



Farm and landscape factors interact to affect the supply of pollination services



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ABSTRACT

Farms can harbor substantial biodiversity, which in turn sustains the supply of ecosystem services. The effectiveness of farm management to enhance biodiversity, however, may be modified by land cover in the surrounding landscape beyond a farmer's direct control. We examined how landscape pattern and farm management affect the abundance and diversity of native bees visiting highbush blueberry in Vermont, USA. We quantified landscape pattern at multiple scales and created an agricultural intensity index that represents farm management practices such as pesticide use, mowed and grain crop area. We observed native bee visitation to assess the supply of pollination service provided to blueberry growers. Across 15 farms, 84 wild bee species were observed visiting highbush blueberry, almost a third of bee species recorded in Vermont. Visitation rate, abundance and species richness increased with the amount of natural area surrounding farms. Less intensively managed farms had higher levels of bee visitation, abundance and a more diverse bee community. Bee communities and the pollination services they provide are influenced by interactions between local management and landscape pattern. In particular, intensive farm management appears to compound the negative effects of landscape simplification. To support native pollinators on their farms, growers should consider farming approaches in the context of the broader landscape.

1. Introduction

Animal-mediated pollination is an important ecosystem service that regulates crop production and quality (Kennedy et al., 2013; Klatt et al., 2014). Pollinator-dependent crops contribute significantly to the global supply of micronutrients (Chaplin-Kramer et al., 2014; Ellis et al., 2015) and are critical to agricultural economies (Klein et al., 2007). Reliance on pollinators is particularly evident in smallholder agriculture, which are susceptible to yield gaps when pollinator densities are low (Garibaldi et al., 2016).

As the demand for agricultural pollination services surges (Aizen and Harder, 2009; Koh et al., 2016), wild pollinator visitation is expected to safeguard against yield limitations (Garibaldi et al., 2013). Although European honeybees *Apis mellifera* L. are frequently employed as crop pollinators, hive failure is increasingly common and managed populations of this pollinator have declined in recent decades (Lee et al., 2015; Neumann and Carreck, 2010). Native bee communities can complement the activity of honey bees and ensure adequate pollination for many economically important crops (Benjamin et al., 2014; Klein, 2009; Kremen et al., 2002). In many cases, native bees are more

efficient pollinators because they visit a greater number of flowers per unit time and transfer more pollen per visit. For example, when compared to honeybees pollinating blueberry, native bees have greater visitation rates and deposit more pollen per flower visit (Javorek et al., 2002). Diverse native bee communities are also active over a range of climate (Rader et al., 2013) and temporal scales (Bartomeus et al., 2011), and therefore provide insurance against single species loss (Winfree et al., 2007).

Agriculture disrupts native bee populations at multiple scales through drivers such as habitat degradation, farm management, pathogens and climate change (Goulson and Hughes, 2015; Potts et al., 2010). At broader scales, altered landscape pattern (i.e. changes in the composition and/or configuration of habitat patches) restricts the temporal and spatial distribution of foraging, nesting and overwintering sites (Kremen et al., 2007). Research into landscape pattern effects on pollinators has focused on the importance of habitat composition (i.e. the number and abundance of habitat patches), and to a lesser extent habitat configuration (i.e. the spatial arrangement of habitat patches) (Kennedy et al., 2013). As central place foragers, the amount and proximity of resource patches affects native bee populations and

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regulates ecosystem service supply, with crop visitation rates declining steeply as farms become more isolated from natural habitats (Ricketts et al., 2008). Changes in landscape pattern can also alter landscape-wide bee species pools, with clear benefits to crop pollination for farms situated in areas with greater extent and proximity of natural habitat (Garibaldi et al., 2011).

At local scales, differences in management can influence the delivery of pollination services to crops. Intensive practices that focus on a few crop species and their specific requirements often leads to input-intensive agriculture (e.g. fertilizer input, pesticide application, habitat simplification and decreased crop diversity) (Tscharntke et al., 2005). Less-intensive management practices, such as organic farming or increasing crop-non-crop heterogeneity, can improve pollinator abundance and richness (Boreux et al., 2013; Kennedy et al., 2013; Kremen and Miles, 2012). Management practices can drive variation in bee communities that translate into differences in pollination services provided to crops. For example, canola seed set was on average 3 to 6 times lower on conventional and herbicide-resistant fields than in organic fields, and this reduced seed set was strongly correlated with reduced abundance of native pollinators (Morandin and Winston, 2005).

Theoretical and empirical work shows that landscape pattern and farm management often interact to influence biodiversity (Batáry et al., 2011; Carvell et al., 2011; Concepción et al., 2012). The intermediate landscape-complexity hypothesis predicts that less-intensive farm management will have the greatest positive effect on farmland biodiversity in simple landscapes, but less so for farms in spatially complex regions, because these farms already have abundant and diverse species pools (Tscharntke et al., 2012, 2005). This pattern holds for many taxa: landscape pattern can determine how strongly farm management affects the diversity of bees (Holzschuh et al., 2007), butterflies (Rundlöf et al., 2008) and spiders (Schmidt et al., 2005). Recent meta-analyses have found that agri-environment practices had the greatest effect on the species richness of multiple taxa (e.g. plants, birds, herbivores, pollinators) in landscapes with low levels of intact natural area (Batáry et al., 2011; Lichtenberg et al., 2017).

The effects of management decisions on biodiversity are clearly context-dependent, but few studies have investigated the resulting effects on ecosystem services (ES). As the biophysical and social conditions by which people obtain benefits from ecosystems, these services can be quantified in terms of supply and benefit. Evaluating ES supply typically involves measuring the presence of species, ecosystems, or ecological processes that contribute to human livelihoods, whereas evaluating ES benefit also involves demand for services, as determined by social and economic factors (Mitchell et al., 2015; Villamagna et al., 2013). For example, crop pollination can be measured as bee visits to crop flowers (supply) or as changes in the value of crop production (benefit) (Ricketts et al., 2016). Ecosystem service supply and benefit are often related; for pollination, increased visitation is known to be associated with improved production across crops and growing regions (Garibaldi et al., 2013).

Here we use crop pollination to examine how landscape pattern interacts with farm management to affect biodiversity and the supply of an ecosystem service. We focus on wild, native bees visiting highbush blueberry (*Vaccinium corymbosum* L.), because pollination is critical to fruit production for this crop (Dogterom et al., 2000; Isaacs and Kirk 2010). We predict that native bee biodiversity and ecosystem service supply would be affected by both farm management and habitat composition and configuration, and that these factors interact, such that less-intensive management practices would have the greatest effect in simple landscapes. Rather than classify farms into simple binary categories (e.g. organic vs. conventional), we use an agricultural intensity index to better capture realistic gradients of management strategies. We use this index, combined with landscape data and observations of native bee pollination, to explore the following questions: (i) Do native bee communities respond to differences in landscape composition and configuration, and does this alter the supply of pollination services? (ii)

Does farm management influence native bee communities and associated pollination services? (iii) Is the effect of farm management on bee communities and derived pollination services dependent on landscape pattern?

2. Methods

2.1. Study system

The Champlain Valley, Vermont, USA (44.45° N, 73.09° W) is an important agricultural region due to rich alluvial soils and a growing period extended by a nearby lake. Land cover in the region is spatially heterogeneous; residential exurban areas and small-scale agriculture are interspersed with second-growth forests dominated by maple (*Acer* spp.), birch (*Betula* spp.) and beech (*Fagus grandifolia*). Agriculture in the region is a mix of pastureland and grain production, along with smaller fruit and vegetable farms. Our study system consists of 15 highbush blueberry farms. None of these farms import honeybee hives for pollination, although a few ($N = 3$) have hives for honey production. Blueberry acreage on these farms ranges from < 0.5 ha to 3.6 ha with a median field size of 1.1 ha.

2.2. Agricultural intensity index

We quantified differences in farm management by creating an agricultural intensity index that included measures of pesticide use, mowed area and grain crop area. To quantify pesticide use across farms, we adapted the environmental impact quotient (Kovach et al., 1992) to develop a pesticide use index based on known impacts to bees. Pesticide use indices have been used with multiple arthropod taxa (Dormann et al., 2007) and this approach is well documented for native bees (Park et al., 2015). We obtained pesticide identity and use information directly from farmers for each managed crop, and if precise application rates were unknown we used the regionally suggested rates for each reported crop (New England Small Fruit Management Guide 2015–2016). We follow Park et al. (2015) by summing across all pesticides (fungicides, herbicides and insecticides) the product of the pesticide's (i) bee impact quotient (BIQ = pesticide toxicity ratings times the half-life on plant surfaces) (Kovach et al., 1992; Morse, 1989), (ii) percentage active ingredient in material sprayed and (iii) maximum application rate (quantity per acre of a given crop) (see Table A.2 for a list of pesticides recorded in this study). This provides a farm level index that is derived from a crop-specific, per-acre calculation of the effects of a farm's pesticide application on bees, and thereby accounts for differences in crop area between farms. We provide measures in terms of acres, because it is the unit relevant to participating land managers. We further captured differences in agricultural intensity by quantifying the extent of grain crops (corn and soy) and mowed areas on and adjacent to study farms. These forms of land use are frequently disturbed, thereby limiting nesting sites, and offer little in terms of floral resources. Moreover, landscape-scale assessments report declines in native bee abundance associated with the conversion of natural habitats to row crops (Koh et al., 2016). We calculated the areal coverage of these two land uses within 300 m of each farm's blueberry crop because this scale encompasses the crop area of observed farms.

Rather than arbitrarily weight management variables based on perceived impact to bee populations, we scaled each variable from 0 to 1 and reduced these continuous variables through principle components analysis (PCA). We use the first principle component score (45% of the overall variation), scaled from 0 to 1, as our agricultural intensity index (AII) (Fig A.1). While PCAs are useful for emphasizing variation and eliminating collinearity between dimensions, the resulting scores are unit-less and their biological relevance becomes abstract. We therefore compared AIIs between farms that self-reported as organic or conventional to ground truth our index. We found that our intensity index is associated with, albeit marginally, whether a farm is organic

practicing (Fig. A.2 ; $F = 3.72$, $P = 0.08$).

2.3. Landscape classification

We used the 2011 National Land Cover Dataset (NLCD 2011) to quantify landscape composition and configuration within radii of 1000 m and 2000 m centered on each blueberry field. All fields in this study are at least 1 km apart. To determine landscape composition surrounding each farm, for each radius, we quantified the proportion of natural area, here defined as the combined area of wetlands, grasslands, shrub and scrublands, mixed forests, deciduous forest and evergreen forest. We also calculated landscape diversity (Shannon Index) using all land cover types for each radius for each farm as another landscape composition measurement. To obtain statistical measures of spatial configuration we used FRAGSTATS 3.4 (McGarigal and Cushman, 2002) to calculate edge density and mean patch size across all land cover types.

2.4. Pollinator observations

We sampled bees on farms over three summers (2013–2015). Although we visited the majority of farms each year ($N = 11$), two farms were sampled for a single year and two farms were sampled during two consecutive years (2014–2015). In each year, we visited each farm at least three times during the bloom period (May to June) to observe bee visitation, abundance and diversity. To standardize pollinator activity observations, we sampled between 09:30 and 14:00 h, under favorable conditions (clear to hazy skies, temperature above 15 °C, and wind speeds less than 3 m/s).

During each farm visit, we randomly selected two observation bushes at two sites: one site at the blueberry crop edge (“edge sites”) and another 50 m from the edge (“interior sites”). To assess farm level pollinator visitation rate and abundance, we performed 10-min observations at each bush (total of 40 min of observation per visit per farm). Observers established a 1-m³ area and recorded all pollinators making legitimate visits to flowers, here defined as an insect landing on a flower and collecting resources from it. For each 10-min period, we recorded the number of individuals visiting blueberry flowers to quantify abundance and the number of flowers visited by each individual to quantify visitation rate. During observations, we assigned flower visitors to eight morphospecies groups: *honey bee*, *Bombus queens*, *Bombus workers*, *big black bee*, *slender black bee*, *tiny black bee*, *green bee*, and *other bee*.

Following each observation period, we sampled pollinator diversity via 10-min aerial netting along one 20-bush transect at each site. Data collectors walked at an even pace collecting flower-visiting bees by hand net, stopping time to process specimens. Within each year, data collectors were rotated among farms and at sites within farms. Transect walks provided bee species richness data, while observations measured bee abundance and the potential supply of pollination services.

2.5. Specimen identification and richness estimation

We identified all collected specimens to species using published and online guides (see Supporting information for identification references). We assigned specimens collected during transect walks to morphospecies groups to illustrate the species composition of each group (Fig. 1; Table A.3).

We use our specimen data to estimate species richness as an index of per farm bee diversity using rarefaction methods (Colwell et al., 2012). This approach is recommended because it corrects for bias due to sampling effort and species’ rarity by estimating and adding the number of undetected species (Colwell et al., 2004). We calculated asymptotic species richness estimators using an incidence-based rarefaction method with the iNEXT software (Chao et al., 2014; Hsieh et al., 2016). We constructed bootstrapped 95% confidence intervals and standard

errors for estimated species richness of all farms (Fig. A.3).

2.6. Weather and other covariates

During each farm visit, we collected data on abiotic covariates including time of observation, temperature, average wind speed and relative humidity. Variation in crop features may also influence bee activity. To account for difference in floral resource availability among farms we recorded the phenological stage of blueberry bloom on a 0–3 scale depending on the relative proportion of senescent flowers. We also assessed the abundance of other flowering plants within a 10 m radius around the observation point. To account for differences in potential bee nesting sites among farms we recorded the proportion of bare ground beneath crop rows, as well as inter-row vegetative state (e.g. tall grass, mowed grass or bare ground).

We found no relationship between native bee visitation rate, abundance or diversity and measured covariates that varied within sites by date (time, temperature, wind speed, blueberry flower density, weed flower density) in single least squares regression ($P > 0.05$). Within the sampled fields, native bee visitation rate did not differ between field edge and interior sites ($F = 0.11$, $P = 0.74$), so we averaged bee activity data for each farm within each year.

2.7. Statistical analysis

We used linear mixed effects models to analyze the effect of landscape composition and configuration, farm management and their interaction on average native bee visitation rate, abundance and diversity. We included year as a random effect in all models. For each main model, we constructed a null model with all fixed effects variables removed and compared AIC values between the two models. As a goodness-of-fit measure we calculated a log likelihood ratio test between fitted and null models (McFadden, 1974).

Pollinators are known to differ in their efficiency in depositing pollen (Ne’eman et al., 2010). To test whether different pollination efficiencies affect our results, we follow Isaacs and Kirk (2010) and scale morphospecies visits according to their reported average per visit pollen deposition for blueberry (Benjamin et al., 2014; Javorek et al., 2002) (Table A.1). We then calculate total per farm pollen deposition as the sum of expected pollen grains deposited across native morphospecies (i.e. excluding *Apis*) within each year. Our most active morphospecies groups were also effective at transferring pollen (Fig. 1; Fig. A.4 ; Table A.1), as such visitation rate and total pollen deposition are strongly correlated ($r^2 = 0.87$, $P < 0.001$) and for simplicity we report results for only visitation rate.

For predicting species richness we took into account the uncertainty associated with each farm’s asymptotic richness estimation. We used the same model structure as above but with a weighted regression in which richness slope estimates are weighted by the inverse of their standard error. This variance is a function of sample coverage and this technique further accounts for differences in sampling effort among the farms (Pelini et al., 2014). To better understand the importance of the specific land cover classes that compose our natural area classification, we used the same model structure as above to relate visitation, abundance and estimated species richness with each land cover class separately.

We tested the effects of farm management by modeling visitation, abundance, and estimated species richness using linear mixed effects models with the AII as a fixed effect and year as a random effect. To examine the interaction between landscape pattern and farm management we first identified the most explanatory scale by regressing all response variables against the proportion of natural areas at both scales. We compared the resulting r^2 values, and used the scale with the highest r^2 value in all subsequent analyses (Holland et al., 2004). Critically, we tested for collinearity between our AII and proportion natural area before testing for significant interactions between them. We

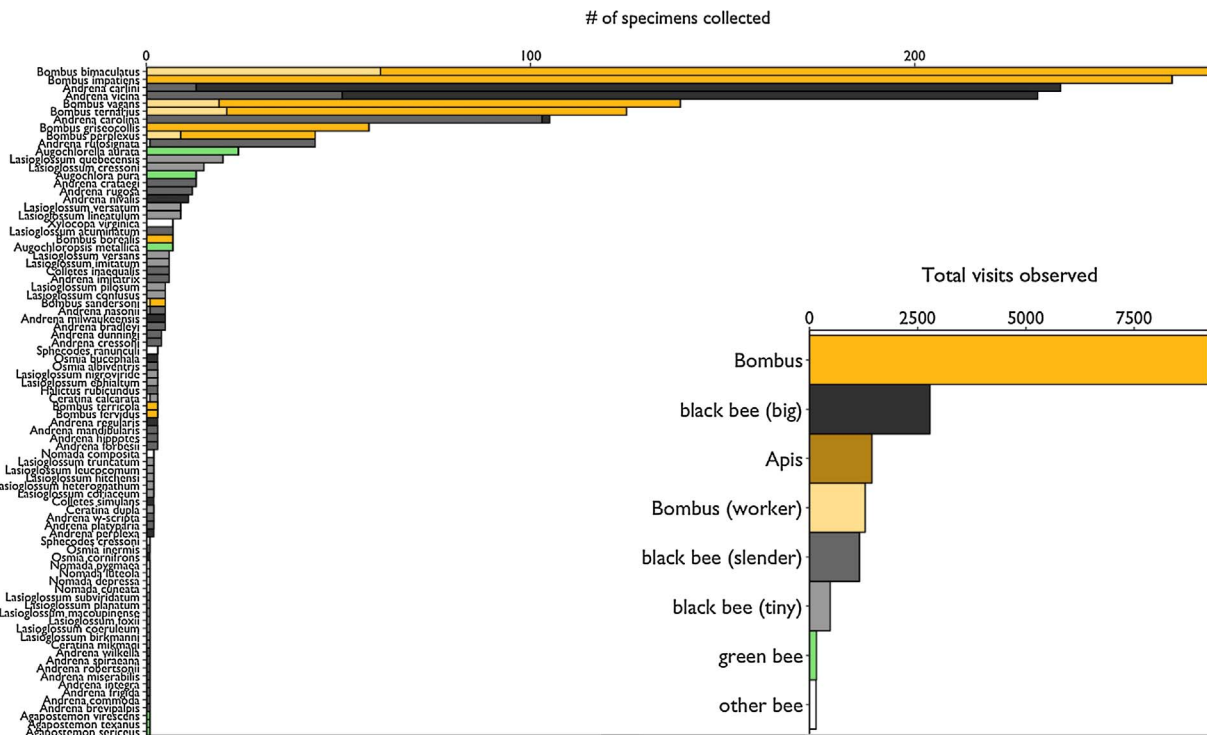


Fig. 1. Rank-abundance plot for species collected. Inset depicts the total floral visits of eight morphospecies observed. To provide information on the species composition of morphospecies groups, the rank abundance plot is color coded according to inset. Some species belong to more than one morphospecies due to caste and sex morphological differences. Non-native species are omitted from the rank abundance plot (see Table A.3 for more information).

found that agricultural intensity and proportion natural area were not related ($|r| = 0.40$, $P = 0.144$). In addition, to avoid the potential problem of multicollinearity between main effects and interaction terms, we mean centered main predictor variables, which has been suggested as a solution of reducing multicollinearity without altering regression slopes or hypothesis tests (Jaccard et al., 1990; Quinn and Keough, 2002). We log-transformed all response variables to meet assumptions of normality and homoscedasticity and performed all statistical analyses in R v.3.2.2 (R Development Core Team, 2013) using packages ‘lme4’, ‘lmerTest’ and ‘MuMin’.

3. Results

3.1. Blueberry-visiting bee community

From 1831 collected specimens we identified 84 bee species belonging to 14 genera (Fig. 1) that were actively visiting blueberry fields during bloom. The most species rich genera were *Andrena* (28 species), *Lasioglossum* (22 species) and *Bombus* (10 species). The four most common species (*B. impatiens*, *B. bimaculatus*, *A. vicina* and *A. carlini*) accounted for 55% of collected specimens (Fig. 1). We focused collection on native species, so we omit a few collected specimens of two non-native species (*Apis mellifera* and *Osmia cornifrons*) from diversity analyses. Sample-based extrapolation of specimen data provided asymptotic richness estimators for each farm for each year (range: 4.13 ± 0.44 – 131.00 ± 118.62 [range estimate \pm standard error]). Estimated species richness was strongly correlated with observed species richness across farms (Pearson’s $r = 0.77$, $n = 39$, $P < 0.001$).

From 118 observation hours we recorded 15,270 floral visits by 3262 individual native bees. Disaggregating by morphospecies and using our specimen records to understand the species composition of each group, we observed 9252 flower visits by *Bombus* queens (10 species inclusive), 1285 by *Bombus* workers (5 spp.), 2783 by big black bees (10 spp.), 1155 by slender black bees (27 spp.), 480 by tiny black bees (27 spp.), 162 by green bees (6 spp.) and 153 by other bees (8 spp.)

(Fig. 1 & Table A.3). With 1444 visits, honeybees made up a relatively small proportion of visits (9%). Native bee visitation rate (21.60 ± 1.07 flower visits per 10-min sample) and abundance (4.61 ± 0.19 individuals per 10-min sample) were much greater than honeybee visitation rate (2.04 ± 1.10) and abundance (0.62 ± 0.07) (visitation: d.f. = 74, $t = 10.56$, $P < 0.001$; abundance: d.f. = 74, $t = 10.19$, $P < 0.0001$).

3.2. Landscape pattern

We found that native bee communities responded consistently to landscape pattern at the larger spatial scale (Fig. 2 & Table A.4), and bee visitation rate ($r^2 = 0.51$, $P < 0.001$), abundance ($r^2 = 0.55$, $P < 0.001$) and estimated species richness ($r^2 = 0.31$, $P < 0.001$) increased with the proportion of natural area at this scale. Landscape diversity had no effect on visitation rates or abundance at either scale, but estimated species richness was positively related to landscape diversity at the larger scale (Table A.4; 1000 m: $r^2 = 0.02$, $P = 0.365$; 2000 m: $r^2 = 0.14$, $P = 0.016$). When examining natural land cover classes individually, we consistently found that visitation rate, abundance and species richness are positively related to deciduous and mixed forest types at both scales, whereas the direction and significance of other land cover classes varied (Fig A.5). Landscape configuration variables (edge density and average patch area) were not significantly related to bee visitation rate, abundance or estimated species richness (Table A.5). Based on a high degree of explained variance, the proportion natural area at the 2000 m scale was used for all remaining analyses.

3.3. Farm management

Native bee visitation ($r^2 = 0.19$, $P = 0.004$), abundance ($r^2 = 0.16$, $P = 0.011$) and species richness ($r^2 = 0.14$, $P = 0.018$) declined with increasing agricultural intensity (Fig. 3 & Table A.6).

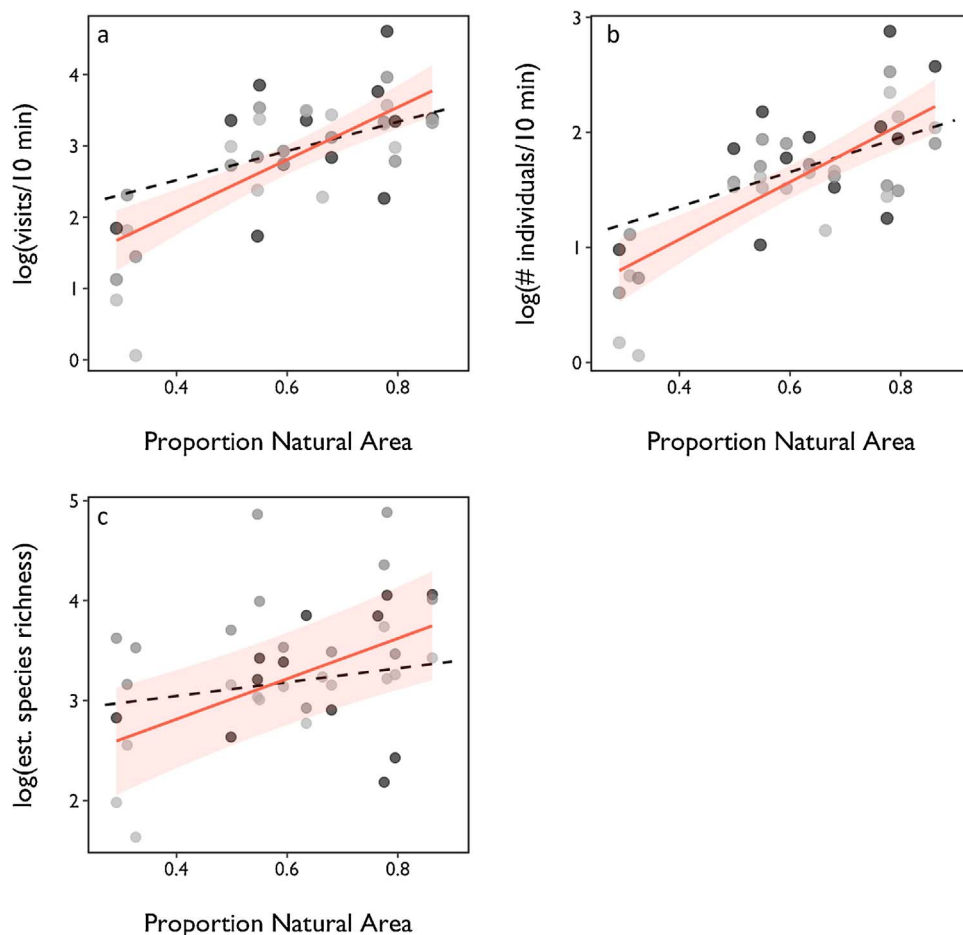


Fig. 2. Effect of proportion natural area on native bee (a) visitation rate (b) abundance and (c) species richness. Points and model fit with 95% confidence intervals for the amount of natural area at the 2000 m scale shown for each of three sampling years (red line and shading). Model fit (black dashed line) for 1000 m scale is also depicted (points not shown). Results are from mixed effects models with year as a random effect. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Landscape moderated effects of farm management

We found a significant interaction between our AII and proportion natural area on visitation rate (7.44 ± 2.29 (interaction slope estimate \pm standard error), $t = 3.25$, $P = 0.002$), native bee abundance (3.42 ± 1.51 , $t = 2.26$, $P = 0.030$) and estimated species richness (6.166 ± 2.15 , $t = 2.86$, $P = 0.007$) (Table A.7). We did not find collinearity between the centered variables and their interactions in multiple linear regression models (all $|r| < 0.5$). We visualize this interaction as a surface of predicted visitation, abundance and richness values bounded by a convex hull containing all observed combinations of proportion natural area and AII (Fig. 4). We did not find a significant interaction between farm management and landscape diversity or the two configuration measures, edge density and average patch size (Table A.8).

4. Discussion

We report here that at least 84 species of wild bees visit highbush blueberry flowers on Vermont farms, representing almost a third of the state's recorded bee fauna (J. Ascher, unpublished data). Bee diversity, abundance and visitation were higher on farms where less intensive practices were employed, and were positively correlated with proportion of natural area in the surrounding landscape. Moreover, farm management and landscape pattern interact such that the negative effects of intensive agriculture on native bee communities are compounded by landscape simplification.

4.1. Landscape effects on native bee communities

We found that landscape composition had a significant effect on native bee communities and derived pollination services, whereas landscape configuration did not. Landscapes with more natural area support robust bee populations because these areas provide access to floral resources, as well as nesting substrates and materials (Williams and Kremen, 2007). Previous studies of bees have found that the amount of natural area surrounding focal sites supports abundant and stable of pollinator communities (Cusser et al., 2016; Garibaldi et al., 2011; Kremen et al., 2002). We also found that the diversity of native bees is positively related to landscape heterogeneity at large spatial scales. Habitat diversity provides variety in forage and nesting sites and wild bees have been shown to prefer patches surrounded by a multiple habitat types (Hirsch et al., 2003). Our results bolster the evidence for a predictive relationship between the extent of natural areas and the supply of pollination services (Garibaldi et al., 2011 and references therein).

Aggregating land cover classes is common practice (Greenleaf and Kremen, 2006; Holzschuh et al., 2012; Klein et al., 2012), yet specific classes can influence native bee communities differently. For instance, we found that the coverage of mixed or deciduous forests is a strong predictor of native bee visitation and diversity (Fig. A.5), because these areas offer abundant nesting substrates (Kremen et al., 2007; Watson et al., 2011). While summarizing land cover illustrates how large-scale landscape patterns influence native bee communities, identifying specific land cover classes can help managers understand what aspects of their landscapes support pollinator populations.

Beyond landscape composition, the effects of habitat alteration are often the result of landscape configuration: the size, juxtaposition and

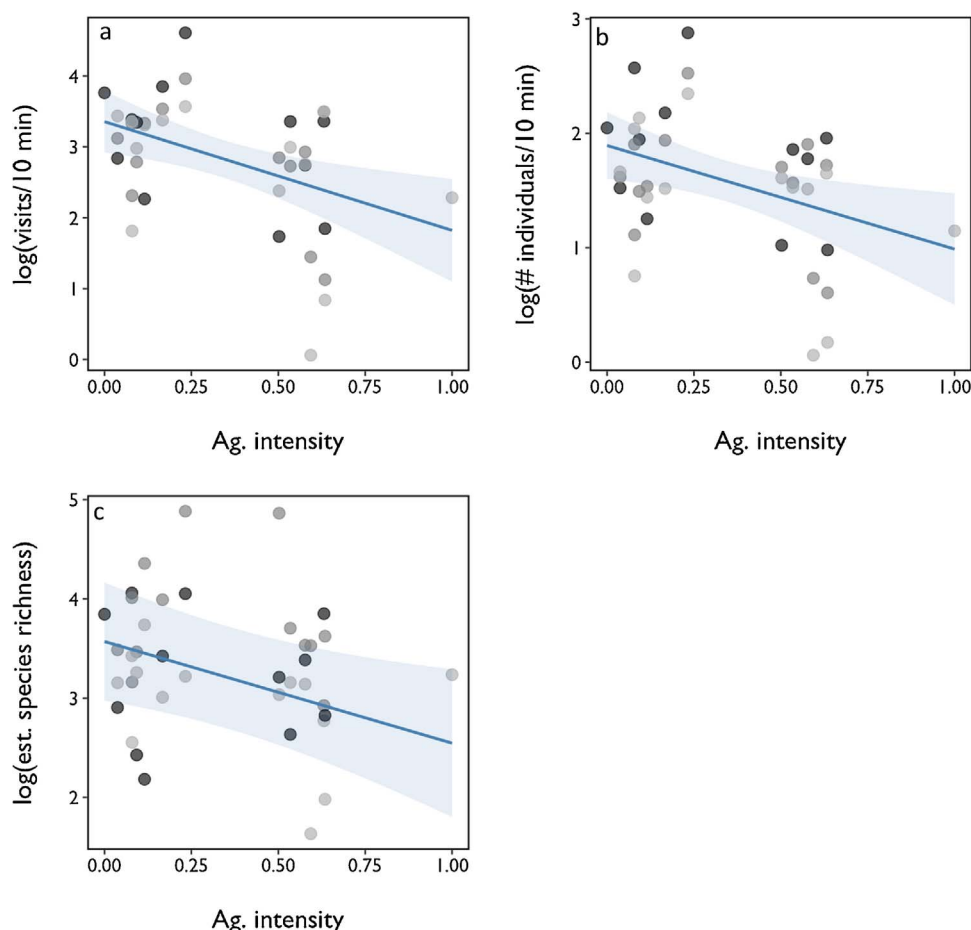


Fig. 3. Effect of agricultural intensity on native bee (a) visitation rate (b) abundance and (c) species richness. Points and model fit with 95% confidence intervals shown for each of three sampling years (blue line and shading). Results are from mixed effects models with year as a random effect. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

orientation of landscape elements. Our analyses of configuration metrics did not reveal any significant relationship between native bee communities and average patch size or edge density. Our results suggest that bees are not responding to edge density at the landscape level, and patchy landscapes with more habitat edges do not factor significantly into predicting bee activity or diversity.

4.2. Farm management effects on native bee communities

Few studies have assessed differences in ecosystem service between farms that vary in management intensity, and the evidence for effects of management actions on pollination services is wanting (Kremen and Miles, 2012; Winqvist et al., 2012). We quantified the supply of pollination services and found that farm management had a significant effect on both the biodiversity of native bees and flower visitation rate. Our agricultural intensity index is useful because it characterizes farm management as a continuous gradient and allows for a more quantitative examination of management intensity (Mas and Dietsch, 2003). Constricting farms to binary categories (e.g. organic vs. conventional) has been criticized (Puech et al., 2014), and composite indices can provide a convenient single measure of agricultural intensity and better characterize local management heterogeneity (Hendrickx et al., 2007; Herzog et al., 2006; Le Féon et al., 2010). Although our measures of pesticide use were farm and crop-specific, we recognize that other management practices likely vary between crops. Additionally, our intensity index provides only a static, early-season snapshot of a farm's management, when in fact management intensity is likely to vary across a growing season as new crops emerge and different practices employed. Future development of continuous management gradients could benefit from considering a suite of crop-specific processes and tracking changes in management intensity over time.

The beneficial effects of less intensive farming for pollinating insects arise from reduced agrochemical use and increased area of resource rich ruderal habitats. Pesticide application directly affects native bees via lethal exposure to insecticides or fungicides (Johnson, 2015) or indirectly by herbicides altering local habitat quality. Less intensive farming practices lead to greater plant diversity in and around farmland habitats (Roschewitz et al., 2005; Winqvist et al., 2011) and these local floral resources can support larger, more diverse local native pollinator populations (Krauss et al., 2005). Farm management differences can also impact community structure: higher floral abundance and diversity on less intensive farms are linked to larger bee populations, but also larger and more robust insect-flower interaction networks (Power and Stout, 2011). Yet, several studies have found an absence of biodiversity benefits from less intensive farming (Clough et al., 2005; Ekroos et al., 2008; Purtauf et al., 2005). These contrasting effects of farm management may be due in part to the crucial mediating role of landscape pattern in determining biodiversity and ecosystem service (Bengtsson et al., 2005).

4.3. Landscape moderated effects of farm management on bee communities

Farm management and landscape composition combined to influence on-farm native bee diversity and ecosystem service supply. Bee communities on more intensive farms in areas with little natural area are less abundant and diverse compared to areas with abundant natural areas. The capacity of natural areas within the broader landscape to buffer the negative effects of farm management may be attributed to more abundant resources or refuge from pesticide exposure. Natural areas provide greater forage and nesting opportunities, allowing for greater population sizes and more diverse species assemblages. In our system, deciduous forest coverage is a strong predictor of native bee

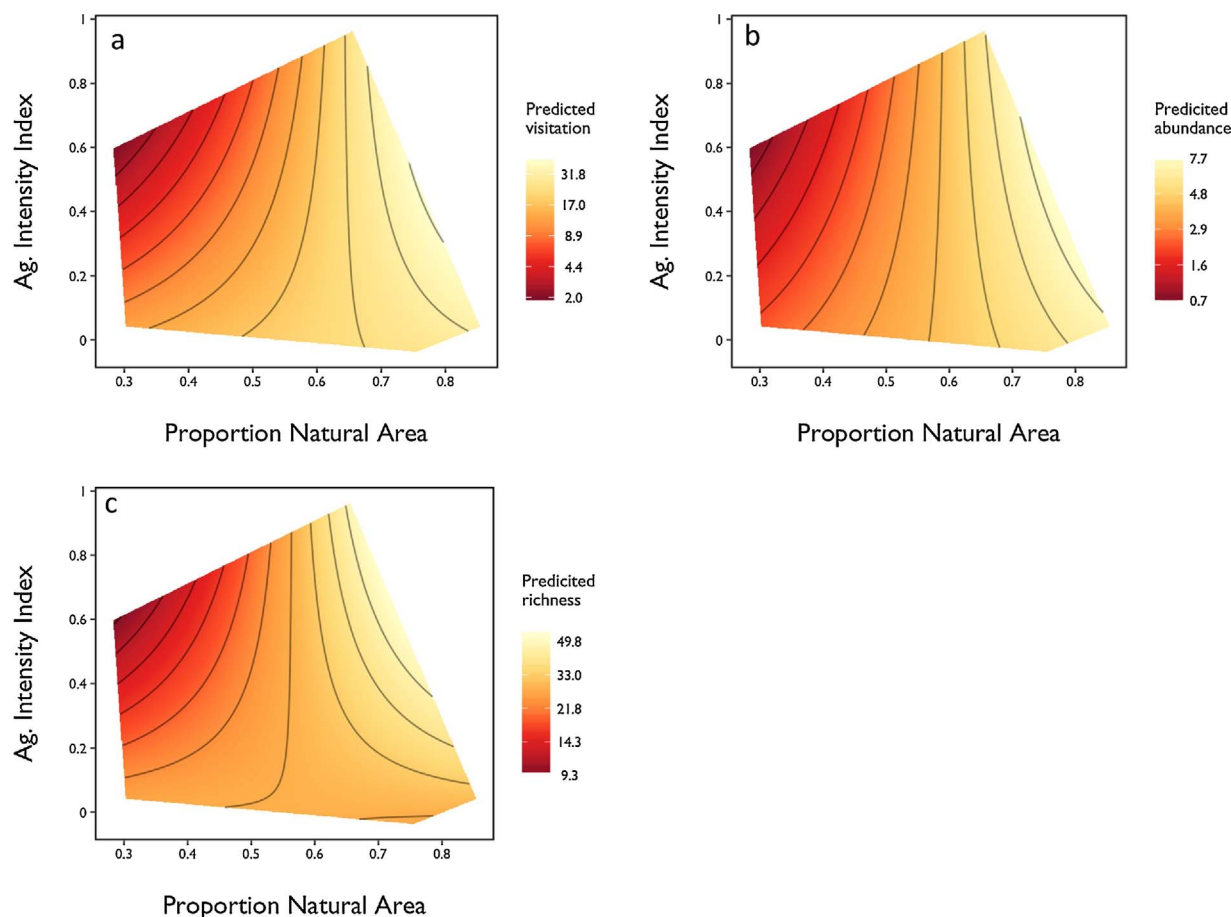


Fig. 4. Response of native bee (a) visitation, (b) abundance and (c) estimated species richness to the interaction of agricultural intensity and the amount of natural area within 2000 m of farm sites. Data are fitted values derived from final mixed effects models and log-transformed. Contour lines indicates areas of similarity. The convex hull delimits the sample space to the range of parameter combinations assessed in our study.

communities (Fig. A.5), resources found in this habitat type are important for early spring pollinators such as those that frequent blueberry (Watson et al., 2011). These same natural areas may also provide refuge from pesticide exposure, an effect of landscape pattern that has been observed for the natural enemies of agricultural pests (Landis et al., 2000).

Previous studies have shown interacting effects of farm management and landscape pattern on biodiversity of bees and other taxa (Dormann et al., 2007; Holzschuh et al., 2007; Roschewitz et al., 2005), but few studies demonstrate a similar interacting pattern for resulting ecosystem services. While theory predicts that biodiversity will be linked to ecosystem service supply (Cardinale et al., 2012), the evidence for this link is conditional on spatial scale and ecosystem service measurement approaches (Ricketts et al., 2016). We show that differences in the supply of an important agricultural ES, crop pollination, depend on the combined effect of landscape composition and farm management.

Our measure of pollination supply (i.e. bee visits flower⁻¹ time⁻¹), is used frequently (Carvalho et al., 2010; Klein et al., 2012; Nielsen et al., 2017; Winfree et al., 2008) but does not capture actual pollen deposition on stigmas or plant reproductive success. Pollinators can differ in the amount of pollen they transfer in a single visit (Cane and Schiffhauer, 2003), and sonicating taxa in particular are expected to pollinate blueberry effectively. In our case, the morphospecies group with the highest visitation rates (*Bombus* spp.) is also known to be an effective pollen vector in blueberry (Benjamin et al., 2014; Javorek et al., 2002; Scott et al., 2016) (Fig. A.4, Table A.3), reinforcing their important role in this system. Compared to other blueberry systems (Blaauw and Isaacs, 2014; Isaacs and Kirk, 2010), Vermont blueberries

are pollinated predominantly by a wild community of bees. This allows for clearer interpretation of their ecological role, but we also recognize that our findings may not hold for systems dominated by managed pollinators.

Similar research in California almond orchards has demonstrated that organic management increased pollinator visitation rate, but flower visitation was only enhanced by organic farming when orchards were surrounded by at least 10% natural habitat (Klein et al., 2012). Here we show that the negative effects of intensive management are strongest in landscapes with < 50% natural area (Fig. 4). Interestingly, as the amount of natural area increases, visitation, abundance and species richness continue to increase, despite agricultural intensity. A similar effect was observed in New York apple orchards: predicted bee abundance and richness were highest where the proportion of natural areas was greatest and pesticide use was most intense (Park et al., 2015). In landscapes with expansive natural areas, levels of organism immigration will be high (Bianchi et al., 2006; Ricketts et al., 2008) and the effects of farm management may be crowded out by increased immigration and dispersal success (Hanski, 2011; Pickett and Thompson, 1978; Tschamtko et al., 2005). A corollary of this effect, is that extensive natural areas can buffer the effect of local disturbances, including more intensive agriculture, through landscape compensation (Tschamtko et al., 2005).

Our results provide support for the intermediate landscape-complexity hypothesis (Tschamtko et al., 2012), which predicts that the effects of less intensive management will be strongest in structurally simple (1–20% natural habitat) rather than in cleared (< 1% non-crop habitat) or complex (> 30% natural habitat) agricultural landscapes. Yet, according to this categorization, our sites are predominately

situated in ‘complex’ landscapes, and the proportion of natural habitat at the 2 km scale (range: 29–86%) is high compared to other study systems: 8–60% (Winfree et al., 2008), 0–62% (Kremen et al., 2004), 1–28% (Steffan-Dewenter et al., 2002). These simple categories of landscape complexity have two limitations. First, they were derived from studies in central Europe, and may not hold for other biomes or regions. Second, they do not emphasize the analogous nature of this dynamic across a range of landscape complexity, albeit with varying magnitude in response. Intermediate landscape complexity is relative and our results provide evidence that the response of pollinator communities to landscape pattern, given differing levels of agricultural intensity, is a continuous relationship even at the upper bounds of landscape complexity.

5. Conclusion

Conservation planning requires action at multiple spatial scales. Our results suggest that management actions taken at the farm scale can be reinforced by landscape planning at broader spatial scales. In landscapes with extensive natural area, bee biodiversity and pollination service levels are high irrespective of agricultural intensity, and under these conditions preservation of natural areas is a priority. Conversely, in landscapes with less natural area, we can expect that local farm management, such as organic practices, could benefit biodiversity and ecosystem service. Our results demonstrate the ecological tradeoffs inherent when farm management is context dependent and bolster calls for cross-scale landscape design in agroecosystems (Landis, 2017). We do not quantify the realized benefit (e.g. improved yield) or costs of supporting pollinator populations in agriculture. The cost to farmers of converting to less intensive farming practices, or the opportunity costs of not intensifying, will vary depending on farm size, climate, soil characteristics and crop types. Future research should strive to integrate ecological and economic tradeoffs of landscape-dependent farm management. The challenge of ensuring food security, while simultaneously sustaining populations of service-providing organisms, will necessarily combine landscape planning and farm management.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2017.08.030>.

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