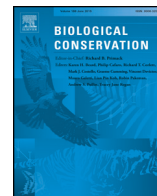




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Bumble bee colony growth and reproduction depend on local flower dominance and natural habitat area in the surrounding landscape

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ABSTRACT

Conservation measures for bees often focus on increasing the diversity and abundance of floral resources. But it has not been clear if observed benefits of floral enhancements result from greater population growth, which is critical for the long-term success of conservation, or from mobile foragers aggregating in high-resource locations. Experimental evidence is only beginning to emerge in favor of the former mechanism and it is not well-established how different aspects of floral resources affect population growth. For example, bumble bee colonies may benefit from greater overall floral abundance, richness, or relative dominance of resource species. Because bumble bees are highly mobile, resource variability in the surrounding landscape is also important for colonies and may mediate local-scale effects. We experimentally assessed the growth and reproduction of bumble bee colonies (*Bombus impatiens*) deployed in grasslands in different local- and landscape-scale resource environments. We found that floral dominance, rather than the overall abundance or richness of floral resources, was the most important local factor for colony growth and reproduction. This may reflect more efficient foraging on a few numerically dominant and abundant resource species. Local- and landscape-scale predictor variables had interacting effects on colony growth and reproduction, suggesting that foraging distance depends on where in the landscape efficiently used resources are located. Our results provide further evidence that conservation strategies aimed at enhancing floral resources can increase bumble bee population growth. However, the most effective form of floral enhancement may vary among bee species.

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1. Introduction

Bees are important pollinators in native plant communities and agricultural systems, and often provide most of the pollen delivery to flowers (Kearns et al., 1998; Ollerton et al., 2011). The decline of some bee species in recent decades is therefore of great concern (Goulson et al., 2008; Cameron et al., 2011; Bartomeus et al., 2013; Goulson et al., 2015). Although factors such as pathogens and low genetic diversity can potentially contribute to the decline of some bee taxa (e.g., bumble bees; Cameron et al., 2011), loss of habitat that provides food and nesting resources is thought to be the primary driver of wild bee declines (Winfree et al., 2009; Potts et al., 2010). As such, conservation measures often promote the preservation of resource-rich natural habitats and floral enhancements (Dicks et al., 2016). These measures generally result in a greater abundance and diversity of bees, but it is not clear if this benefit is directly related to increased population growth or if highly mobile foragers merely aggregate in high-resource areas (Carvell et al., 2007; Williams et al., 2015; Crone and Williams, 2016). We are aware of only one study that

has made the important link between resource availability and bumble bee population growth (Crone and Williams, 2016).

At local spatial scales, such as within a crop field or patch of grassland, the abundance and diversity of floral resources is often positively correlated with the abundance and diversity of the bees observed there (Potts et al., 2003; Hines and Hendrix, 2005). Greater bee abundances within these locations may reflect greater local population growth rates, as well as the attractiveness of local resources to mobile foragers (e.g., bumble bees) nesting elsewhere in landscape (Mandelik et al., 2012; Kennedy et al., 2013). The composition of the surrounding landscape may also be important for mobile species (Holt, 1993). For example, the area of natural habitat in the landscape is often positively correlated with the abundance and diversity of bees (Kremen et al., 2002; Klein et al., 2003; Steffan-Dewenter, 2003; Kennedy et al., 2013; Bennett and Isaacs, 2014), suggesting that a greater amount and continuity of food resources in the surrounding landscape may directly support the growth of locally nesting and mobile populations (Schellhorn et al., 2015). However, it is also possible that landscapes high in natural cover support local bee abundance and diversity through spillover or mass effects (Shmida and Wilson, 1985; Rand et al., 2006), rather than directly enhancing the growth of locally nesting populations. It can be challenging to differentiate potential mechanisms of these local- and landscape-scale effects on bees without measuring factors directly related to population growth.

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Different aspects of local- and landscape-scale resource environments are important for supporting bee population growth, including the overall amount of floral resources, dominance of particular resource species, and the species richness of resources. Locally, the overall abundance of resources may be important for providing energy and nutrients for colony growth and reproduction (Westphal et al., 2009; Crone and Williams, 2016). Alternatively, floral dominance provides an opportunity for foragers to focus their resource collection effort on a small number of abundant and rewarding species. For example, mass flowering crops can enhance colony growth and local abundance (Westphal et al., 2009; Persson and Smith, 2013) but it is not clear if the benefit comes from resource abundance per se or if some benefit is derived from an ability to focus foraging effort on a single numerically dominant resource for a portion of the growing season. Lastly, the species richness of flowering plants may also be important (Jha and Kremen, 2013), especially if greater richness provides a more consistent resource supply throughout the season. Moreover, bumble bees can be limited by the protein provided in pollen (Vaudo et al., 2015), so a greater number of different floral species may provide more complete sources of pollen and other nutrients necessary for worker and queen production (Tasei and Aupinel, 2008).

At a landscape scale, a greater amount of natural habitat often benefits bees but not all natural habitats provide similar floral resources. In an agricultural region of California, for example, natural habitat is composed of riparian, oak woodland and savannah, and chaparral habitats, the area of which are positively correlated with the abundance of the floral resources that benefit bumble bee colony growth and reproduction (Williams et al., 2012; Crone and Williams, 2016). But in areas where natural habitat may provide relatively few floral resources, such as in the pine forests of southern New Jersey, natural habitat area can be negatively correlated with bee abundance and richness (Winfree et al., 2007). Thus, in order to understand the effects of natural habitat area on populations it is important to determine the composition of natural habitat area in landscapes and the degree to which different habitats provide resources.

Agriculture dominates the Midwestern United States, where much of the diverse perennial land cover has been converted to annual row crops and where there is increasing intensification of cropped land use (Foley et al., 2005; Lark et al., 2015). Grassland and woodland habitats comprise much of the remaining natural habitat in the region. Both can provide nesting sites, but grasslands can support abundant and diverse bee communities (Bennett and Isaacs, 2014; Spiesman and Gratton, 2016) through the floral resources that can provide nectar and pollen throughout the growing season. Woodland habitat, in contrast, generally offers floral resources for only a limited period in the spring when ephemeral herbaceous plants and trees are in bloom (Rogers, 1981).

In this study, we used colonies of the common eastern bumble bee, *Bombus impatiens* Cresson, set within grassland habitats located across southern Wisconsin (WI) and Michigan (MI), USA to examine how the local floral community and the amount of natural habitat in the surrounding landscape affect colony growth and reproduction. We used a model selection procedure to assess the relative importance of different local- (total floral abundance, floral dominance, and floral species richness) and landscape-scale (area of natural habitat) effects on *B. impatiens* colonies. This experimental framework allows us to assess how different components of a multiscale resource environment influence factors directly related to bumble bee population growth.

2. Material and methods

2.1. Study sites

Our study was conducted at 32 grassland sites in southern Wisconsin (20 sites) and Michigan (12 sites), USA (Appendix A) in 2014. Sampling at each site occurred within a standard 50 m × 100 m area set within a larger grassland field. Grassland fields ranged from approximately 5–25 ha, many of which were former agriculture lands (>10 years old)

that had been seeded with a mix of native prairie species. These grassland fields accounted for approximately 1–20% of the total grassland habitat within a 2000 m radius. The plant communities at these sites were composed of switchgrass (*Panicum virgatum* L.) and big blue stem (*Andropogon gerardii* Vitman) with a diverse mix of native forb species including tall goldenrod (*Solidago altissima*), wild bergamot (*Monarda fistulosa* L.), purple coneflower (*Echinacea purpurea* Moench), cup plant (*Silphium perfoliatum* L.), and red clover (*Trifolium pratense* L.), all highly attractive plants for bees (Tuell et al., 2008).

Grassland sites were set within a largely agricultural region. Crops in study landscapes were mainly corn and soybean with some alfalfa and winter wheat. These crops likely provide few floral resources for bumble bees but floral resources can be abundant along roadsides and field margins (J. Hemberger unpublished data, R. Isaacs unpublished data). Study landscapes also included other natural woodland habitats, which were mainly composed of an overstory of deciduous trees such as *Acer saccharum* Marshall, *Tilia americana* L., and *Fagus grandifolia* Ehrh. (Rogers, 1981). In the spring, the understory can provide some floral resources for bees including *Claytonia virginica* L., *Erythronium albidum* Nutt., and *Allium tricoccum* (Hanes) A.G. Jones (Rogers, 1982; Mallinger et al., 2015). However, many woodlands are heavily shaded and therefore provide very few floral resources for much of the growing season (Rogers, 1981; Rogers, 1982), especially during the mid-summer period of our study. We selected sites to span a gradient in the area of natural (or semi-natural) habitat in the surrounding landscape as well as a gradient in local flowering plant diversity to enable determination of the importance of these factors for bumble bee colony growth and reproduction.

2.2. Assessing local- and landscape-scale resource availability

2.2.1. Local scale

The flowering plant community at each site was sampled within two 2 m × 100 m belt transects on two occasions after colony establishment: once in mid-July and again in mid-August. In Michigan, the relative floral abundance of each species was estimated as the count of individual plants in flower within the belt transects. In Wisconsin, belt transects were divided into a grid (4 × 100) and the relative floral abundance of each species was estimated as the count of 0.5 m × 0.5 m grid cells in which flowers of each species were present. The total relative abundance of floral resources was estimated as the sum of each species relative abundance across all sample periods. Because WI and MI floral abundances were quantified in different ways within belt transects, we used the residuals of a linear model, with state (WI or MI) as an independent variable and total abundance (ln-transformed) as the dependent variable, as an index of total relative floral abundance in the analyses described below. State had no significant effect on total floral abundance ($F_{1,29} = 0.209, P = 0.651$). The count of all species occurring within sites was used as an estimate of floral species richness. We calculated community-level floral dominance as $1 - J$, where J is Pielou's evenness metric (Pielou, 1975). Dominance therefore increases as the proportion of total abundance is increasingly concentrated in a smaller number of species instead of being distributed more evenly among species. Floral data from one of the MI sites were not available, so it was excluded from all analyses involving local floral data.

2.2.2. Landscape scale

We used the 2014 Cropland Data Layer (CDL; USDA National Agriculture Statistics Service, 2014) within a geographic information system to determine the area of natural habitat within a 2 km radius of the center of each grassland site (colonies were placed within 30 m of the centroid of sites). The area of natural habitat was calculated by summing the areas of grassland (based on CDL classes: grass/pasture, switchgrass, other hay, and herbaceous wetlands) and woodland (deciduous, evergreen, and mixed forest and woody wetlands) habitats within this radius. The proportional area of natural habitat was used in our analyses.

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