



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.

2.3. Bumble bee colonies

Colonies of *B. impatiens* were purchased from Koppert Biological Systems (Howell, MI). *Bombus impatiens* is native to the study area and is a relatively common bumble bee species at the research sites (Spiesman and Gratton, 2016). Two colonies per site were set out at Wisconsin sites and three colonies per site were set at Michigan sites for approximately 6–7 weeks during the period between July 7 and August 28, 2014. Before being set in the field, each colony was weighed to the nearest 0.1 g. Initial weights included the plastic box housing the colony as well as the colony itself, but not the sugar water solution used for supplementing nectar resources within the colony, which was included as part of the colony setup. Colony boxes were not opened prior to the study for a more detailed assessment of initial condition (e.g., counting workers) in order to minimize disturbance. However, based on four extra colonies that were purchased in the same batch as experimental colonies and immediately examined at the start of the experiment, each colony contained one queen and on average 14.3 workers (± 5.1 SD). Within a research site, replicate colonies were set up at least 100 m from the field edge and at least 50 m from each other. The sugar water solution was removed from the Wisconsin colonies but remained in the Michigan colonies during the study period.

Before placement, the vegetation within a 1 m \times 1 m area was trimmed to the ground and a 1 m \times 1 m sheet of landscaping fabric was pinned down for the colony to rest upon and to suppress plant growth. Colony boxes were housed within corrugated plastic containers to provide shade, and secured to the ground on top of plastic milk crates. Tangle-Trap (The Tanglefoot Company, Grand Rapids, MI) applied around the base of colonies was used to deter ants, and coarse wire mesh was secured to the face of containers to deter small mammals. During the study period, colonies were checked periodically for disturbance and the vegetation around them was kept trimmed back. Despite attempts to exclude ants, four bumble bee colonies (one in Wisconsin and three in Michigan) were invaded, resulting in poor colony health relative to others at their respective sites. These four colonies were therefore excluded from all analyses. Before colonies were removed from the field, the setting on the colony entrance was set to only allow re-entry (no outgoing bees) for a period of 24 h so that foraging bees could return to the colony. Colonies were then closed and brought back to the lab where they were immediately frozen until processing.

We assessed colony performance over the duration of the field study using metrics of colony growth and reproductive potential. Relative colony growth rate (G) was quantified as $G = 100 \times ((M_f - M_i) / M_i) / D$, where M_i is the initial colony mass, M_f is the final mass (measured in the same way as initial mass described above) and D is the number of days a colony was left in the field. Relative colony growth is therefore a measure of the relative percent change per day in the combined mass of all individuals in the nest, resources stored within the nest (honey and pollen), and the nest itself (waxy cells). Colony growth rate was highly correlated with other measures of colony performance, including the number of workers (Pearson $r = 0.906$, $P < 0.001$), and the mass ($r = 0.975$, $P < 0.001$), area ($r = 0.914$, $P < 0.001$), and number of brood cells in colonies ($r = 0.935$, $P < 0.001$) at the end of the study period. Our count of brood cells included all full and emerged worker, male, and queen cells.

The reproductive potential of each colony was quantified as the count of queen cells in colonies at the end of the experiment. Although males contribute to reproduction, the number of queens produced is a good indicator of reproductive potential because queens must overwinter and establish new colonies (Williams et al., 2012). Queen cells can be reliably differentiated from worker and male cells and leave a record of queen production after they have left the nest.

2.4. Statistical analysis

We used linear mixed-effects models to examine the impact of local- and landscape-scale effects on relative colony growth rates. We

compared alternative models that took the general form: *colony growth* ~ *state* + *local* + *landscape* + *local* \times *landscape*, where *local* was either the index of relative floral abundance, floral dominance, or floral species richness, and *landscape* was the proportion of natural habitat area within a 2 km radius surrounding the colonies. State was included as a fixed effect to account for factors such as differences in handling between research teams that may have affected growth. We set out multiple *B. impatiens* colonies per site (2 in WI and 3 in MI), therefore site was also included in each model as a random effect to account for any shared site-level variance. All analyses were performed in R v3.2.4 (R Development Core Team, 2016). Alternative models were evaluated based on the Akaike Information Criterion corrected for small sample sizes (AICc), and the model with the lowest AICc score was considered the best model (Burnham and Anderson, 2002). We also calculated AICc model weights (w), which indicate the likelihood that a model would be the best model in replications of the experiment. The relative importance of each of the terms in the models was determined using importance weights ($w +$). Relative importance weights were calculated for each term by summing w across all models in which the term occurred (Burnham and Anderson, 2002). AICc, AICc model weights, and importance weights were calculated using the *MuMIn* package (Barton, 2016). Mixed-effects model analyses were performed using the *lme4* package v1.1–11 (Bates et al., 2015) and fit using maximum likelihood. Significance levels for the best model were included for completeness and assessed using type III Wald chi-square tests (*car* package; Fox and Weisberg, 2011).

The number of queens produced by each colony (i.e., reproductive potential) was analyzed in terms of local floral dominance, natural habitat area, and their interaction. These were the local- and landscape-scale predictors included in the best model of colony growth (see Results: Colony growth). Many colonies produced no queens resulting in a relatively large number of zeros and overdispersion. Therefore, following Crone and Williams (2016), we compared three models (based on AICc) that account for these factors. Models 1 and 2 were zero-inflated negative binomial mixture models that can combine two components: a zero component that addresses how predictors affect the probability that queens are produced, and a count component that addresses how predictors affect the number of queens produced. Both the count and zero components were modeled in (1) and only the count component was modeled in (2). The *pscl* package (Zeileis et al., 2008) was used to fit zero-inflated models. Model 3 was a generalized linear mixed-effects model, with a Poisson distribution. State was included as a fixed effect and site included as a random effect. A unique colony identifier was also included in this model as a random effect to help correct for overdispersion (Elston et al., 2001).

3. Results

3.1. Colony growth

Comparison of AICc values and model weights for the competing models showed that the dominance of the local floral community, the area of natural habitat in the surrounding landscape, and their interaction best predicted colony growth ($w = 0.955$; Appendix B; Table B.1). This model was substantially better than the next best model, which included an index of total relative floral abundance, natural habitat area, and their interactions (Δ AICc = 6.62, $w = 0.035$). Local floral dominance ($w + = 0.96$) was therefore much more important for bumble bee colony growth than an index of relative floral abundance ($w + = 0.04$) or flowering plant species richness ($w + < 0.01$). There was no evidence in favor of important interactions between different local-scale predictors (results not shown).

Local floral dominance was positively correlated with the relative abundance (ln-transformed) of the numerically dominant plant species in both Wisconsin ($r = 0.60$, $P = 0.004$) and Michigan ($r = 0.74$, $P = 0.015$; Fig. 1A). However, floral dominance was uncorrelated with

total relative floral abundance in both Wisconsin ($r \leq 0.01$, $P = 0.985$) and Michigan ($r = 0.40$, $P = 0.247$; Fig. 1B). A single flowering plant species tended to occur in high relative abundance at sites with high dominance, but the identity of that species varied among sites. Eight different plant species represented the most abundant species at the 11 (upper third) sites with the highest dominance (*Solidago altissima* L., *Trifolium pratense* L., *Silphium perfoliatum* L., *Medicago sativa* L., *Rudbeckia hirta* L., *Erigeron annuus* (L.) Pers., *Lotus corniculatus* L., *Desmodium canadense* (L.) DC., and *Chamaecrista fasciculata* (Michx.) Greene), with no species being dominant at more than two sites. Previous flower observations conducted at the same research sites confirm that these plant species are commonly visited by *Bombus*, including *B. impatiens* (Spiesman and Gratton, 2016, Bennett and Isaacs unpublished data).

Natural habitat, which was primarily composed of woodland and grassland, ranged from 21.2 to 90.2% of the landscape. However, as the total area of natural habitat in landscapes increased, natural habitat was increasingly composed of woodlands ($r = 0.58$, $P = 0.001$) and decreasingly composed of grasslands ($r = -0.58$, $P = 0.001$; Fig. 2A). Total

woodland area in the landscape increased linearly with greater natural habitat area ($F_{1,29} = 103.9$, $P < 0.001$), while total grassland area in the landscape varied non-linearly with the area of natural habitat, ($F_{2,28} = 7.6$, $P < 0.002$; Fig. 2B). Annual crop habitat made up most of the remainder of landscapes, the total area of which was negatively correlated with natural habitat area ($r = -0.91$, $P < 0.001$). Therefore, when natural habitat area is high, the landscape is composed mainly of woodland habitat that provided few floral resources during the study period (Rogers, 1981). As natural habitat area decreases from its maximum, total woodland area decreases and grassland area increases, peaking at an intermediate level of natural habitat (Fig. 2A). As natural habitat decreases further, grassland area necessarily decreases as it is replaced by crop habitats that likely support pollinators along their margins. We therefore interpret natural habitat area as negatively correlated with the amount of floral resources for *B. impatiens* in the surrounding landscape (Winfrey et al., 2007). Thus, while grassland area may seem a more straightforward measure of potential resource availability for bumble bees in the landscape than the amount of total natural area, subsequent analyses showed

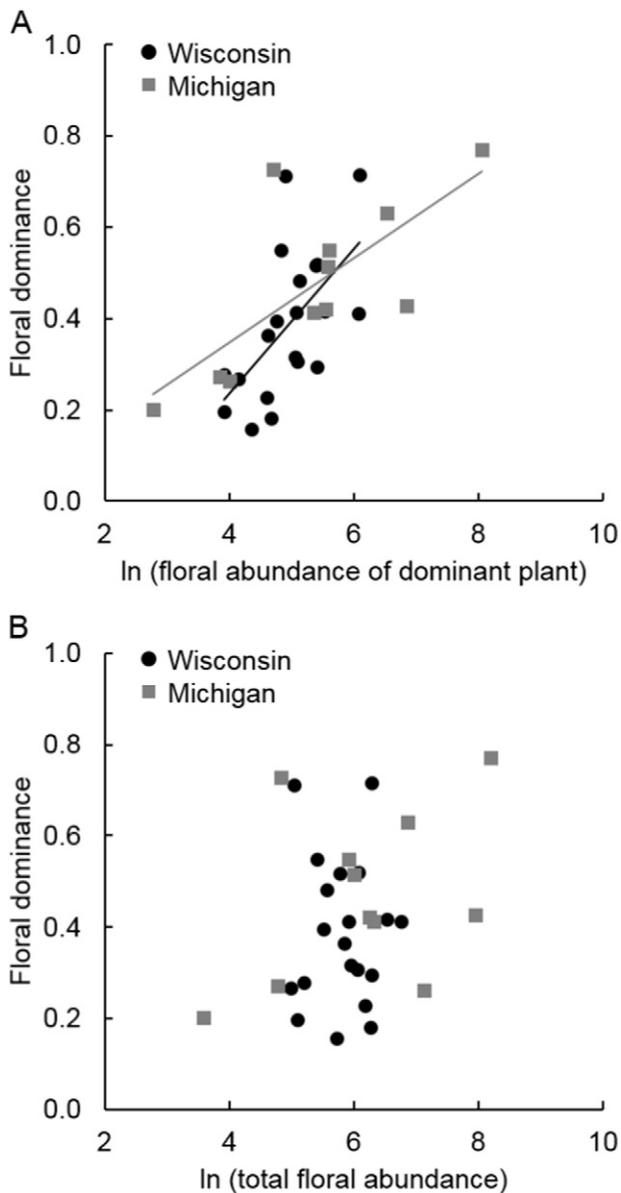


Fig. 1. Relationships between local floral dominance and (A) the floral abundance of the most numerically dominant flowering plant species at grassland sites, and (B) the total floral abundance at these sites in Wisconsin (black circles) and Michigan (gray squares). Fit lines were based on OLS regression.

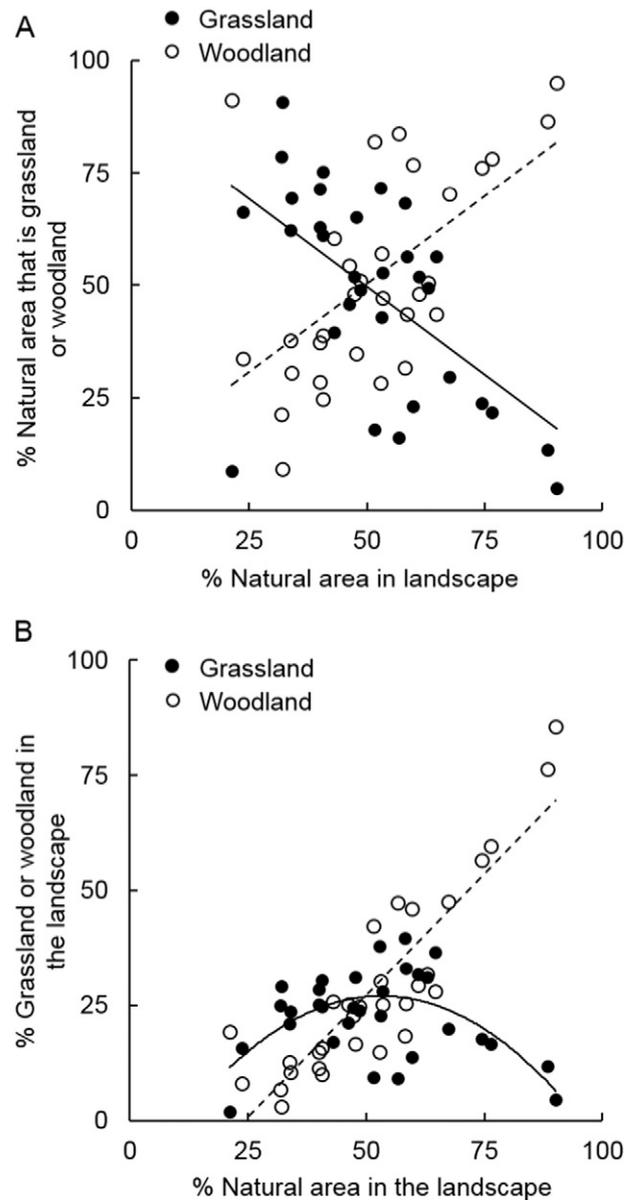


Fig. 2. Relationship between the percent area of natural habitat in the surrounding landscape (2000 m radius) and the percent of natural area that is grassland (black circles) or woodland habitat (open circles) area (A), and the percent area of grassland or woodland habitat in the landscape (B). Fit lines were based on OLS regression.

that natural area explained *B. impatiens* colony growth much better than either grassland, woodland, or agriculture area (Table B.2). Moreover, given the complex relationships among grassland, woodland, agriculture, and natural area in the landscape (Fig. 2), in this system natural area better represents potential floral resources than do any of the specific habitat categories alone (i.e., grassland, woodland, or agriculture area).

After accounting for a state effect, the relative growth rate of bumble bee colonies increased with greater local floral dominance and decreased with increasing area of natural habitat in the surrounding landscape. However, colony growth was dependent on an important interaction between local- and landscape-scale predictors ($w+ = 0.95$; Table 1, Fig. 3A). When local floral dominance was low, colony growth decreased with increasing natural habitat area in the landscape (Fig. 3B), whereas when local floral dominance was relatively high, there was no correlation between colony growth and the amount of natural habitat in the landscape (Fig. 3C). From the other perspective, when natural habitat area in the surrounding landscape was high, there was a positive effect of floral dominance on colony growth (Fig. 3D), whereas when natural habitat area was low, there was no relationship between floral dominance and colony growth (Fig. 3E). Multicollinearity among predictor variables was low and residuals were normally distributed. A Mantel test with state as a blocking factor (to account for differences in colony handling) and 9999 permutations revealed no significant spatial autocorrelation of residuals ($r = 0.194, P = 0.367$).

3.2. Queen production

Mean queen production per site (log-transformed) was highly correlated with relative colony growth ($r = 0.84, P < 0.001$). The best model of local- and landscape-scale effects on queen production was a zero-inflated negative binomial model that included both count and zero components (Model 1; Table B.3). Model 1 was substantially better than the next best model; a generalized linear mixed-effects model with a Poisson distribution (model 3, $\Delta AICc = 6.25$). The best model showed a significant state effect but no effect of local- or landscape-scale predictors on the probability that queens were produced (zero component, Table 2A). However, the number of queens produced depended on an interaction between local floral dominance and the area of natural habitat in the surrounding landscape (count component, Table 2B, Fig. C.1), and the patterns of this response were similar to those observed for relative colony growth (Fig. 3).

4. Discussion

A large body of research has shown that the abundance and diversity of bees generally increases with greater local abundance and diversity of plant resources and with greater amounts of resource-providing habitat in the surrounding landscape (Kennedy et al., 2013). The idea that greater resource availability increases bee population growth is intuitive, but the positive association could also reflect aggregation of mobile bees in high-resource areas (Scheper et al., 2013; Williams et al., 2015). We found that the growth and reproduction of colonies of the bumble bee *B. impatiens* depends on interacting effects of local- and landscape-scale factors

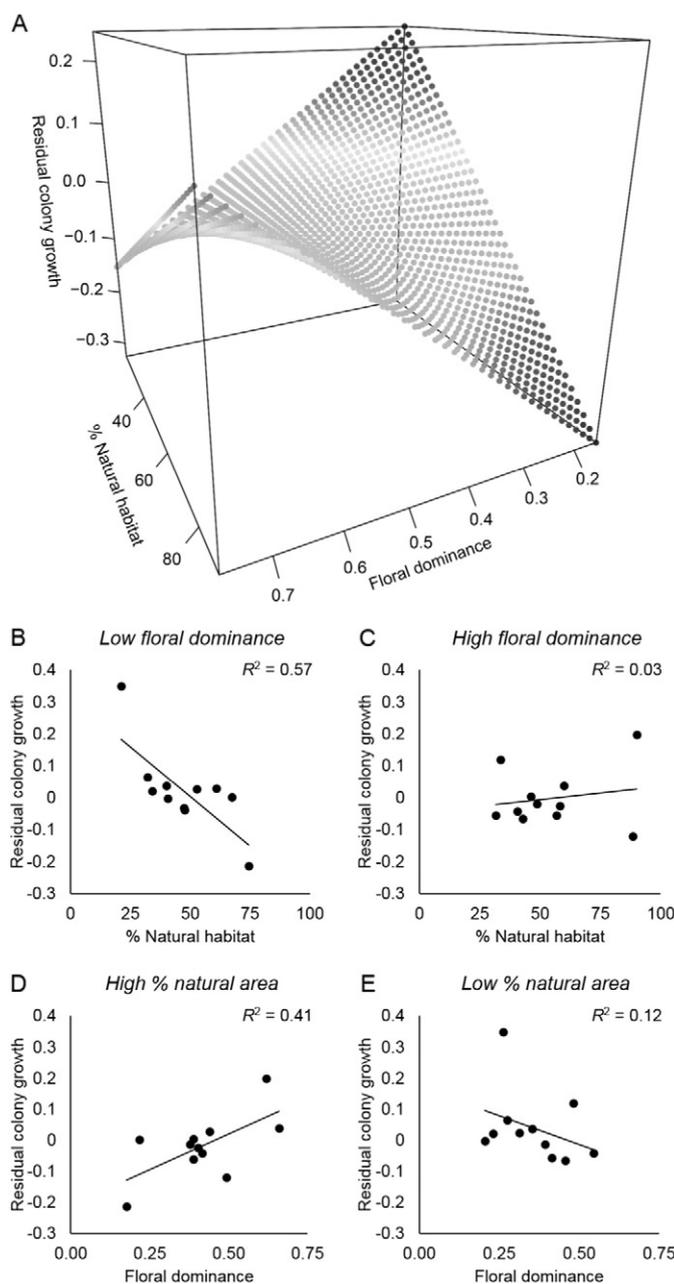


Fig. 3. Interacting effects of local floral dominance and the percent area of natural habitat in the surrounding landscape on the relative growth rate of *Bombus impatiens* colonies. (A) Fitted surface is from the best linear mixed-effects model with residual colony growth plotted after accounting for the state effect. (B–E) For easier interpretation of the interaction effect, the relationship between local- and landscape-scale factors and colony growth is shown near each edge of the fitted surface. “High” and “low” approximately correspond to the upper and lower third of values for each variable. Each point is the mean residual colony growth at a site after accounting for a significant state effect.

Table 1

Linear mixed-effects model of the response of *Bombus impatiens* relative colony growth to local-scale (floral dominance) and landscape-scale (% natural habitat in the surrounding landscape) predictors from the best model (see Appendix B). Site was included as a random effect. Importance weights ($w+$) are based on AICc comparisons among models (Appendix B).

	Estimate	SE	χ^2	df	P	$w+$
Intercept	2.199	0.232	89.6	1	<0.0001	
State	-0.839	0.071	139.0	1	<0.0001	1.00
Dominance	-2.292	0.535	18.3	1	<0.0001	0.96
Natural area	-2.572	0.434	35.1	1	<0.0001	1.00
Dominance × Natural area	4.262	0.929	21.1	1	<0.0001	0.95

associated with floral resource availability, supporting the emerging evidence that food resource availability at multiple scales directly benefits bumble bee population growth (Crone and Williams, 2016).

Our study also reveals that the benefit of additional food resources for bumble bee population growth may not be as simple as “more is better”. Locally, higher floral dominance was more important for *B. impatiens* colony growth and reproduction than total floral abundance in our study region. In landscapes high in natural habitat area (Fig. 3D), colonies tended to gain more weight and produce more queens with greater floral dominance. The reasons for the benefit of floral dominance for *B. impatiens* are not clear, but it is possible that foraging efficiency is improved at locations where one or two flowering plant species provide most of the potential

Table 2
Zero-inflated negative binomial model of the response of *Bombus impatiens* queen production (number of queen cells) to local-scale (floral dominance) and landscape-scale (proportion natural habitat in the surrounding landscape) predictors from the best model of colony growth. Zero component results (A) show how predictors affect whether or not queens were produced and count component results (B) show how predictors affect the number of queens produced. θ describes the shape parameter.

	Zero component				Count component			
	Estimate	SE	z-value	P	Estimate	SE	z-value	P
Intercept	−3.355	4.619	−0.726	0.4675	6.366	1.106	5.754	<0.0001
State	3.990	1.433	2.783	0.0054	−2.127	0.472	−4.506	<0.0001
Dominance	−5.537	14.829	−0.373	0.7088	−7.997	2.730	−2.929	0.0034
Natural area	0.093	0.085	1.090	0.2759	−0.048	0.021	−2.264	0.0236
Dominance × Natural area	−0.147	0.274	−0.535	0.5924	0.108	0.044	2.459	0.0139
ln(θ)					0.062	0.288	0.215	0.8300

nectar and pollen resources. Foraging on a small subset of dominant resource species may reduce search and/or handling time, and would fit optimal foraging predictions of how bumble bees should allocate their foraging effort (Pyke, 1980; Hodges, 1981). This efficiency would be expected to benefit colony growth and reproduction, with the benefit being enhanced as dominant resources are present in greater abundance. Foraging efficiency may also increase with greater nutritional value of resources. For example, two of the species that achieved high numerical dominance in our study were tall goldenrod (*S. altissima*) and red clover (*T. pratense*). These species tend to be nutritionally rewarding for bumble bees (Heinrich, 1979; Carvell et al., 2006), which may also promote reproduction (Rundlöf et al., 2014). Further research may determine how the nutritional value of dominant floral species contributes to foraging and colony performance (Vanderplanck et al., 2014; Vaudo et al., 2016).

The percent area of natural habitat surrounding study sites was important for explaining bumble bee colony growth and reproductive potential. However, interpreting the effects of natural habitat is not straightforward because the proportion of grassland and woodland habitat comprising natural habitat varied with the amount of natural habitat in the surrounding landscape. In low-floral dominance locations, colony growth and reproduction decreased with greater natural habitat area in the landscape (Fig. 3B). This may be because in landscapes with high natural land cover, woodland dominates, providing few floral resources for bees in the summer (Winfree et al., 2007; Mandelik et al., 2012; Mallinger et al., 2016). On the other hand, when natural area is relatively low, what natural habitat is present is composed mainly of high-resource grasslands and other habitats, such as agricultural field margins that also have the potential to provide floral resources (Williams et al., 2015). Therefore, our results agree with other recent studies showing that bumble bee colony growth depends on landscape-scale factors related to resource availability (Williams et al., 2012; Crone and Williams, 2016), and that bumble bee responses to natural habitat may be negative when natural habitat provides few resources (Winfree et al., 2007). It is interesting, however, that neither grassland nor woodland area alone explained colony growth as well as their sum (i.e., natural habitat). Further work incorporating more detailed measurements of landscape-scale floral resource availability may help to explain this result. For example, given the variability in floral resources among seminatural areas and the importance of local floral dominance, landscape-scale effects of resource availability may reflect patchiness in dominance of rewarding species that is not well-captured by simple measures like habitat area.

Bumble bees can exhibit great flexibility in the distances over which they will forage for food resources (Jha and Kremen, 2013) and this may be critical for persistence in landscapes where resources are heterogeneously distributed in space and time (Vasseur et al., 2013). This flexibility may help to explain the interaction between local- and landscape-scale effects on colony growth and reproduction in our study. For example, if landscape-scale resource availability is low, bumble bees may depend on local-scale resources, and vice versa. On the other hand, if sufficient resources are present locally, foraging closer to the colony may help minimize some of the energetic costs of foraging and offer little incentive to utilize resources in the surrounding landscape (i.e., resulting

in no relationship between colony growth and landscape context when local dominance is high). Rundlöf et al. (2008) found a similar interaction between local- and landscape-scale effects on richness and abundance of European bumble bees sampled on conventional and organic farms, suggesting that our results from experimental colonies reflect patterns present in natural populations.

5. Conclusions

Our results highlight that the population growth of the bumble bee *B. impatiens* can depend on factors related to the availability of key floral resources at different spatial scales. This supports the findings of a recent study on the western US species, *B. vosnesenskii* (Crone and Williams, 2016). However, unlike recent studies we found that floral dominance had the greatest local-scale benefit for colony growth and reproduction rather than the overall amount of floral resources present (Crone and Williams, 2016) or the richness of floral resources (Jha and Kremen, 2013). Conservation strategies aimed at increasing floral resources may therefore need to be tailored to target species, as current programs for florally-rich plantings have been shown to differentially affect various groups of bees (Williams et al., 2015; Wood et al., 2015). Bees that benefit from high floral dominance environments, such as the common *B. impatiens* in our study, may respond positively to the expansion of mass flowering crops (Westphal et al., 2009), whereas rare bee species may be more likely to benefit from diverse floral communities (Potts et al., 2003). Therefore, landscape-scale conservation of bees may require complex landscapes composed of patches of locally dominant floral resources and locally diverse patches of floral resources to maintain robust populations of the greatest variety of bee species (Tscharntke et al., 2012).

The interacting effects of local- and landscape-scale factors related to resource availability suggest that *B. impatiens* can adaptively alter its foraging distance depending on where efficiently-utilized resources are present, as found for other bumble bee species (Jha and Kremen, 2013). Local conservation measures aimed at supporting species with similar responses to local- and landscape-scale resources may therefore be most effective at locations set within resource-poor landscapes. Similarly, landscape-wide conservation measures will have the greatest benefit for species in resource-poor locations. Understanding these interactions can help direct conservation programs to where they will have the greatest benefits.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.12.008>.

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