



## Local resources, linear elements and mass-flowering crops determine bumblebee occurrences in moderately intensified farmlands



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### ABSTRACT

There is consensus that land-use change is a main driver behind the recent declines of many pollinator populations in Europe. However, it is still not adequately understood how the local resource quality and landscape composition influence pollinators, and if and how the effects vary in space and time. We analysed the influence of landscape- (2 km radius) and local scale- (50 m transects) resources on bumblebee species richness and abundance during two years in South-eastern Norway, where agriculture is highly modernised but landscapes still show limited spatial homogenization. Local flower density and species richness were strongly positively associated with bumblebee densities and species richness, but higher landscape-level flower species richness were linked to lower local bumblebee abundances. Early and late mass flowering crops had clear, but contrasting, effects. The total area of early flowering crops had a consistent negative impact on bumblebee density and species richness throughout the season, while late flowering crops had a positive impact in the beginning of the season before their bloom, suggesting a carry-over effect from previous years. The negative effects of early flowering crops could be due to competition of bumblebees with honey-bees, which are widely used in these crops. Bumblebee density and species richness were clearly negatively correlated with the total area of forest and flower-poor land use areas, including grass fields and cereals. In contrast, bumblebees were positively associated with most linear elements in the landscape (especially pasture and cropland verges), except for roads, which negatively affected bumblebee densities, possibly due to increased mortality, since the quality of the flower resources did not differ from other linear elements. Our results show that the quality and the spatial and temporal distribution of flower resources within the landscape are important drivers for bumblebees, but can create counterintuitive distribution patterns depending on the temporal and spatial resolution of the survey. Increasing flower resources in linear elements and the amount of late mass-flowering crops may be viable management measures to improve conditions for bumblebees in moderately intensified landscapes.

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### 1. Introduction

Crop pollination is increasingly recognised as a major component of global food security. Pollinator conservation and status assessments are now receiving considerable attention due to increasing threats to pollinators and reports of considerable pollinator population declines (Potts et al., 2016, 2010; Vanbergen et al., 2013) together with estimated pollination deficits (Garibaldi et al., 2016). Bee density and diversity are important for the

delivery of a resilient pollination service to flowering crops and wild plants (Garibaldi et al., 2014; Rogers et al., 2014). It has been observed that higher pollinator diversity leads to increases in fruit and seed set of focal plants and is an important predictor of crop yields worldwide (Garibaldi et al., 2016; Lowenstein et al., 2015), possibly through improved matching between different pollinator and crop species (Cardinale et al., 2006; Rosenfeld, 2002). Bee populations are also sensitive to weather conditions which can result in large year to year variation in population sizes. Mediated by species-specific responses, pollinator diversity helps to maintain stable pollination services by buffering against this variation, since it increases the likelihood that some species respond favourably to the fluctuating weather conditions (c.f.

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“response diversity” in Elmquist et al., 2003; Garibaldi et al., 2014; Kremen et al., 2002). Accordingly, simplification of pollinator communities has been linked to decreased stability of seed production (Bommarco et al., 2012), and may be one reason for a lower stability of yields in pollinator-dependent crops compared to other crops (Potts et al., 2016).

Simplified landscape composition that result from agricultural intensification (Fjellstad and Dramstad, 1999; Ricketts et al., 2008; Steffan-Dewenter et al., 2002; Tscharrntke et al., 2005) is among the critical factors that affect bee populations in the industrialized world. Higher cover of large and homogenous cropland areas is linked to pollinator population declines (Potts et al., 2010; Senapathi et al., 2015; Vanbergen et al., 2013) and more heterogeneous landscapes are associated with higher bumblebee species richness and densities (Rundlöf et al., 2008), for example through provisioning of complementary floral resources (Mallinger et al., 2016). Furthermore, many studies show that higher proportions of cropland and decreased semi-natural habitats result in lower bee species richness (Garibaldi et al., 2011; Ricketts et al., 2008).

Several studies focus on the effects of land use on pollinator density and diversity (e.g. Carre et al., 2009; Goulson et al., 2010; Ricketts et al., 2008) as well as on their foraging behaviour (e.g. Jha and Kremen, 2013). These however, have often been conducted in highly homogenous landscapes with intense agricultural production (but see Diaz-Forero et al., 2013). Still, many agricultural landscapes in the Western world consist of long established patchworks of cropland and other land uses, often constrained by abiotic factors such as topography. This is especially true in our study area in Norway, where the spatial simplification and homogenization of the agricultural landscape has been relatively limited. In such settings, other factors, such as habitat quality and the continuity of food resources could be more relevant than the amount of available nesting sites or foraging distances (Garibaldi et al., 2011; Ricketts et al., 2008), which has been emphasised previously (Lonsdorf et al., 2009). As in much of the Western world, the quality of the landscape elements has also been highly transformed in Norway; pastures, lays, and meadows have been largely converted into cereal or grass production using modern techniques, and many small fields have been conglomerated into larger units (Fjellstad and Dramstad, 1999). Hence, current land uses within the established agricultural landscape and their impacts on habitat quality, including the composition of crop-fields, are likely important drivers of pollinator occurrences (Kennedy et al., 2013; Ricou et al., 2014).

For instance, in addition to non-crop habitats, flowering crops are an important resource for pollinators (Rundlöf et al., 2014), a factor considered also in spatial models of pollination services (Zulian et al., 2013). Mass-flowering crops constitute a pulse resource, highly concentrated in time, with strong effects on pollinator population structure (Diekötter et al., 2010, 2014; Hanley et al., 2011; Holzschuh et al., 2013, 2016). This can result in temporal effects both between (Rundlöf et al., 2014) and within years (Riedinger et al., 2015), as well as spatial effects (Montero-Castaño et al., 2016). The crop phenology in Norway allows us to study the effects of early and late mass-flowering crops separately. The main early mass-flowering crops bloom in early to late May and can provide large pollen sources for newly emerging queens, when communities of workers are still relatively small. These are likely important early season resources for bumblebees in the region of our study. Early pollen sources are often cited as important food sources for bumblebees (O'Rourke et al., 2014) but the commonly employed example of willows (*Salix* spp.) are often sparsely distributed throughout an entire region, making it difficult to assess their importance. The other main mass-flowering crops flower in the middle of July – August, offering resources in a period clearly separated from the early ones.

Despite the attention given recently to the effect of the quality of landscape elements on pollinators (Kennedy et al., 2013; Ricou et al., 2014), current knowledge is insufficient to provide reliable models of pollination services to support local decisions, which often rely on expert-based scoring of flower resource suitability (Lonsdorf et al., 2011; Zulian et al., 2013). Frequently, natural habitats such as wetlands, heathland and woodland are given equal importance (Steffan-Dewenter et al., 2002; Woodcock et al., 2013), which may be one reason behind the lack of correspondence between bee richness and the area of semi-natural habitat in these studies, and which is typically found in studies that aggregate land-uses to a lesser degree (Garibaldi et al., 2011; Lonsdorf et al., 2009). Further, recent studies highlight the importance of botanical attributes of landscape elements for pollinators, showing for instance, that richer plant assemblies in riparian margins can support more pollinators than grassland fields (Cole et al., 2015).

In modern agricultural landscapes, the linear elements that border the major land use types – field margins, road verges and forest edges – are generally considered to provide a large proportion of the food resources (Hanley and Wilkins, 2015) and nesting places for bees, and have been used as spatial indicators of the capacity of agro-ecosystems to generate pollinator services (Zulian et al., 2013). However, the positive impact of their presence on the landscape level abundance of pollinators have not been widely confirmed. In addition, although pollinator studies often consider various spatial scales, ranging from farm to landscape level effects (e.g. Kennedy et al., 2013; Kovacs-Hostyanszki et al., 2013), the very local (transect level) effects have seldom been analysed together with landscape level effects (but see Diaz-Forero et al., 2013).

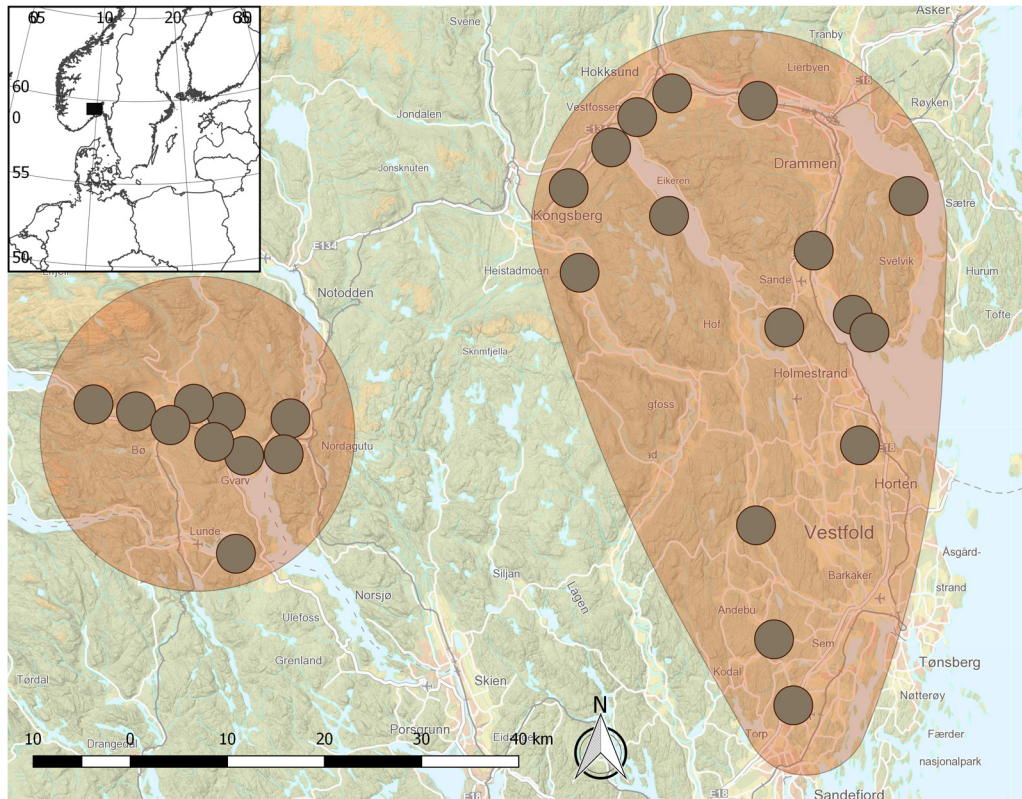
Bumblebees form an important pollinator group in Norway (Totland et al., 2013) and are abundant enough to enable the collection of sufficient data for several species. Since bumblebees have an impressive ability to locate suitable flower resources (Olsson et al., 2015) and can fly up to several kilometres to forage (Osborne et al., 2008), we expect bumblebee assemblies to be affected by different features of the landscape, with impacts at different scales.

In this study, we investigate the importance of landscape configuration and resource quality on bumblebees in relatively spatially heterogeneous, but highly modernised agricultural landscapes. We map the flower resources both at the local (transect) and landscape scale, and use study landscapes centred on either early or late mass-flowering crops (or none for control). By simultaneously addressing the transect and landscape levels, with repeated samples spanning two years, we are able to explore potential spatial and temporal aggregation effects. We hypothesised that the 1) habitat quality in terms of local flower resources and the amount of resources within a landscape would be main determinants of bumblebee density and species richness, and that 2) early and late mass flowering crops would synergistically enhance bumblebee populations. Due to the temporal variation of flower resources and the active forage seeking behaviour of bumblebees, we further hypothesised that 3) temporal and spatial aggregation effects would influence the bumblebee distributions. Lastly, we wanted to explore to what extent 4) land-use heterogeneity influenced bumblebees in these moderately homogenised landscapes.

## 2. Material and methods

### 2.1. Study area and field sites

The area studied was the south-eastern part of Norway in the counties of Vestfold, Telemark and Buskerud (see Fig. 1). This region contains a range of landscape types, including some of the most intensified agricultural landscapes in Norway, which are dominated by cereal production, interspersed with vegetables and



**Fig. 1.** Map with locations of the 26 study landscapes of 2 km radius (plotted to scale) in southern Norway covering in total 327 km<sup>2</sup>. The study locations were divided into east and west clusters for the analysis as shown.

fruit and berry production, as well as landscapes dominated by forests, with interspersed agricultural activity. The landscape units in the study (see below) were clustered in two geographical areas, the West with abundant fruit production in addition to crops, and the East containing mostly agricultural crops, but with fruit production in some landscapes.

We used digital land-cover maps (Björdal and Bjørkelo, 2006) to delimit 26 circular areas of 2 km radius (hereon, 'landscapes') with varying composition of land uses. Although maximum flight distances of bumblebees can be several kilometres, most foraging movements recorded are less than 1 km (Hagen et al., 2011 and references therein), making 2 km radii a reasonable choice. The centre points of the landscapes were selected according to their closeness to apple orchards and red clover seed production fields in 2013, representing early and late mass-flowering crops, respectively. Only 6.1% of the area of early mass-flowering crops was made up of berries which bloom over an extended period of time, so these agricultural units represent an early-season resource that is distinct from the late mass-flowering crops of red clover and spring-sown rapeseed. The individual landscapes thereby sample a gradient of landscapes with high agricultural activity (maximum of 58% agricultural land and 23% forest) to landscapes dominated by spruce and pine forest (minimum of 2% agricultural land and 80% forest). In total, the study area comprised 327 square kilometres, which were mapped according to their land use. Bumblebees were recorded along transect walks (see below) covering approximately 11 ha. It is possible that the individual transects were also influenced by features outside the delimited landscape unit area of 2 km radius, as transects were spread within these circles and could be located close to the border. However, this would have added to the unexplained variability in the data, but not likely introduced systematic biases. Distances between the study landscape centres ranged from 2.5 to 64 km. The minimum

distance between the two clusters were 33 km and the distance between the centres 57 km. Further details of the landscapes are available in the Supplementary material.

## 2.2. Bumblebee and transect sampling

Within each landscape, we established 50 m transects located along linear features, with transects types classified as road, field, forest and pasture edges based on the Norwegian Land Resource Map 1:5 000 AR5 classes 12, 21 & 22, 30, and 23, respectively (Björdal and Bjørkelo, 2006). The number of transects and transect types within each landscape was proportional to the total length of each linear feature type in a landscape, varying between 6 and 30 transects per landscape, with a mean of 21, and 535 transects in total for the study. The sampling effort was thereby scaled to the amount of linear elements in the landscape. Transect positions were recorded with a GPS and mapped to enable the same location to be revisited. We conducted a total of seven visits to each transect, one visit each month between May and August in 2013 and one in May, July and August in 2014. The recording was done during dry weather conditions between the hours 09:00 and 18:00.

At each transect we walked approximately 5 min per visit, allowing for additional time for specimen handling and species identification, and recorded the number and species of bumblebees within 2 m on both sides. Individuals of *B. lucorum*, *B. soroeensis*, *B. magnus*, *B. cryptarum* and *B. terrestris* were aggregated into one group for the analyses because it was not always possible to distinguish the species identity accurately in the field. Additional individuals for which species could not be determined in the field were collected and identified in the laboratory. We also recorded when bumblebees were observed on flowers and which flower species (total of 4919 observations on 104 different flower species/families). This data was used later for weighting the



importance of flower species when calculating the density of flower resources (see below).

At 5 m from the starting point of each transect we delimited a plot of 2 × 5 m, in which we recorded all open flowers. The registered flower units differed depending on the type of flower but the same flower unit was consistently recorded within species. Flower units included individual flowers (e.g. Convolvulaceae), flower clusters (e.g. Apiaceae), flower heads (e.g. Asteraceae and clovers), racemes (e.g. other Fabaceae), and flower stalks (e.g. Campanulaceae and Ranunculaceae). When flower density was very high and homogeneous in terms of species composition in the 2 × 5 m plots, we used a 1 × 2 m sub-plot for flower counts, and the values were extrapolated to the 2 × 5 m plot. In the case of shrubs, we recorded their height and the area they covered within the 2 × 5 m plot, and whether the species was flowering. A few species were recorded at a genus or family level due to difficulty in reliable identification in the field. Within these groups, the species had similar flower traits.

### 2.3. Variables

We used the total number of bumblebees and the total number of bumblebee species recorded per transect visit as dependent variables in the statistical models.

We calculated the length of the linear elements (road, field-, forest- and pasture edges, see above) and the area of land use classes using digital land use/land-cover maps (Björdal and Bjørkelo, 2006). In addition, we ground-truthed the landscapes in 2014 and recorded the crop species in the agricultural fields. The land uses were combined into five different main categories; 1) early mass-flowering crops (including fruit orchards and cultivated berries) 2) late mass-flowering crops, (including peas, clover and oilseed rape) 3) forests (including all forests classes in AR5) 4) flower-poor areas (including grass fields and cereal crops) 5) grasslands (including pastures, meadows and fallows). We used these same categories also to calculate a Shannon's land use diversity index for each landscape which summarizes the number of land use categories and evenness of the total area of the different land use types within each landscape.

We calculated the flower resources both at transect and landscape level. Flower species richness at transect level was calculated as a number of species flowering during the transect visit. Only open, non-withered flowers were recorded. Because of the varying numbers of transects in different landscapes, we estimated the total species richness within the landscapes, using the "specpool" function from the Vegan package (Oksanen et al., 2016) in R (R Core Team, 2016). These estimates were not correlated with the number of transects in a landscape, and could therefore be used as an unbiased estimate of the total species richness within a landscape.

Due to the differences in flower morphology and counting methods (see above), flower counts were not directly comparable between species, but the measure is comparable among transects and landscapes (Rundlöf et al., 2014). We standardized the amount of flower resources per species in each transect in relation to the total number of flower counts of that species in the same sampling period (month of sampling). To account for differences in the quality of plant species as flower resource, we weighted these standardized flower counts by the total bumblebee visitation rate for each plant species/family during the same sampling period. These standardized and weighted values were then summed up to represent a flower density estimate at each transect. Similarly, at the landscape level, we summed up the relative number of flowers of each flower species within the landscape during the sampling period, weighted them with the plant specific visits during that sampling period and then summed these up for each landscape.

Local daily temperature averages were obtained from the Norwegian Meteorological Institute (<http://www.met.no>), which are interpolated for a 1 × 1 km grid based on local weather stations (Mohr, 2008; Tveito et al., 2000).

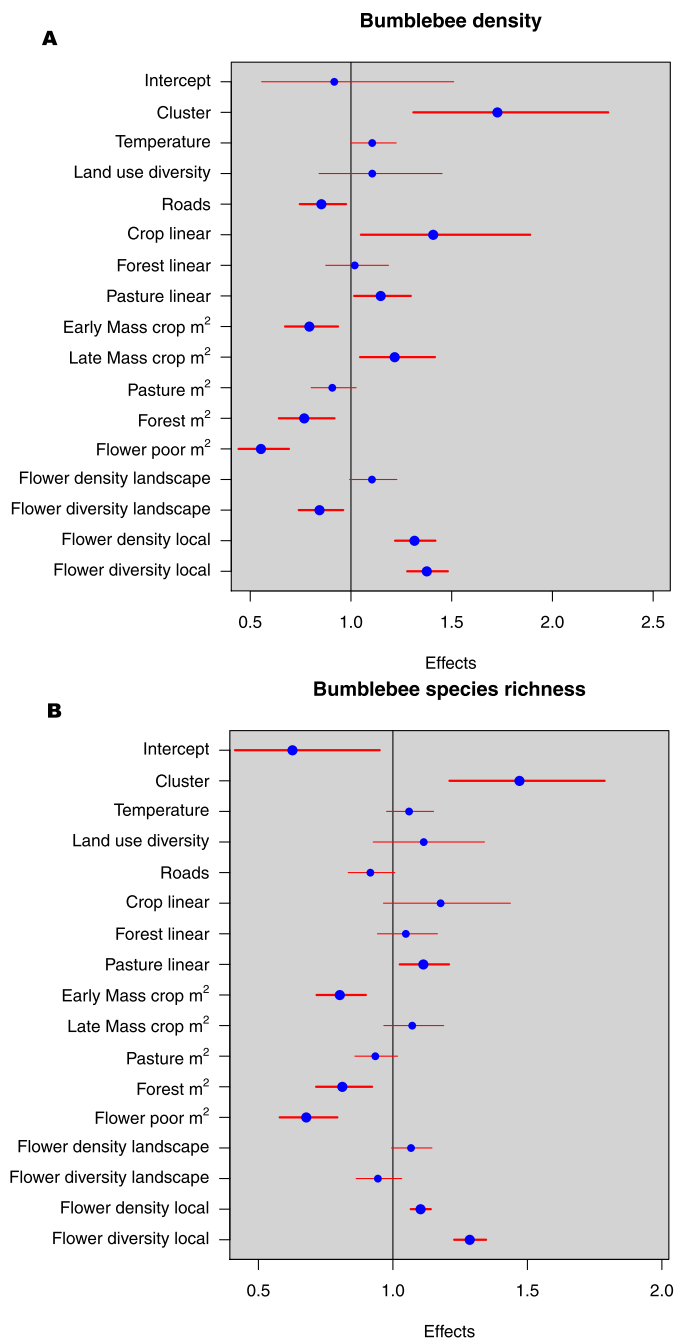
### 2.4. Statistical analyses

We built separate models for bumblebee species richness and density using the glmmADMB package (Fournier et al., 2012; Skaug et al., 2016) in R (R Core Team, 2016). We used a negative binomial distribution and log link function which is suitable for over-dispersed count data and for modelling the zero-inflation from transect samples with no bumblebee observations. We fitted models that included all explanatory variables of interest a priori: i.e. areas of the five different land uses (see above) within each landscape, Shannon's land use index for each landscape, flower species richness and density at landscape and transect level, the total length of the four different linear elements (field, forest and pasture edges and roads) per landscape, and temperature as a covariate. Due to the spatial division of the study landscapes, we divided the landscapes into a western and an eastern cluster and added this as a factor in the models. We report and discuss all parameter estimates together with their uncertainty, as they were considered interesting a priori, and to avoid problems with spurious results associated with rule-based model selection (Burnham and Anderson, 2002; Gelman and Hill, 2007; Reichert and Omlin, 1997). We included transect\_id, landscape\_id and sampling period as random effects to account for spatial aggregation effects and repeated observations. In addition, we fitted separate models to investigate possible seasonal effects of early and late mass-flowering crops on bumblebees. The models included the total area per landscape of either early or late mass-flowering crops, their interaction with sampling period, and the east-west clustering factor as explanatory variables, using glmmADMB with negative binomial distribution and transect\_id and landscape\_id as random effects. With all analyses, we accounted for zero inflation in the models when it improved the model fit based on AIC values. Similarly, we used families as "nbinom" or "nbinom1" depending on which produced lower AIC values. All explanatory variables were standardized (using  $\frac{x_i - \bar{X}}{sd(X)}$ ) to improve model fit and interpretability (Zuur et al., 2009). Furthermore, we checked the generalised Variance Inflation Factor (VIF) for all models to test collinearity of the variables (Fox and Monette, 1992). These were found to be <1.38 for all variables which are considered acceptable. Spatial autocorrelation of the measured variables was calculated as Moran's I using the R package "ape" and was very low (<0.08) and not significant for any of the models.

## 3. Results

### 3.1. Flower resources

Local flower species richness and density had positive effect on both bumblebee density and species richness (Fig. 2, Table 1). Transects with one standard deviation more flower species had on average 38% (95% conf.int: 28% to 48%) more individuals of bumblebees and 29% (95% conf.int: 23% to 35%) more bumblebee species. Landscape level flower density likewise had estimated positive effects on local bumblebee density and species richness although the 95% confidence intervals overlapped zero. Interestingly, after accounting for the local flower resources, a higher flower species richness in the surrounding landscape negatively affected local bumblebee density. There was a similar tendency for species richness, although this effect was more uncertain.



**Fig. 2.** Results from the generalised linear mixed models of bumblebee density (a) and diversity (b) with negative binomial distribution and log link function. All fixed explanatory variables included in the model are shown. The dots show the exponent of the model estimate for each variable, corresponding to a multiplicative model, such that e.g. a value of 1.5 indicates a positive effect of 150% and a value of 0.5 represents a negative effect of 50%. The lines represent the 95% confidence intervals, and variables not crossing 1 (representing the cut between positive or negative influence in the model) are presented with thicker lines and larger dots. Early Mass crop and Late Mass crop refer to early mass-flowering crop and late mass-flowering areas, respectively. ‘Cluster’ indicates West and East landscape clusters. Land use diversity corresponds to the Shannon index calculated on land use/land-cover types.

Landscapes with one standard deviation more flower species had on average 16% (95% conf.int: –28% to –4%) less bumblebee individuals and 5.6% (95% conf.int: –13 to 3%) fewer bumblebee species per transect. The results were qualitatively the same in a model containing only landscape level explanatory variables (not

shown), indicating that this is not an artefact of the multilevel model.

### 3.2. Land uses

Bumblebee density and species richness were not clearly related to land use diversity (Shannon land use diversity index) within the landscapes, and the parameter estimate showed considerable uncertainty. Adding second degree polynomials, allowing for a humped-backed effect, did not improve the models and are not reported further. In contrast, both bumblebee density and species richness were clearly negatively correlated with the total area of forest and flower-poor land use areas, including grass fields and cereals (Fig. 2). Flower-poor areas showed the strongest effect of all explanatory variables; landscapes with one standard deviation more flower-poor land uses had on average 45% (95% conf.int: –56% to –31%) less bumblebee individuals and 32% (95% conf.int: –42% to –21%) less bumblebee species. In the present study, flower-poor land areas together comprise on average 21% (sd 12) of the total area in the landscapes and make up the vast majority of the croplands. Areas with one standard deviation more forest had 19% (95% conf.int: –29 to –8%) less bumblebee individuals. There was also a tendency that bumblebee density and species richness were negatively influenced by the total area of pasture, but this effect was uncertain with confidence intervals overlapping zero.

### 3.3. Mass flowering crops and interaction with sampling time

Early and late mass flowering crops had clear, but contrasting, effects; the total area of early flowering crops within the landscapes had a negative impact on bumblebee density and species richness, while late flowering crops had a positive impact on bumblebee density (Fig. 2, Table 1). The effect of late mass-flowering crops on bumblebee species richness was also positive but more uncertain. Landscapes with one standard deviation more early mass-flowering crops had on average 21% less bumblebee individuals (95% conf.int: –33% to –6%) and 20% (95% conf.int: –28% to –10%) less bumblebee species. Landscapes with one standard deviation more late mass-flowering crops had on average 22% more bumblebee individuals (95% conf.int: 5% to 42%) and 7% (95% conf.int: –3% to 19%) more bumblebee species.

The effect of the area of late mass-flowering crops within each landscape interacted clearly with sampling time: larger areas of late mass-flowering crops were associated with higher bumblebee species richness and density only in the early registrations in May (Fig. 3, Table 2). Later in the season, from June to August, the relationship was in general negative, with clear negative effects on bumblebee diversity in July and August, and on bumblebee density in July. In contrast, there were no signs of interaction effects between early mass-flowering crops and sampling period (Table 2). Thus, there was no evidence that the negative effect of early mass-flowering crops was dependent on sampling period.

### 3.4. Linear features

Both the total length of pasture and cropland edges were positively related to bumblebee density and species richness, although the 95% confidence interval overlapped zero for the effect of cropland edge on bumblebee species richness. Landscapes with one standard deviation more pasture edge or more cropland edge had 15% (95% conf.int: 2% to 30%) and 41% (95% conf.int: 5% to 89%) more bumblebee individuals, and 11% (95% conf.int: 3% to 21%) and 18% (95% conf.int: –3% to 44%) more bumblebee species, respectively. In contrast, the length of forest edges had a lower

**Table 1**

Results of the generalised linear mixed models for bumblebee density and bumblebee species richness. Year, transect ID and Sampling time were included in the model as random factors.

	Bumblebee density				Bumblebee species richness			
	Estimate	Std. Error	z value	Pr(> z )	Estimate	Std. Error	z value	Pr(> z )
Flower species richness local	0.32	0.04	8.57	0.00	0.25	0.02	10.72	0.00
Flower density local	0.27	0.04	7.08	0.00	0.10	0.02	5.70	0.00
Flower spec. richn. landscape	-0.17	0.07	-2.56	0.01	-0.06	0.05	-1.26	0.21
Flower density landscape	0.10	0.05	1.84	0.07	0.06	0.04	1.82	0.07
Flower-poor m <sup>2</sup>	-0.59	0.11	-5.18	0.00	-0.39	0.08	-4.85	0.00
Forest m <sup>2</sup>	-0.26	0.09	-2.90	0.00	-0.21	0.06	-3.20	0.00
Pasture m <sup>2</sup>	-0.10	0.06	-1.56	0.12	-0.07	0.04	-1.57	0.12
Late mass-flower crop m <sup>2</sup>	0.20	0.08	2.54	0.01	0.07	0.05	1.31	0.19
Early mass-flower crop m <sup>2</sup>	-0.23	0.08	-2.75	0.01	-0.22	0.06	-3.79	0.00
Pasture linear	0.14	0.06	2.22	0.03	0.11	0.04	2.56	0.01
Forest linear	0.02	0.08	0.24	0.81	0.05	0.05	0.87	0.38
Crop linear	0.34	0.15	2.28	0.02	0.16	0.10	1.61	0.11
Roads	-0.16	0.07	-2.33	0.02	-0.09	0.05	-1.82	0.07
Land use diversity	0.10	0.14	0.72	0.47	0.11	0.09	1.15	0.25
Temperature	0.10	0.05	1.92	0.05	0.06	0.04	1.40	0.16
Cluster	0.55	0.14	3.88	0.00	0.39	0.10	3.88	0.00
Intercept	-0.09	0.25	-0.34	0.73	-0.47	0.21	-2.20	0.03

estimated influence, with the uncertainty overlapping zero broadly for both bumblebee density and species richness.

Unexpectedly, the total length of roads had a negative effect on bumblebee density. There was a corresponding estimated negative effect on bumblebee species richness, although the confidence interval here overlapped zero. Landscapes that had one standard deviation more length of roads had on average 15% (-25% to -2%) less bumblebee individuals and 8% (95% conf.int: -17% to 0.7%) less bumblebee species. None of these effects appear to be clearly related to the flower resources of the different linear landscape elements, or the local bumblebee densities in each respective

linear element category (Supplementary material), suggesting that these were not driven by aggregation effects.

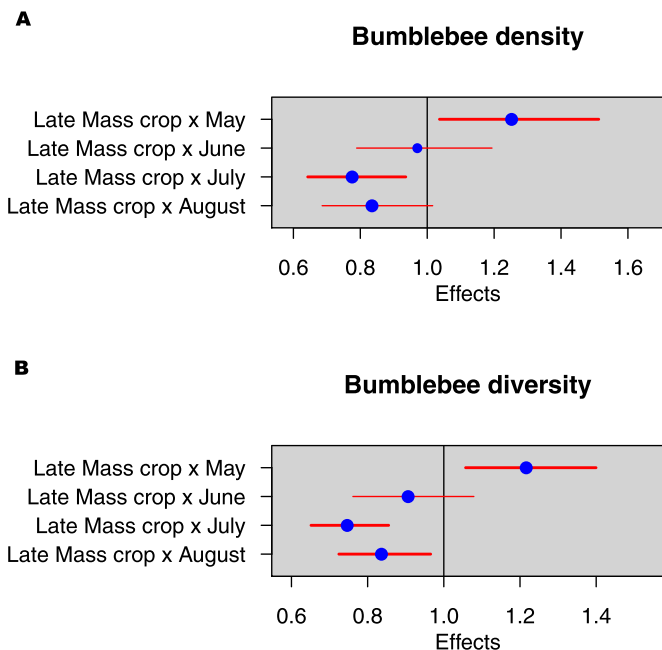
### 3.5. Random effects and spatial clustering

The random effect of sampling period accounted for most of the variation with a variance of 0.25 and 0.17 for the density and species richness models, respectively. Individual transects in turn, had an estimated variance of 0.14 and 0.03, and individual landscapes 0.005 and 0.002 for the density and species richness models, respectively. The west-east clustering showed clearly higher abundances and species richness in the western cluster than in the eastern (Fig. 2).

## 4. Discussion

### 4.1. Flower resources

We found clear evidence that bumblebee density and species richness are positively affected by the local flower species richness and density, which is congruent with most previous findings (Cole et al., 2015; Ebeling et al., 2008; Potts et al., 2003). For example, Potts et al. (2003) found that bee species richness was linked to floral species richness, and flower abundance has been found to be a good indicator of bee patch use (Bennett et al., 2014). Ebeling et al. (2008) also found that increasing plant diversity enhances and stabilizes pollinator visits. The local flower species richness was a particularly important determinant of local bumblebee richness, suggesting that bumblebees have the ability to effectively locate their preferred flower resources. Taking into account these strong effects of the local flower resources, the landscape level density of flower resources showed an additional but weaker and more uncertain positive effect on bumblebees. In other words, increasing the amount of flowering plants leads to greater density and species richness of bumblebees, and in addition it is likely that there is a spill over effect from the wild flower resources in the surrounding landscape. This could act both within the current year, with the regional level of flowering resources boosting population numbers, or between years as a result of increased reproduction. Since foraging is directed toward the most rewarding foraging habitat patches as determined by quality and distance, the actual foraging habitat will likely include a wide range of forage qualities close to the nest, but a much narrower range farther away. Our results support previous evidence for spatial aggregation at



**Fig. 3.** Results of generalised linear mixed models exploring the interaction between sampling time and the amount of late and early mass-flowering crops in the landscapes for bumblebee density (a) and species richness (b) with negative binomial distribution with log link. Late Mass Crop refer to late mass-flowering crops. The dots show the exponent of the model estimate for each variable, similar to Fig. 2. The lines represent the 95% confidence intervals, and variables not crossing the 1 (representing the cut between positive or negative influence in the log linked model) are presented with thicker lines and larger dots.

**Table 2**  
Results from the generalised linear mixed models of bumblebee density and bumblebee species richness with interaction between sampling time and mass-flowering crops as explanatory variables. Year and transect ID were included in the model as random factors.

	Bumblebee density				Bumblebee species richness			
	Estimate	Std. Error	z value	Pr(> z )	Estimate	Std. Error	z value	Pr(> z )
Intercept	−0.54	0.11	−4.80	0.00	−0.79	0.09	−8.90	0.00
Cluster	0.34	0.15	2.25	0.02	0.24	0.11	2.22	0.03
Late Mass crop × May	0.22	0.10	2.34	0.02	0.20	0.07	2.74	0.01
Late Mass crop × June	−0.03	0.10	−0.28	0.78	−0.10	0.09	−1.11	0.27
Late Mass crop × July	−0.25	0.10	−2.65	0.01	−0.29	0.07	−4.22	0.00
Late Mass crop × August	−0.18	0.10	−1.80	0.07	−0.18	0.07	−2.44	0.02
June	−0.24	0.11	−2.18	0.03	−0.31	0.10	−3.17	0.00
July	1.57	0.10	16.11	0.00	1.10	0.08	14.68	0.00
August	0.96	0.10	9.47	0.00	0.69	0.08	8.59	0.00
Early Mass crop × May	0.11	0.10	1.01	0.31	0.01	0.09	0.11	0.91
Early Mass crop × June	−0.09	0.12	−0.76	0.45	0.00	0.11	−0.01	0.99
Early Mass crop × July	0.03	0.10	0.32	0.75	0.07	0.08	0.88	0.38
Early Mass crop × August	−0.02	0.10	−0.18	0.86	0.04	0.08	0.49	0.63
Intercept	−0.54	0.11	−4.80	0.00	−0.79	0.09	−8.90	0.00

attractive resources (e.g. Walther-Hellwig and Frankl, 2000; Osborne et al., 2008; Redhead et al., 2016) and pollination models that incorporate foraging behaviour, which assume that bees selectively use those parts of the landscape that enhances their fitness, avoiding foraging in other parts of the landscape (Olsson et al., 2015). Still, the results indicate that increasing the total amount of flower resources within a landscape will increase landscape level pollinator density and species richness, which could in turn lead to higher flower visitation and likely more stable and effective pollination of both crops and wild plants (Bommarco et al., 2012; Rogers et al., 2014). For example, a recent study by Garibaldi et al. (2016) showed the benefit of increasing pollinator density and richness on crop yield in a wide range of agricultural crops.

Interestingly, after taking into account the strong positive effect of local flower density and species richness, there was a negative influence of the landscape level flower species richness on local bumblebee densities, and a similarly negative, but less certain effect on species richness. This additional but opposite effect to local flower richness is counterintuitive at first glance. However, bumblebees actively search the landscape and are likely to aggregate at particularly attractive local flower resources, as this study indicates. Jha and Kremen (2013), for instance, documented longer mean foraging distances in patches where flower plant richness was high and variability in flower cover between patches within landscape low. This means that a distributed high diversity of flower resources within a landscape could lead to a dilution of bumblebee at the local scale. Other studies also provide some evidence of impacts of flower resources on the spatial aggregation of bees (e.g. Osborne et al., 2008; Redhead et al., 2016; Walther-Hellwig and Frankl, 2000). Bennett et al. (2014) found a negative influence of flower richness on total bee visitation rate, but they suggested that the negative effect of flower richness at small scales could be an artefact of other factors that are correlated with flower richness, and we cannot exclude that this could also be the case here.

#### 4.2. Landscape composition

Earlier studies have associated habitat and landscape heterogeneity with higher biodiversity (Benton et al., 2003; Holzschuh et al., 2007; Martins et al., 2014). In our study, while there was positive estimated effects of land use heterogeneity on bumblebee species richness and density, these estimates were rather low and

had considerable uncertainty. A possible reason for this result could be the coarse scale of the land use categories that were used for calculating the land use heterogeneity index (five categories). A more detailed description of the habitats might be needed for revealing a hypothetical positive effect. However, given the relatively high heterogeneity of the entire region, it is reasonable that variation in landscape heterogeneity will here have less effect. In contrast, we found strong negative effects of flower-poor areas – here representing mainly cereal crops and grass fields – on bumblebee species richness and density, indicating that at least this category is relevant despite being broad. Typically, this category represents large monoculture fields with few flowers and other resources for bumblebees and are expected to show negative correlation with pollinators on a landscape scale (Holzschuh et al., 2007; Steffan-Dewenter et al., 2002).

The amount of forested area within a landscape had a negative effect on bumblebees. This contrasts with earlier studies where forested areas are considered as natural or semi-natural habitats and are generally expected to have positive impacts on numbers and diversity of bees (Garibaldi et al., 2011; Kremen et al., 2004; Zulian et al., 2013). However, some studies have indicated a negative correlation between forest cover and bee abundance and diversity (Carre et al., 2009; Mandelik et al., 2012; Winfree et al., 2007). Possible differences between these studies could be both the quantity and quality of forests within the landscapes, and the kind of resources they provide. Forest stands are thought to be relatively low quality for foraging but possibly providing nesting substrate (Roulston and Goodell, 2011). In the present study area, even the most intensively farmed landscapes have a fair amount of forest left; the forest cover in the landscapes varied between 23 and 80 percent. Considering the relatively high dispersal abilities of bumblebees (Dramstad, 1996; Osborne et al., 2008), this could mean that resources in forests might not be limiting for bumblebees in these landscapes. In addition, most bumblebee species found in the agricultural landscapes are not forest specialists, but rather associated with agricultural management, and therefore a negative association with forests is not unexpected (Ødegaard et al., 2015; Åström et al., 2016).

Lastly, the area of pastures had weak negative, and uncertain effect on bumblebee species richness and density. Pasture is defined in the Norwegian Land Resource Map as an agricultural area that could be used for pasture, but not harvested by machine, and is therefore a broad category. Overall, there were very few semi-natural grasslands with a high abundance of flowering plants



in the study area, and it is likely that these areas classified as pastures represent in general poor foraging areas for bumblebees.

#### 4.3. Linear elements

The borders between two land use types delimit distinct habitats throughout the landscapes, which, together with roads, constitute what we have called 'linear elements'. In modern agricultural landscapes, which are mostly devoid of non-crop flowering plants, these linear elements constitute a major resource for pollinators. Our data show varying effects of these linear elements which indicates clear differences in the way the different types of linear elements influence bumblebees.

We observed positive effects of the amount (total length) of pasture borders in the landscapes on both bumblebee density and species richness. Pasture borders did not have particularly high levels of flower resources or bumblebee occurrences (see Supplementary material), suggesting that their benefit to bumblebees may not be primarily as a provider of forage areas. One can speculate that these linear elements provide suitable nesting habitats for bumblebees, as pastures are less frequently sprayed with insecticides, and not shaded by forest, thus providing favourable micro-climates (Herrera, 1995).

Forest edges, in turn, had weak influence on both bumblebee density and species richness. This is in contrast to common conceptions, as earlier studies (Bennett et al., 2014) have found that bees often forage in areas close to forest edges. The weak effect of forest edges may be a result of that forests are not a scarce resource in these regions, that most bumblebee species are not forest specialists, or that forest edges are associated with forest area, which had a clear negative influence on bumblebees.

Crop borders had in our study a positive but variable effect on bumblebee density, with the effect on bumblebee species richness being positive, but more uncertain. The uncertain influence of crop borders is possibly due to different management regimes of croplands. To our knowledge, after consulting with the local agricultural extension service, there are no agro-environmental schemes implemented in the area to enhance the quality of field margins as pollinator resources, and as a result, they are mostly very narrow with wild flowers growing outside the managed area. However, the type of crop and the use of pesticides or herbicides vary, as well as local ground conditions, which results in variability among field edges in their quality as pollinator resource providers. Still, these results indicate that field borders have the potential to provide valuable resources for bumblebees, if properly managed.

In contrast to all other linear elements, the amount of roads had a negative influence on local bumblebee density, and also a negative but more uncertain effect on bumblebee species richness. The negative influence of roads is not likely explained by differences in flower resources along roads compared to other linear elements in the landscape, nor that bumblebees aggregate especially to roadsides. Roadsides showed flower resources on par with cropland edges and had bumblebee occurrences in similar range as the other transect types (see Supplementary material). In contrast, Hanley and Wilkins (2015) attributed higher local bumblebee abundance to higher flower abundances along roads. The negative influence of roads could have various explanations, including increased mortality due to traffic collisions, sub-optimal timing of mowing, herbicide application, salt spreading at winter time, or pollution. These results indicate that there might be a trade-off between increasing bumblebees by augmenting roadside flower resources and potential loss of bumblebees by unforeseen negative effects. Given the current attention that roadside flower resource management is receiving as a potential tool to improve forage resources for bees (e.g. Hopwood, 2008; Mac Cana, 2013), these unexpected negative effects ought to be investigated further.

#### 4.4. Mass-flowering crops and seasonal variation

Unexpectedly, we found a clear negative effect of the total area of early mass-flowering crops within the landscapes on bumblebee density and species richness, and this effect was consistent regardless of sampling time. This consistency suggest that the negative effect is not due to temporary aggregation in the fruit orchards during bloom. We also observed a high dominance of managed honey bees within the fruit orchards (unpublished), indicating that this resource was relatively little used by bumblebees. The negative influence of early mass-flowering crops on bumblebees could thus be the result of competition from managed honeybees. Almost every apple orchard kept honey bees to secure efficient pollination, and the foraging range of honey bees are sufficient to influence the entire landscape of study. It is also possible that bumblebees are affected by insecticide sprayings or other agrochemicals commonly used at the orchards, but this seems less likely due to the seeming lack of aggregation of bumblebees within the orchards. Insecticide sprayings are also relatively limited, especially during the blooming period (personal communication with apple farmers). Further, early mass-flowering crops may have little impact on bumblebee colony size early in the season, and may act as 'flower-poor' elements in the landscape after the blooming period, depending on how the orchard understorey is managed (i.e. composition of the grassland).

In contrast, there was a strong positive effect of the area of late mass-flowering crops within landscapes on bumblebee density, and similar but less certain effects on bumblebee species richness. The positive effect of late mass-flowering crops is congruent with findings that mass-flowering crops increase colony size of *B. terrestris*, *B. vosnesniskii* and *B. pascuorum* (Herrmann et al., 2007; Westphal et al., 2009; Williams et al., 2012).

There was clear evidence of an interaction between sampling time and the presence of late mass-flowering crops, showing that landscapes with more late mass-flowering crops had higher bumblebee density and species richness early in the season in May, while we documented lower bumblebee density and species richness from June to August, when red clover and spring-sown oilseed rape are in bloom. This was especially evident for the July sampling, when the red-clover starts to bloom. We suggest that the positive influence of late mass-flowering crops early in the season is a carry-over effect from higher bumblebee reproduction in previous years. Although farmers in our study region typically rotate crops between years and fields, this rotation is centred around the farms and crop types within a landscape are relatively stable between years. As a result, we cannot specifically disentangle the effect of previous and current year crops. This would require a higher turnover of area of mass-flowering crops in the landscapes, or considerably more landscape replicates. However, a recent study from Sweden also shows a positive correspondence of bumblebee queen density with the area of a late mass-flowering crop, red clover (*Trifolium pratense*) (Rundlöf et al., 2014). The suggested mechanism is that red clover provides resources late in the season when colony sizes are largest and the production of reproducing individuals takes place. Therefore resource demand is high during this time and late-season flowering resources can be a bottleneck for reproduction. Riedinger et al. (2015) also documented higher densities of bees the following year in landscapes with high cover of oilseed rape.

We attribute the negative association between bumblebee occurrences and late mass-flowering crop areas in June–August, to that the late mass-flowering crops attract bumblebees from the surrounding landscape, where the survey transects were located. Note that this effect is independent of the quality or quantity of the local resources at transects in these landscapes. This is in line with the aggregation effects of non-bombus bees shown by Riedinger



et al. (2015) in landscapes with increasing oilseed rape cover. Rundlöf et al. (2014) also found larger densities of bumblebees in the mass-flowering fields than in the field borders during mass-flower crop bloom, and the attractiveness of red clover to bumblebees well known (e.g. Carvell et al., 2006; Fussell and Corbet, 1992; Pywell et al., 2005). Another study has shown lower bumblebee abundances in grasslands in landscapes with oilseed rape during blooming (Holzschuh et al., 2011) while Hanley et al. (2011) documented increased bumblebee numbers during field-bean blooming in transects adjacent to the fields. All these studies indicate powerful aggregation effects of mass flowering crops that may temporarily affect the densities in the surrounding landscape.

There are also reports that wild plants are likely to share the same pollinators as oilseed rape (Stanley and Stout, 2014), thus possibly increasing between-plant competition for pollinators. Our results therefore raise questions about the impact of the mass-flowering crops on wild flowers that flower at the same time, if the mass-flowering crops are drawing individuals from the landscape (Diekötter et al., 2010; Holzschuh et al., 2011; Rundlöf et al., 2014).

## 5. Conclusions

This study shows that the abundance and species richness of bumblebees in moderately modified agricultural landscapes is strongly influenced both by the local and the distributed flower resources throughout the landscape. The local amount and diversity of wild flowers, which to a high degree are located along linear elements in the landscape, as well as the area of late mass-flowering crops, was found to have the strongest positive influence on bumblebee densities and species richness. Increasing the amount of these resources throughout the landscapes appears to be viable management targets for bumblebees, also in moderately homogenised landscapes. The highly mobile foraging behaviour of bumblebees caused spatial aggregation at attractive flower resources, which diluted the bumblebees in landscapes rich in resources, with counterintuitive responses to regional flower diversity as a result. These aggregation effects also had a temporal signal, corresponding to the bloom of late mass-flowering crops, causing temporary, negative relationships between the observed numbers of bumblebees and the amount of flower resources within the landscape during bloom. These findings highlight the complex nature of pollinator surveys and warns against making conclusions based on surveys of insufficient spatial and temporal span.

Somewhat worryingly, early mass-flowering crops, here represented by fruit orchards that bloom around the emergence of hibernating queens, had negative effects on bumblebees. A likely mechanism for this result is competition by managed honey bees centred at the early mass-flowering crops, but this needs to be further studied to be concluded. Consequently, pollination-dependent crops both benefit from the landscape-level species pool of pollinators, but also greatly influence wild pollinators. At the same time, this valuable resource for wild pollinators is affected also by factors beyond the individual farmer's management control.

Apart from mass-flowering crops, the bulk of the food resources for pollinators where situated along linear elements that dissect the landscape, and the dominating crop fields of grass and cereal negatively affected bumblebee density and diversity. Simplification of the landscape with flower-poor monocultures and merging of land parcels therefore has negative consequences for pollinators also in relatively heterogeneous agricultural landscapes such as the ones in our study. Lastly, the unexpected negative effect of the amount of roads within the landscapes on bumblebees raise questions of the appropriateness of increasing flower resources on road verges as a conservation measure, and encourages further study.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2016.12.039>.

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