Contents lists available at ScienceDirect



Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

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



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ARTICLE INFO

Article history: Received 13 July 2016 Received in revised form 22 December 2016 Accepted 24 December 2016 Available online 23 January 2017

Keywords: Bombus Pollinators Linear features Mass-flowering crops Landscape ecology Agricultural landscapes Ecosystem services

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 Elmqvist 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; Tscharntke 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 cropfields, 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

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