site</sub>				19 <sub>Site</sub>			
Observations	114				114			
$R^2_m/R^2_c$	0.37/0.65				0.26/0.65			
<hr/>								
<i>Fixed effects</i>	Diversity				Cuckoo bees			
	$\beta$	<i>SE</i>	<i>t</i>	<i>p</i>	$\beta$	<i>SE</i>	<i>t</i>	<i>p</i>
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
<i>Random effects</i>								
$\sigma^2$	0.08				0.35			
$\tau_{00}$	0.02 <sub>Site</sub>				0.17 <sub>Site</sub>			
<i>N</i>	19 <sub>Site</sub>				19 <sub>Site</sub>			
Observations	114				114			
$R^2_m/R^2_c$	0.33/0.42				0.23/0.49			
<hr/>								
<i>Fixed effects</i>	Long-tongued				Short-tongued			
	$\beta$	<i>SE</i>	<i>t</i>	<i>p</i>	$\beta$	<i>SE</i>	<i>t</i>	<i>p</i>
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

(continued)



**Table 3.** (continued)

<i>Fixed effects</i>	Long-tongued				Short-tongued			
	$\beta$	SE	<i>t</i>	<i>p</i>	$\beta$	SE	<i>t</i>	<i>p</i>
<i>Random effects</i>								
$\sigma^2$	0.34				0.43			
$\tau_{00}$	0.26 <sub>Site</sub>				0.23 <sub>Site</sub>			
<i>N</i>	19 <sub>Site</sub>				19 <sub>Site</sub>			
Observations	114				114			
$R^2m/R^2c$	0.33/0.62				0.38/0.62			
<hr/>								
<i>Fixed effects</i>	Early emerging				Late emerging			
	$\beta$	SE	<i>t</i>	<i>p</i>	$\beta$	SE	<i>t</i>	<i>p</i>
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				
<i>Random effects</i>								
$\sigma^2$	0.41				0.34			
$\tau_{00}$	0.38 <sub>Site</sub>				0.26 <sub>Site</sub>			
<i>N</i>	19 <sub>Site</sub>				19 <sub>Site</sub>			
Observations	114				114			
$R^2m/R^2c$	0.21/0.64				0.25/0.56			

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;  $\sigma^2$ , variance;  $\tau_{00}$ , 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.

(Supporting Information Fig. SA3d, Table 3, LRT = 10.60, df = 1,  $P = 0.001$ ).

## Discussion

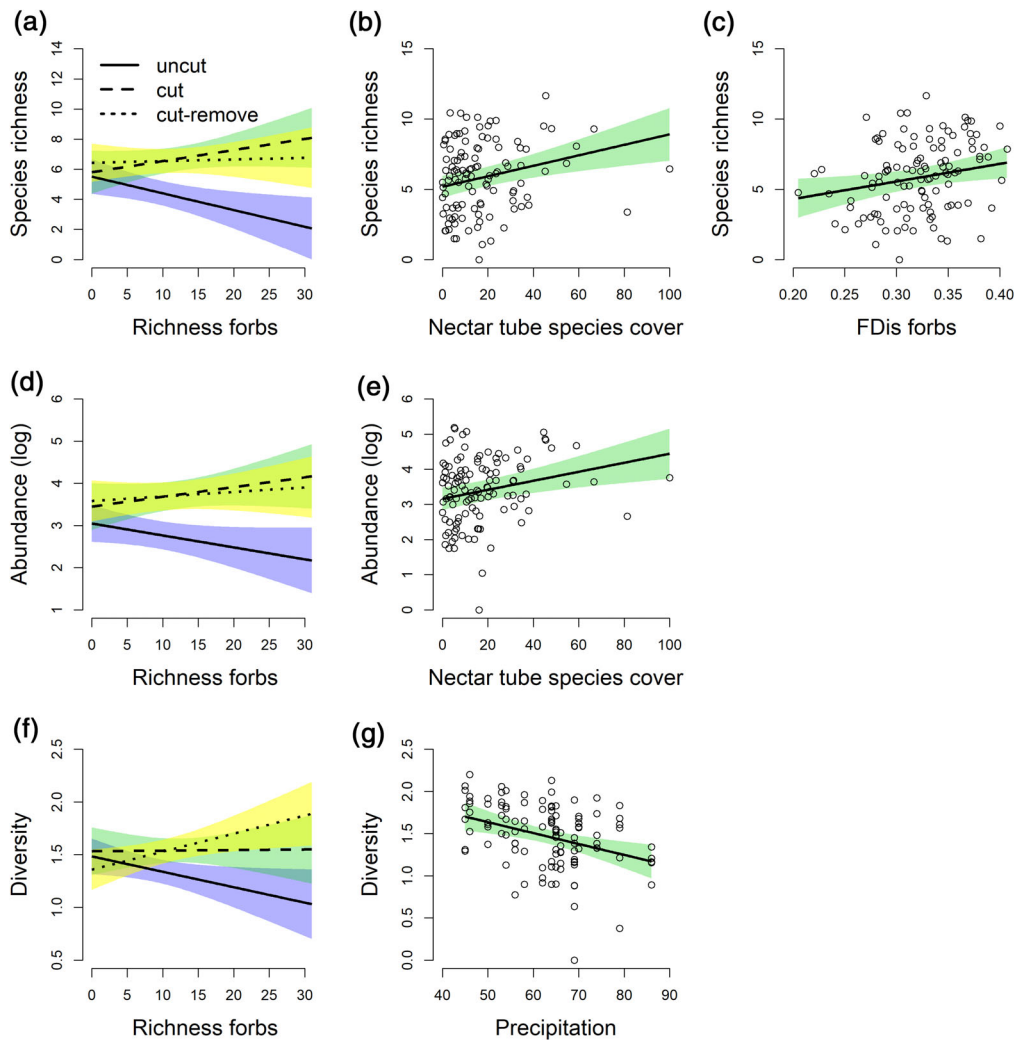
Experimental clearing of the vegetation in power-line clearings enhanced the habitat quality for bumble bees, irrespective of woody debris retention or removal. Our study clearly demonstrates the positive effects of maintenance clearing on bumble bees in the first years after cutting. The treatment effects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

### *Species richness, abundance and diversity*

The large difference between the two types of cleared plots and the uncut treatment plots showed that the effect of

maintaining vegetation in an early successional phase has a pronounced positive effect on the taxonomic responses of 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, increased forb species richness in the cleared treatment plots enhanced the habitat quality for bumble bees. This agrees with previous studies documenting a higher bumble bee richness and abundance where there is a higher 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 more bumble bee species are found in sites containing more flowers with nectar tubes, irrespective of treatment. This is a result that was expected since bumble bees are well known for their preference for plants with high nectar content (Goulson *et al.*, 2005; Pywell *et al.*, 2006).

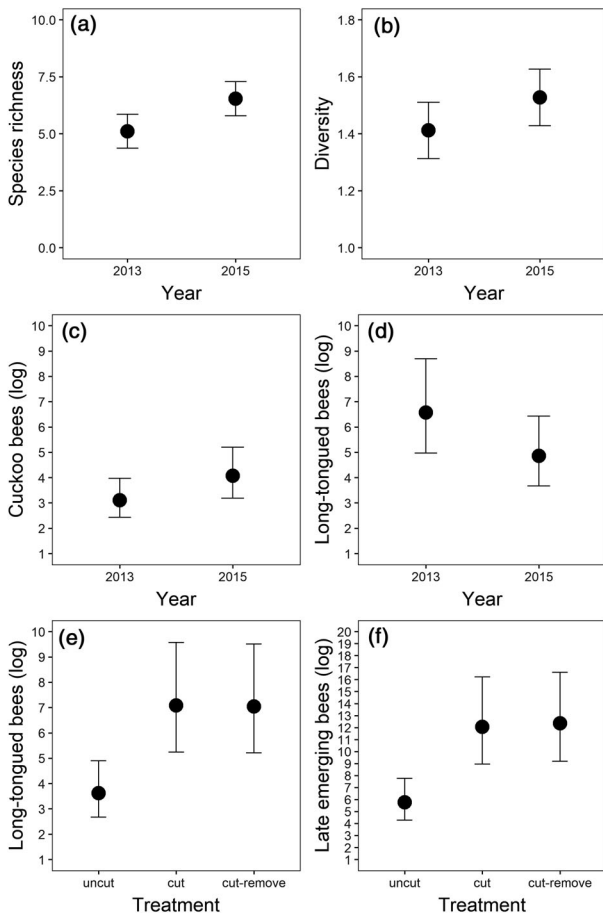
Woody debris removal did not seem to increase bumble bee habitat quality compared with the plots where cut woody debris was left to decay. This result was somewhat surprising and contradicts previous findings where woody debris removal had an added positive effect on solitary bees in power-line clearings (Sydenham *et al.*, 2016; Steinert *et al.*, 2020). 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



**Fig 3.** Effect of treatments and explanatory variables on taxonomic responses of bumble bees: The treatment effect (treatments: uncut, cut, cut-remove) on (a) bee species richness with increasing 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 average monthly 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. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

treatments, i.e. the forb richness was not significantly different between the treatments at each site (Steinert *et al.*, 2018). However, woody debris removal may enhance the functional diversity of forbs specifically in areas with high site productivity (Steinert *et al.*, 2018). This is likely because productive sites produce more woody debris inhibiting the growth or availability of flower resources. But bumble bees are robust dispersers and may not be limited by the woody debris or 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, compared to bumble bees nesting below ground. Nevertheless, leaving the

woody debris to decay on the ground may be beneficial for both below and above-ground nesting species, because bumble bees prefer nest entrances concealed by dense vegetation or different types of debris (Lanterman *et al.*, 2019). 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 bumble bee diversity in both types of cleared treatment plots can also be attributed to the bumble bees' ability to forage over large areas (Osborne *et al.*, 2008a), indicating that different types of habitats with flower resources within a 1–2 km radius are likely to be visited, irrespective of distances between the treatment plots.



**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

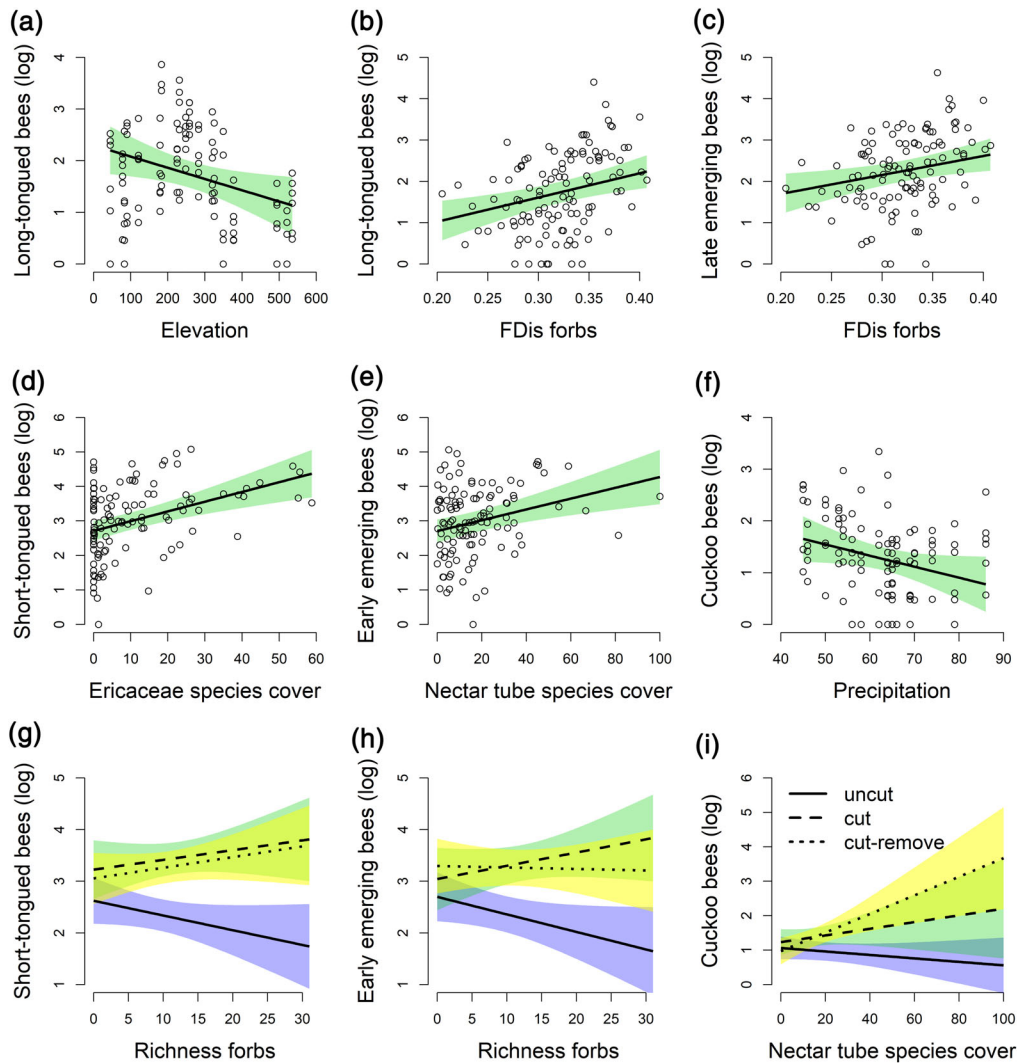
In addition to identifying the effects on species richness, abundance and diversity, a further aim was to determine to what degree these practices retain the functional diversity of bumble bee communities. By taking functional trait groups into account, we were able to identify the effects on the vulnerable long-tongued and late-emerging species. The long-tongued species preferred the cleared habitats, 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 were more abundant the first year. 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 heterogeneous landscapes within our study area.

Late-emerging species were markedly more abundant in the two types of 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. Therefore, these functional groups also responded positively to the increased forbs species richness in both the cleared treatments, similar to the taxonomic responses. The short-tongued species also positively responded 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. 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 emerging species. Possibly this is because willow or *Salix* species can also be found outside the power-line clearings and would only be present in the cleared 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) (Supporting Information Fig. SA2).

The cuckoo bees preferred the treatments where woody debris was removed in areas with increasing cover of forb species with nectar tubes. This could be because cuckoo bees are commonly attracted to sun-exposed rich flower resources. But it could also indicate that the cut-remove habitats with a high cover of nectar species would support more stable populations of their host species because 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 eusocial *Bombus* species in this study. 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 improved habitat quality, through their host dependency (Sheffield *et al.*, 2013). Given the dependency on



**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 (m.a.s.l.), 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. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

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 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 km (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, and knowledge about the effectiveness of habitat interventions for conservation purposes is important to inform management. Our research demonstrates the importance of early successional habitats for species diversity and functional trait groups of bumble bees. Woody debris in the field layer and the regrowth during 3 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 in areas with certain environmental conditions (Steinert *et al.*, 2018), and this functional diversity may benefit the more vulnerable long-tongued and late-emerging 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 prove to be valuable alternative natural or semi-natural grassland habitats for bumble bees in forests when flower-rich early successional vegetation is left undisturbed over several years. This is 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 increasing 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 (Russell *et al.*, 2018). This may redistribute 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 prefer the habitats in power line clearings when they are recently cut, particularly when there is a high richness of forbs, in comparison to habitats left uncut for more than 4–9 years. This suggests that increasing the frequency of cutting may benefit bumble bee communities particularly in areas with a high richness of forbs in the landscape. To promote bumble bees, we suggest that a more frequent cutting of vegetation than the current standard practice of long 10–12 year intervals, may contribute to the floral vegetation over the spatial and temporal scales required for bumble bees.

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## Authors contribution

M.S. performed the analyses, wrote the first draft of the manuscript and led the writing of the manuscript. K.E. and S.R.M. designed and initiated the experiment. M.S. and M.A.K.S. 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.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in [GBIF] at [http://doi.org/\[DOI\]10.15468/6iunbi](http://doi.org/[DOI]10.15468/6iunbi).

## Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

### Appendix S1: Supplementary Information

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