Landscape-scale resources promote colony growth but not reproductive performance of bumble bees

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Abstract. Variation in the availability of food resources over space and time is a likely driver of how landscape structure and composition affect animal populations. Few studies, however, have directly assessed the spatiotemporal variation in resource availability that arises from landscape pattern, or its effect on populations and population dynamic parameters. We tested the effect of floral resource availability at the landscape scale on the numbers of worker, male, and queen offspring produced by bumble bee, *Bombus vosnesenskii*, colonies experimentally placed within complex agricultural-natural landscapes. We quantified flower densities in all land use types at different times of the season and then used these data to calculate spatially explicit estimates of floral resources surrounding each colony. Floral availability strongly correlated with landscape structure, and different regions of the landscape showed distinct seasonal patterns of floral availability. The floral resources available in the landscape surrounding a colony positively affected the number of workers and males it produced. Production was more sensitive to early- than to later-season resources. Floral resources did not significantly affect queen production despite a strong correlation between worker number and queen number among colonies. No landscape produced high floral resources during both the early and late season, and seasonal consistency is likely required for greater queen production. Floral resources are important determinants of colony growth and likely affect the pollination services provided by bumble bees at a landscape scale. Spatiotemporal variation in floral resources across the landscape precludes a simple relationship between resources and reproductive success as measured by queens, but nonetheless likely influences the total abundance of bumble bees in our study region.

Key words: Apoidea; Bombus; bumble bee; floral resources; landscape structure; pollinator; reproductive success.

Introduction

Resource availability is a critical factor determining the dynamics of populations over space and time. For mobile organisms that forage beyond single habitat patches, resources must to some extent be determined by landscape composition and structure. For bees, for example, the overall abundance of floral resources in the landscape will be a function of the density of flowers within different habitat types and the amounts of these habitats within the flight range of individual foragers (Kremen et al. 2007, Osborne et al. 2008). Within the landscape, the distance to resource patches and associated foraging energetics determine the profitability of resources (Orians and Pearson 1979, Cresswell et al. 2000). For many animal species, including bees, resources also vary temporally throughout the season (Tepedino and Stanton 1980, Bowers 1985), creating a spatiotemporally dynamic resource landscape that de-

fines the abundance and profitability of resources at any place and time (Lonsdorf et al. 2009). Although it is not the only factor affecting populations (Borer et al. 2006), resource abundance thus provides one likely mechanism linking landscape structure with the patterns of animal abundance and distribution.

The role of resource distribution in determining population dynamics is additionally important in the context of landscape change. Anthropogenic land use change is a primary driver of species endangerment globally (Millennium Ecosystem Assessment 2005, Pereira et al. 2010). Although many studies have documented how the loss and fragmentation of native/ natural habitat affect animal and plant populations and communities (Debinski and Holt 2000, Tischendorf et al. 2005), only a few studies have examined whether resource availability resulting from (or related to) land use change drives changes in population abundance (Abraham et al. 2005). Spatially explicit assessment of resources and their relation to populations or population dynamic parameters are few (van Riper 1984, Hines and Hendrix 2005, Knight et al. 2009). Here we tested the effect of landscape-level floral resource abundance

on the growth and reproductive performance of bumble bee colonies across a landscape varying in habitat composition. Instead of conducting population censuses, which might display temporal lags in response to floral resources and can misrepresent population responses (Knight et al. 2009, Roulston and Goodell 2011), we measured the numbers of workers, males, and queens produced (i.e., offspring production). Offspring production in bees is strongly affected by pollen and nectar shortfalls (Sutcliffe and Plowright 1988, Cartar and Dill 1991) and should thus depend on the abundance and distribution of such resources in the landscape (Potts et al. 2003, Williams and Kremen 2007, Westphal et al. 2009).

Recent studies have documented the effect of landscape composition on native bee communities including bumble bees (Klein et al. 2002, Kremen et al. 2004, Knight et al. 2009), and meta-analyses pinpoint extreme habitat loss as the most consistent disturbance factor linked to declines in bee abundance and diversity (Winfree et al. 2009, Williams et al. 2010b). Bumble bees are a group of particular conservation concern globally (National Research Council 2007, Williams and Osborne 2009, Cameron et al. 2011). They are key pollinators of native plant populations and crops throughout the Northern Hemisphere. Declines of bumble bees in Europe have been linked to loss of preferred forage resources in changing agricultural landscapes (Carvell et al. 2006, Goulson et al. 2008, Knight et al. 2009). To date, however, most studies have correlated bumble bee abundances either with floral resources in small patches of restored vegetation (Pywell et al. 2005, Carvell et al. 2007), or with the area of different habitat categories at the landscape scale without quantifying continuous differences in resources available among habitat types (Mand et al. 2002, Westphal et al. 2003, Knight et al. 2009). Although the latter provide important insights about resource landscapes, they do not directly quantify floral resource availability. Most studies also rely on indirect measures of bee abundance, such as density based on genetic variation among sample foragers in the landscape. Thus the mechanistic relationship between bumble bee distributions, population dynamics, and floral resource availability at the organism-appropriate scale is poorly known (Elliott 2009). Such information is central to understanding how populations perform in different landscape contexts, and to predicting population responses to anthropogenic landscape change.

Bumble bees are central-place foragers whose colonies persist over many months and produce dozens to hundreds of foraging workers with relatively large foraging ranges (Osborne et al. 1999, 2008, Walther-Hellwig and Frankl 2000). Colonies integrate floral resources from across the landscape surrounding the colony and throughout the growing season (Heinrich 1979a, b). Because worker number changes over the season, colonies may be differentially sensitive to resource availability at different times of the season. Earlier in the season when there are fewer workers, colonies may have difficulty locating and capitalizing on dispersed resources. Later in the season, a larger worker force may be able to gather flower resources from a wider portion of the landscape and thus may be able to produce offspring even in a landscape with a low density of floral resources.

We combine a well-resolved landscape classification with field surveys of flower abundance and flower use by bumble bees to quantify the flower resources available in the landscape. Using bumble bee colonies placed throughout the landscape, we test the following hypotheses about how floral resources in the landscape affect bumble bee colony growth and reproduction: (1) floral resource abundance in the landscape will be positively correlated with the amount of natural or seminatural habitat such that resource abundance might help to explain previously documented effects of landscape composition on bee populations and communities; (2) the numbers of worker, male and queen offspring produced will depend on the floral resource abundance in the landscape; (3) resource abundance varies temporally through the season, and production of workers and queens will be more sensitive to resource availability early in the season when the number of foragers in a colony is lower.

METHODS

General design

To test the effect of floral resource abundance on the performance of bumble bee colonies, we placed two hand-reared colonies of Bombus vosnesenskii at each of 39 sites in a mixed agricultural-natural region in Yolo and Solano Counties in the Central Valley of Northern California, USA. The landscapes surrounding sites spanned a gradient that varied in the proportion of natural habitat (chaparral, oak woodland, oak savannah, and riparian; Kremen et al. 2004). To account for potential effects of the local habitat in which the colony was located on colony performance, we placed colonies at replicate sites in three habitat types: conventional row crop agriculture, organic row crop agriculture, and riparian habitat. Sites representing each local habitat type spanned the landscape gradient. Conventional farms all grew sunflower monocultures on the field adjacent to colonies. In contrast, organic farms grew a variety of row crops, without the use of inorganic fertilizers, synthetic pesticides, or herbicides. Riparian sites were located along two separate drainages (Cache and Putah Creeks) and contained mixtures of native and alien plant species (Williams and Kremen 2007). We began the study with colonies at 14 conventional farm sites, 13 organic farm sites, and 12 riparian sites, but colonies at one riparian site were lost to vandalism and at one conventional farm site were lost to Argentine ants (Linepithema humilis). To improve spatial independence, all sites were located at least 2.5 km apart. We tested for

spatial autocorrelation in our data using a Mantel test of geographic distance among sites and number of workers produced and queens produced (our main response variables). We found no significant correlations (workers Mantel $r = -0.062$, $P = 0.908$; queens $r = -0.034$, $P = 0.675$; R ade4 package [Dray et al. 2007]).

Floral resource landscape

We modeled the availability of floral resources in the landscape surrounding each *B. vosnesenskii* colony by combining information about the spatial locations of different land cover types surrounding each colony with field measurements of floral densities on each land cover type. We first classified the landscape within 2 km of each colony into 20 land cover categories (Appendix A), using GIS crop commodity layers from the University of California Cooperative Extension office for Yolo County, which provides crop and land cover data for all agricultural parcels. For areas where there were no data in the Yolo county layer, we used a vegetation/land use layer created for the region based on maximum likelihood supervised classification of a Landsat 7 Thematic Mapper image (Raytheon Remote Sensing, Santa Barbara, California, USA; see Kremen et al. [2004] for a detailed description). We added roadsides using the regional transportation layers buffered to 10 m (Tiger roads; LocalRoadsTiger and MajorRoadsTiger; data *available online*).[5] All agricultural parcels not growing orchard crops were visually inspected during the growing season to determine current crop type.

For each non-crop land cover category (natural habitats and roadsides), we used quadrat sampling at five representative sites stratified throughout the landscape to assess the density of flowers of all plant species. We measured flower densities at these sites at three-week intervals between April and July. For crop land cover types, we assessed flower density when the crop was at peak bloom at five representative sites. At the same three-week intervals as for the non-crop habitats, we surveyed all crop fields within the 2 km radius of each nest site and assigned each field a percentage of peak bloom for that crop type. We were thus able to approximate the temporal dynamics of resources available to each bumble bee colony over the season for all land cover types.

Total floral resource availability for each colony was then estimated by aggregating over the area located within a 2 km radius. Previous analysis of bumble bees in this study system used 2000 m as the scale of analysis, basing the choice on the maximum foraging range for this species, inferred from body size (Greenleaf et al. 2007). Rather than considering all resources equally over the area, values were down-weighted as a function of distance from the nest. This approach more accurately represents the foraging ecology of bumble

bees. Although bumble bees are capable of flying several kilometers or more during foraging trips (Goulson et al. 2002), they most often forage closer to the colony (Walther-Hellwig and Frankl 2000, Osborne et al. 2008). In addition, because flight is energetically expensive, the net value of a resource should decrease with its distance from the colony (Cresswell et al. 2000). We weighted all resources within 2 km of the nest according to a simple negative exponential function:

$$w = e^{-D/\alpha}$$

where D is the distance in meters separating the resource from the colony, and α is the typical flight distance for the species. Following Lonsdorf et al. (2009), we used 1035 m as a reasonable estimate of α for *B. vosnesenskii*. Under this weighting scheme, a given floral resource located 2 km from the colony is only ~15% as valuable as it would be in the absence of weighting. To simplify the computation, we discretized space using a 100×100 m grid before applying the weighting function. For comparison, we also calculated total resources without distance weighting. Although specific values differed, the overall patterns and significance were consistent between the weighted and unweighted approaches, and thus we report results only for the distance-weighted function.

We filtered our flower data to include flower densities only from plant species whose pollen was known to be collected by *B. vosnesenskii* based on pollen samples from returning workers (N. M. Williams and C. Kremen, *unpublished data*) and two years of surveys in our study region (Williams et al. 2010a). The correlation between flower density of all species vs. only the species used by *B. vosnesenskii* was high ($r = 0.98$); nonetheless, throughout the paper, floral abundance refers specifically to those species used by *B. vosnesenskii*.

Colony growth and reproductive performance

We monitored colonies weekly using nighttime counts of all individuals and visual nest inspection to determine when they had become moribund, or reached the end of their productive life span, which we defined as either having a dead queen and no remaining larvae, or producing no new eggs or larvae for three weeks. Weekly visual inspections of nests also allowed us to determine the timing of queen offspring production. Moribund colonies were brought to the laboratory, frozen, and dissected. We counted the total number of worker and male offspring produced, the presence of queen offspring, and number of queen offspring produced for each colony based on the number of brood cells it had produced over its life span. Although the brood cell size of *B. vosnesenskii* workers varies considerably, there is a discrete size difference between workers and males vs. queen cells. Male brood cells could not be consistently distinguished from worker brood cells and were therefore included in the worker count for all analyses (Goulson et al. 2002). Although this inclusion blurs the distinction between worker and

[5] http://www.atlas.ca.gov/download.html#/casil/transportation

reproductive output by the colony, population dynamics are likely to be affected most by queen output because queens must overwinter and establish new colonies. These are stages of the life cycle with expected high mortality for reproductives. For this reason too, queen production served as our proxy for colony reproductive success, even though a colony may achieve reproductive success through male production. During the dissections, we also counted all nest-associated insect fauna including putative parasites and commensal species.

All colonies used in the study were reared from queens collected within the region and housed in the lab under consistent conditions and fed identical fresh honey-bee-collected pollen and sugar-water diets until they exceeded a standard size of 23 workers (Greenleaf 2005). The colony was then moved to a wooden "field" box and placed into the field site. Colonies were placed into the field between 12 April and 21 April. Boxes were protected from ants with Tanglefoot (Contech, Victoria, British Columbia, Canada) and were placed under shade structures to prevent overheating (Appendix B). Details of colony rearing are provided by Greenleaf (2005).

Statistical analysis

At each study site, we calculated floral resources available in the landscape surrounding each colony as the summed floral densities over species and sampling periods throughout the season. We tested its correlation (Proc CORR, SAS 8.2, log-transformed; SAS Institute, Cary, North Carolina, USA) with the proportion of natural habitat surrounding the sites at the same spatial scale. A positive relationship between these two variables would be consistent with the hypothesis that resource availability is one mechanism behind pollinator response to natural habitat loss. We also examined differences in seasonal resource dynamics among landscapes surrounding our sites. We tested for differences in spring (March–May) and summer (June–July) flower resource abundance between sites located in landscapes dominated by natural habitat vs. those dominated by agriculture using ANOVA (Proc GLM, SAS 8.2). We defined landscapes dominated by natural habitat as those containing $\geq 20\%$ natural habitat (all but one $>37\%$) within 2 km of the colony and landscapes dominated by agriculture as those containing $\leq 10\%$ natural habitat (most of these $<5\%$). Here our goal was to identify important seasonal shifts in resources that could affect colony growth and reproduction.

We tested the effect of resource availability on the number of workers and males produced, likelihood of producing queen offspring and the number of queens produced at a site. Offspring numbers were tested using generalized linear models (Proc GLM, SAS 8.2) and likelihood of queens being produced using logistic regression (Proc LOGIT, SAS 8.2). Although bumble bee colonies to some degree integrate resources used over the life of the colony, they may be more sensitive to resource availability at some times of the season than

others (Suzuki et al. 2007, Westphal et al. 2009). It is also possible that worker, male, and queen production are differentially affected by resource availability during different seasons (Bowers 1985, Westphal et al. 2009). To examine the influence of temporal patterns of resource abundance, we compared the fit of two models using AIC values, one with resources assessed over the whole season, and another with resources split into spring and summer resources. Both models included flower abundance, local nesting habitat type, and their interaction. We included the number of days a colony was in the lab as a covariate in the analysis to account for effects of supplemental feeding and the timing of placement in the field on number of offspring produced. Residuals were normally distributed and thus response variables were not transformed for analysis.

RESULTS

Patterns of resource abundance

The abundance of flowers used by *B. vosnesenskii* varied dramatically among study landscapes and through the season (Fig. 1). Average total flower abundance in the landscape surrounding a site differed more than four-fold among study landscapes (21.5–99.5 million flowers within 2 km of a colony; average 58.4 ± 21.6 million flowers [mean $\pm$ SD]), but did not differ among colonies in different local habitats (habitat type; $F_{2,30} = 1.67$, $P = 0.20$). Floral resources positively correlated with the proportion of natural/seminatural habitat in the landscape for sites located in different habitats (combined $\rho = 0.81$, $P < 0.001$, $n = 36$ sites; riparian $\rho = 0.84$, $n = 11$, organic farm $\rho = 0.84$, $n = 12$, conventional farm $\rho = 0.81$, $n = 13$). Flower abundance also showed distinct seasonal patterns that differed among landscapes. Spring and summer floral abundance differed significantly and in opposite directions between landscapes dominated by natural habitat vs. agriculture (landscape-type $\times$ season interaction, $F_{1,68} = 207.4$, $P < 0.001$); however, the magnitude of differences was more pronounced in spring than in summer (Appendix C). Natural land cover types on average had more abundant spring-flowering plants than did most crop lands (Fig. 1), such that at sites surrounded by a high proportion of natural habitat, flower abundance was relatively high in late spring and declined thereafter (high-spring/low-summer; Figs. 1 and 2). At sites surrounded by a high proportion of agricultural land, flower abundance was initially relatively low but showed a pulse in summer caused by mass-flowering crops, such as sunflower and tomato (low-spring/pulse-summer; Fig. 2). High-spring/low-summer sites also tended to have more abundant floral resources overall compared to low-spring/pulse-summer sites

Effect of floral resources on colony performance

The abundance of flowers in the landscape surrounding a colony significantly affected the combined number of workers and males it produced ($F_{1,29} = 9.86$, $P =$

A) Spring (March–May)

B) Summer (June–July)

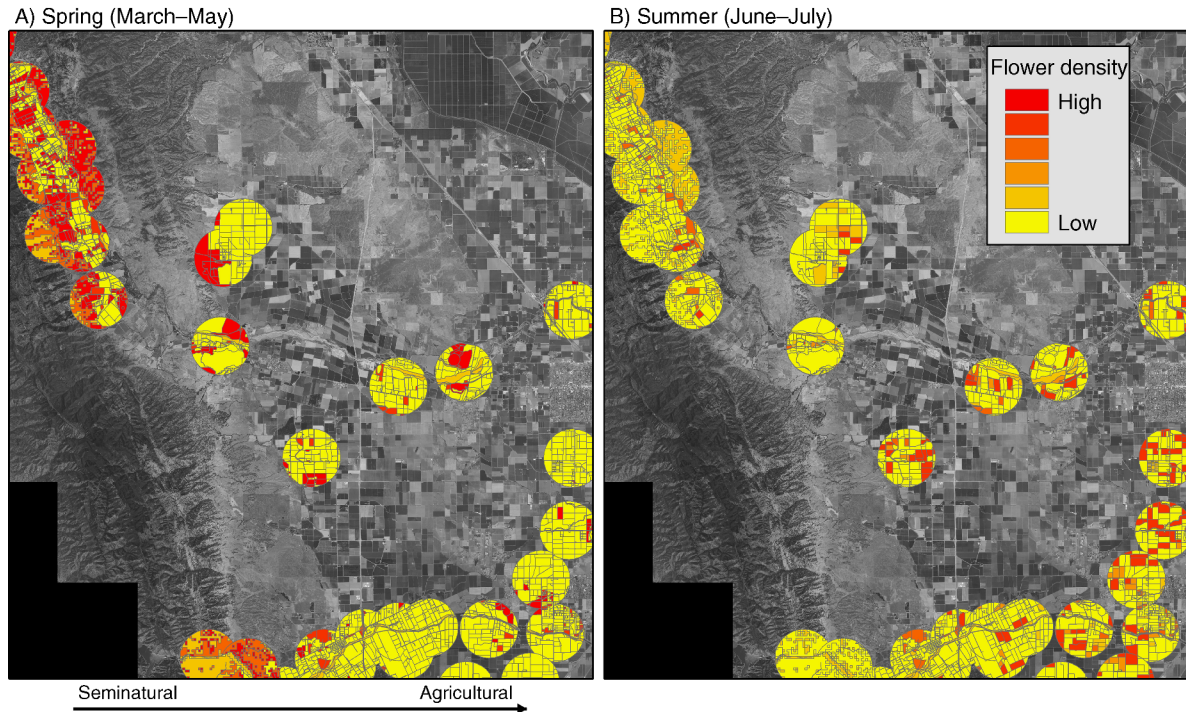Seminatural   Agricultural

Fig. 1. Seasonal changes in resource landscapes around *Bombus vosnesenskii* colonies: densities of flowers used by *B. vosnesenskii* in different areas in (A) spring and (B) summer. Each circular sector is 2 km in diameter. Flower density range is 0–33.3 flowers/m^2. Not all study landscapes are shown.

0.004). Colonies at sites with greater total resources produced more workers and males over the course of the season (Fig. 3A). The local habitat type in which a colony was located did not significantly affect worker and males numbers ($F_{2,29} = 1.16$, $P = 0.33$), nor did it modify the effect of landscape-level resources (habitat × resource interaction; $F_{2,29} = 1.23$, $P = 0.31$). The model with resources split by season fit nearly equally to the model with season-long totals ($\Delta AIC = 0.68$), and revealed that only early-season (spring) resources significantly affected combined worker-male production (spring $b = 4.06 \pm 1.54$, $t_{1,26} = 2.63$, $P = 0.01$; summer $b = -0.50 \pm 4.6$, $t_{1,26} = 0.11$ $P = 0.91$; where b's are the partial regression coefficients of number of worker and male offspring produced on distance-weighted floral resources in the landscape surrounding a colony). Neither spring nor summer resources showed a significant interaction with local habitat type (habitat × spring, $F_{2,26} = 0.47$, $P = 0.63$; habitat × summer $F_{2,26} = 1.08$, $P = 0.35$).

Colonies with more abundant floral resources in the surrounding landscape were no more likely to initiate queen production (Wald $\chi^2 = 0.01$, $P = 0.91$) and did not produce significantly more queens ($F_{1,29} = 1.62$, $P = 0.21$; Fig. 3B). Queen production also showed no response to spring vs. summer seasonal resources (spring $F_{1,30} = 1.98$, $P = 0.17$; summer $F_{1,30} = 0.44$, $P = 0.51$). The likelihood that a colony produced queens depended the

numbers of workers and males it produced (Wald $\chi^2 = 13.3$, $P < 0.001$), and, of the colonies that produced queens, those with more workers produced more of them ($F_{1,52} = 5.46$, $P = 0.02$).

DISCUSSION

Several recent syntheses of the effects of anthropogenic disturbance on native pollinators report negative impacts of isolation from natural habitat on the abundance and species richness of native bees (Carre et al. 2009, Winfree et al. 2009, Williams et al. 2010b). Those studies and others posit that the loss of floral resources is one driver of bee declines. Exceptions to the general pattern of habitat loss and native-bee declines also appear consistent with an effect of resource availability. For example, Winfree et al. (2007) showed a positive effect of agriculture on the abundance and diversity of wild bees, probably because heterogeneous agricultural landscapes provide superior floral resources for bees compared to the natural pine barrens and woodlands in their study region. Here we showed that flower abundance strongly correlated with the proportion of natural habitat in the landscape at the same spatial scale and that bumble bee colonies produced fewer workers and males in landscapes with fewer floral resources. These results provide a mechanistic link from habitat loss through floral resources to an effect on bee offspring production. Direct tests of loss of seminatural
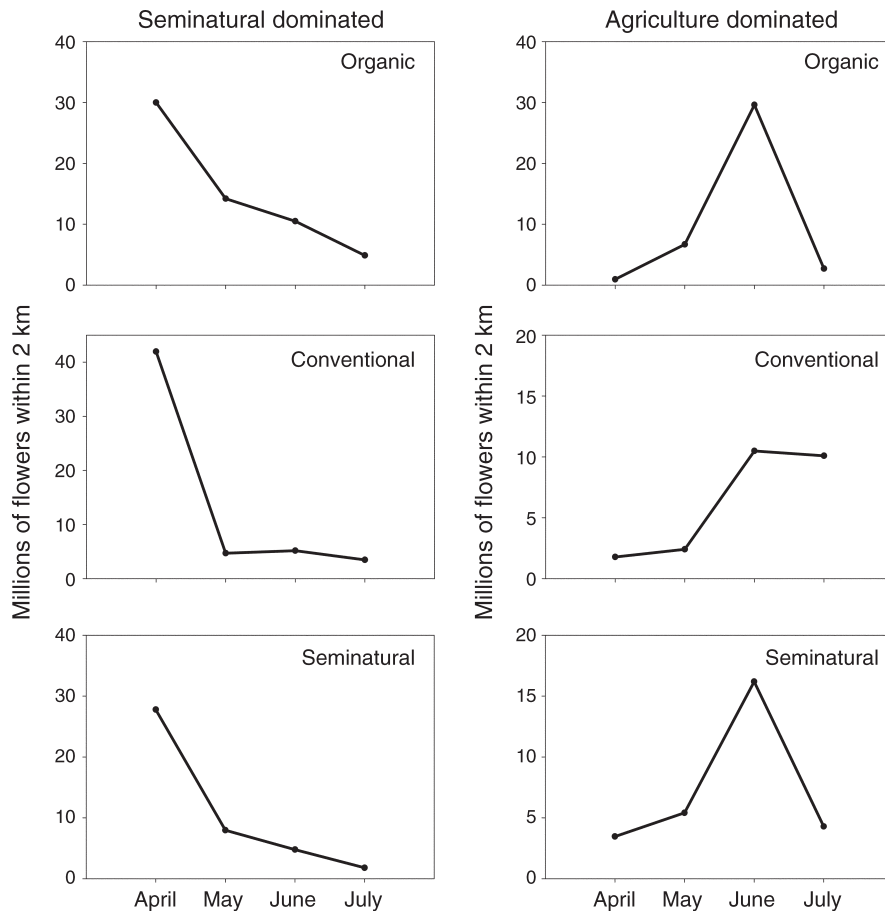
FIG. 2. Change in landscape-level floral abundance with season. The left-hand column shows examples of the "high-spring/low-summer" pattern associated with sites in landscapes with high proportions of seminatural habitat. The right-hand column illustrates the "low-spring/pulse-summer" pattern found in parts of the landscape dominated by agriculture. Each panel shows a representative site from the three local habitat types (seminatural, conventional row crop, organic row crop). Flower values are weighted by distance from the colony and thus do not represent raw counts.

habitat also show a negative effect on *B. vosnesenskii* colony performance in our study landscape (Greenleaf 2005). Our results are consistent with other investigations of bumble bees and landscape change. Estimated colony number, colony size, and colony survival over the season can all be affected by the area of forage-providing habitat within the landscape (Bowers 1985, Herrmann et al. 2007, Knight et al. 2009, Goulson et al. 2010) including the area of mass flowering crops (Westphal et al. 2009).

Further support for the importance of landscape-wide floral resources as determinants of colony performance comes from the lack of interaction with the local habitat type in our study. In contrast, studies investigating local vs. landscape composition on bee abundance frequently have found that high-quality local habitat is most important for bees in degraded landscapes (Heard et al. 2007, Williams and Kremen 2007, Rundlof et al. 2008). The interaction effect is partly due to food subsidies provided by local habitat elements (e.g., diverse crop systems) that offer persistent flower

resources to offset the dearth of such resources in the degraded landscapes (Williams and Kremen 2007). Our focus on the resource landscape as a whole subsumed local and landscape components and revealed the key underlying resource effect on colony performance, appropriate for highly mobile species that use resources from many different habitats (Darvill et al. 2004, Osborne et al. 2008, Westphal et al. 2009).

Contrary to our predictions, despite the strong effect of floral abundance on combined worker–male numbers, the abundance of floral resources did not clearly affect the number of queens a colony produced. Population dynamics in bumble bees are a function of the number of queens produced (reproduction) and the probability of colony establishment and survival (survival). If we accept queen production as a reasonable proxy for reproductive success, we did not find strong evidence that the quality of the resource landscape clearly influences this element of bumble bee population dynamics. Larger colonies that did not produce queens may have realized reproductive success through male

function, which we were not able to separate from allocation to workers (Ings et al. 2006, Westphal et al. 2009). Although male reproductive success is important from a genetic and evolutionary perspective, female reproduction will likely be the principal determinant of population dynamics (but see Zayed and Packer 2005).

The contrasting effects of floral resources on worker and male production vs. queen production were likely caused in part by the distinct spatiotemporal pattern of flower abundance within the season (i.e., high-spring/low-summer in natural dominated landscapes vs. low-spring/pulsed-summer in agriculture-dominated landscapes) combined with differential sensitivity of workers vs. queens to seasonal resource availability. Combined worker–male production was sensitive to floral resource limitation in the spring but not in the summer. Spring resources likely affect worker numbers rather than males, which are rarely produced at this time. Colonies located in landscapes with more abundant spring floral resources produced more workers early in the season. These workers could then potentially gather sufficient resources to maintain colony growth, despite sparser floral resources later in the season. Colonies in landscapes with relatively poor spring resources produced fewer workers early and thus might not be able to capitalize on the higher floral resource densities available to them later in the season. The greater sensitivity of worker numbers to early-season resources also likely reflects the seasonal transition in colony life-history from production of workers to production of queens and males.

Queen production, in contrast, depends on floral resources throughout the season (Westphal et al. 2009) and no landscapes in our region provided consistently high resources throughout the season. Abundant early-season floral resources allow colonies to produce more workers, which gather the food necessary to produce more queens. Later-season resources are needed to provision developing queen brood (Bowers 1986, Beekman and Van Stratum 1998, Pelletier and McNeil 2003). In our landscape, colonies at sites with good spring resources could increase worker numbers, but did not consistently have enough flower resources later in the season. Colonies at sites with poor spring resources were not consistently able to reach large enough sizes to produce large numbers of queens.

These sorts of spatiotemporal dynamics are likely to apply across many landscapes; for example in northern temperate woodland–grassland landscapes, which have abundant wildflowers primarily in spring within wooded habitats, and primarily in summer within grasslands and on farms. Their effect on limiting bee populations will depend on the degree to which spring vs. summer resources are negatively correlated spatially, and on the length of the flight season of the bee. Westphal et al. (2009) found a similar relationship between seasonal resources and bumble bee colony performance. Abundant early-season resources from mass-flowering crops
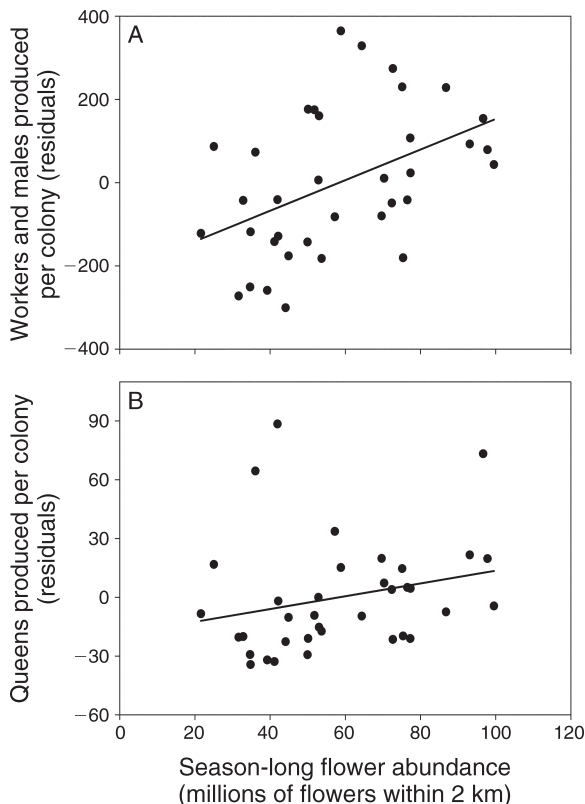

FIG. 3. (A) Residual total number of workers and males and (B) residual total number of queens produced per site as a function of seasonal total flower abundance in the landscape surrounding the colonies. Flower values are weighted by distance from the colony and thus do not represent raw counts. Residuals represent those after controlling for the effect of rearing duration on number of workers or queens a colony produced.

increased worker numbers, but were not sufficient to enhance colony reproduction (queen and male production) in landscapes depauperate of flower resources later in the season. Likewise Bowers (1985) showed that mid to later season resources strongly affected colony persistence and the transition to production of reproductive offspring. Some of the residual variation in queen (and worker) numbers in our study may also arise because we used flower abundance as a proxy for pollen and nectar resources. The quantity and quality of pollen and nectar vary among flower species (Roulston and Cain 2000).

Although we cannot rule out the possibility that other habitat-related factors such as differential rates of nest predation or parasitism drove the landscape pattern and floral resources were simply correlated (Goulson et al. 2002, Carvell et al. 2008), we think that such effects are unlikely in our study. We found no cleptoparasitic *Bombus* species in any colonies upon dissection at the end of the season. Although colonies showed various levels of attack by the wax moth *Vitula edmundsii*, as well as several species of Coleoptera and Diptera,

infestation levels were uncorrelated with worker numbers or with landscape composition ([nest parasites per nest] – [workers produced per nest], Kendall $\tau = 0.02$, $P = 0.81$, $n = 71$ colonies; [mean parasite per site] − [percentage of natural habitat], $\tau = 0.06$, $P = 0.60$, $n = 36$ sites). We did not measure the incidence of internal parasites for any colony, but hand rearing of queens within the lab at colony initialization probably helped to filter out infected queens from the study.

Most previous studies of bumble bee responses to resource availability have surveyed free-flying bees at floral resources (e.g., Pywell et al. 2005, Heard et al. 2007). We focused instead on offspring production by colonies placed into the field. Our approach avoids the pitfall that foraging workers may simply be attracted to rich floral areas (Heard et al. 2007) and provides a more direct estimate of population dynamic variables. By placing colonies of standard size directly into the field, we also filtered out variation related to colony establishment. This filter however prevented examination of the effect of early spring resources on nest establishment. Nest establishment is an important factor in determining population density and persistence within the landscape (Goulson et al. 2010), and since the foundress queen alone forages to support the nascent colony, it might be a period when colonies are particularly sensitive to resource limitation (Suzuki et al. 2009). Nonetheless, because bumble bee species do not store substantial amounts of pollen and nectar, a consistent supply of floral resources remains important throughout the season. In future, it will be important to quantify colony establishment and density directly to understand the effect of landscape-level resources on bumble bee persistence (Knight et al. 2009, Goulson et al. 2010). We also were not able to reliably distinguish between worker brood cells and male cells when measuring colony size. By pooling these individuals with workers we likely overestimate worker number, and increase the among-colony variation in combined worker–male number. This variance inflation could reduce the power to detect a resource effect. That we nonetheless found such an effect is encouraging.

Although the reproductive output of colonies was not significantly affected by the resource landscape surrounding them, the abundance of flowers in the landscape may strongly influence the pollination services provided by bumble bees. Bumble bees are key pollinators of native plants across many ecosystems and are a dominant native pollinator of many crops in north temperate regions (Corbet et al. 1991, Williams 1996, Thorp 2003). In ours and other study systems, they are among the most efficient pollinators of multiple crop types (Kremen et al. 2002, Winfree et al. 2008). Most of this pollination is provided by worker bees; thus, larger colonies will deliver greater pollination service to crops.

Bumble bee colonies responded strongly to differences in floral resources in the surrounding landscape, and less abundant floral resources were consistently correlated with the loss of natural habitat and increases in intensive agriculture. Decreases in floral resources appear to be one important driver behind bee responses to landscape change. The lack of abundant resources throughout the season likely helps to explain why bumble bees are rare to absent in the intensively farmed portion of our study region (Larsen et al. 2005). The particular importance of early-flowering forage resources for bumble bee colonies combined with the relative paucity of such early-flowering species in agricultural habitats has important implications for management and restoration of pollinators in degraded landscapes. Colonies are potentially unable to capitalize on floral resource pulses that occur in summer because they have not produced large enough worker forces. Increasing the abundance of early flowering resources in intensive agricultural landscapes might therefore bolster bumble bee colonies and populations in general.

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SUPPLEMENTAL MATERIAL

Appendix A

Land cover types with floral densities averaged over the entire study season (*Ecological Archives* E093-091-A1).

Appendix B

Photo of a field nest box containing a *Bombus vosnesenskii* study colony (*Ecological Archives* E093-091-A2).

Appendix C

Flower abundance in different regions of the landscape in spring and summer (*Ecological Archives* E093-091-A3).