

Pollinator body size mediates the scale at which land use drives crop pollination services

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Summary

1. Ecosystem services to agriculture, such as pollination, rely on natural areas adjacent to farmland to support organisms that provide services. Native insect pollinators depend on natural or semi-natural land surrounding farms for nesting and alternative foraging resources. Despite interest in conserving pollinators through habitat restoration, the scale at which land use affects pollinators and thus crop pollination services is not well understood.

2. We measured abundance of native, wild bee pollinators and the pollination services they provided to highbush blueberry *Vaccinium corymbosum* L. crops at 16 sites that varied in the proportion of surrounding agricultural land cover at both the field scale (300-m radius) and the landscape scale (1500-m radius). We designed our study such that agricultural land cover at the field scale was uncorrelated with agricultural cover at the landscape scale across sites. We used model selection to determine which spatial scale better predicted aggregate bee abundance, abundance of large versus small bees and crop pollination services.

3. We found that, overall, bees responded more strongly to field-scale than to landscape-scale land cover, but the scale at which land cover had the strongest effect varied by bee body size. Large bees showed a negative response to increasing agricultural cover at both scales, but were most strongly affected by the landscape scale. Small bees were negatively affected by agricultural land cover but only at the field scale, while they had a small positive response to agricultural cover at the landscape scale.

4. Aggregate pollination services from native bees were more strongly influenced by field-scale agricultural cover, due to the combined effects of both large and small bees responding at that scale.

5. *Synthesis and applications.* Bee abundance and pollination services were strongly determined by field-scale agricultural cover, suggesting that field-scale set-asides may provide significant benefits to pollination services. Further, we found that pollinators respond differently to land use depending on body size, but all groups of bees benefit from decreasing agricultural cover at the field scale. Therefore, small-scale modifications to habitat can have significant impacts on both pollinator abundance and pollination services to crop plants.

Key-words: agricultural intensification, agro-ecosystems, bees, blueberry, ecosystem services, land-use change, spatial scale

Introduction

Ecosystem services are benefits that natural and semi-natural areas provide to people (Daily 1997). Ecosystem services (ES) are particularly important to agriculture, which benefits from abiotic functions such as water filtration and nutrient cycling, as well as biotic functions such

as pest control and pollination (Zhang *et al.* 2007). Biotic ES often rely on mobile organisms that move between natural habitat and agricultural fields (Kremen *et al.* 2007). Thus, fields closer to more natural habitat cover tend to receive more ES (Ricketts *et al.* 2008; Chaplin-Kramer *et al.* 2011). However, the scale at which land cover has its strongest effects on pollinator abundance and pollination function is not well understood. In the last decade, researchers have begun to separate localized, field-scale effects from large-scale landscape and regional

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effects on ecosystem service provision (Swift, Izac & van Noordwijk 2004; Thies, Roschewitz & Tschardt 2005; Werling *et al.* 2011; Kennedy *et al.* 2013). Most changes in agricultural practice that are designed to improve ES in agricultural fields, such as intercropping, organic farming and habitat restorations such as hedgerows and field margins, typically occur at the individual field scale as a result of decisions by individual farmers, rather than as a concerted effort across multiple farms at the landscape scale. These types of field-scale changes are appealing because interested farmers can implement them on their own land, but whether they are effective for restoring ES is largely unknown (but see Carvalheiro *et al.* 2011; Carvalheiro *et al.* 2012; Klein *et al.* 2012; Kennedy *et al.* 2013).

The spatial scale at which land use has its strongest effects on ecosystem services will be determined by the species-specific response of the most important (in terms of function) ecosystem service providers. Different groups of ecosystem service providers (ESPs) are likely to respond to the landscape at different scales (Peterson, Allen & Holling 1998; Kremen 2005) because body size affects the scale at which organisms perceive the landscape and use resources (Ritchie & Olff 1999). Thus, the conservation of agricultural ES will be most effective when we focus our efforts on mitigating the effects of agricultural intensification at the scale that will have the greatest positive impact on populations of ESPs, possibly by preservation or restoration of natural habitat at that scale. Most previous studies that have explored questions of body size, land use and ESP populations have compared landscapes where land use is positively correlated across scales (Steffan-Dewenter *et al.* 2002; Schmidt *et al.* 2008), which makes the relative importance of the field and landscape scales difficult to separate. Other studies have considered local management (e.g. organic vs. conventional farming methods) as a proxy for actual measurements of vegetation cover (Schmidt *et al.* 2005; Kennedy *et al.* 2013). Comparisons of response to land use at different scales based on body size have been addressed for some organisms, such as grassland birds (Concepción & Díaz 2011) and aphid–parasitoid wasp interactions (Thies, Roschewitz & Tschardt 2005), but despite the well-documented association between pollinator body size and spatial scale of foraging (Greenleaf *et al.* 2007), these comparisons have been difficult to address for pollinators (Mayer *et al.* 2011). Some recent studies (Bommarco *et al.* 2010; Jauker *et al.* 2012) have found that bee body size affects bee abundance in remnant habitat patches of different sizes, which represent <1% of total land use in the study region. However, these studies focus primarily on bees in natural habitat and not on ESPs visiting crop plants.

Agricultural land-use intensification is likely reducing crop pollination services world-wide through its negative effects on native, wild pollinator populations. Seventy-five per cent of the leading global crop plants benefit from animal-mediated pollination, primarily provided by bees

(Superfamily: Apoidea), both domesticated and wild (Klein *et al.* 2007). Although it has long been assumed that domesticated honeybees (*Apis mellifera* L.) are responsible for most crop pollination services, a recent global synthesis found that wild species account for almost half of pollinator visits to crop flowers and are associated with greater subsequent crop production than honeybees alone (Garibaldi *et al.* 2013). The loss of natural and semi-natural habitats associated with agricultural expansion reduces native bee populations, presumably through removing non-crop food and nesting resources (Winfrey *et al.* 2009); likewise, isolation from natural habitat is known to decrease pollinator visitation rate to flowering agricultural crops (Ricketts *et al.* 2008). Here, we use native, wild bees and the crop pollination services they provide as a model system to explore the relative importance of different spatial scales in determining the effect of agricultural land cover on ecosystem services provided to agriculture.

Specifically, we use the model system of pollination services delivered by wild bees to commercial highbush blueberry, *Vaccinium corymbosum* L., in New Jersey, USA, to investigate the following questions: (i) At what spatial scale does land cover most strongly affect the delivery of crop pollination services – the field scale or the landscape scale? and (ii) What is the role of bee body size in determining these spatial scale effects? In order to robustly separate the relative influence of different spatial scales, we designed our study such that land cover at the farm scale and land cover at the landscape scale were uncorrelated.

Materials and methods

STUDY SYSTEM AND STUDY DESIGN

Our study system consisted of 16 commercial high bush blueberry farms in southern New Jersey. This is an intensive blueberry production region which makes New Jersey the fourth largest producer of commercial blueberries in the United States (USDA-NASS 2011). All study sites were conventionally managed but used low-input management, defined as spraying with fungicides and insecticides fewer than six times during the growing season (from petal drop to fruit harvest). Although blueberry is partially parthenocarpic (Mackenzie 1997; Eck 1988), pollination is associated with increased fruit set and fruit weight, as well as decreased ripening time (Eck 1988; Dogterom, Winston & Mukai 2000; MacKenzie 2008; Isaacs & Kirk 2010), all of which increase the value of the crop to growers. All study fields were monoculture stands of either the 'Duke' or 'Bluecrop' variety. Both varieties are self-fertile, meaning that they do not require outcross pollen from another variety (Ehlenfeldt 2001), and they bloom near-synchronously within a year. All farms used the recommended stocking densities for honeybees of 1–3 hives acre⁻¹.

To statistically separate the importance of land cover to pollinators at each scale, we selected farms such that agricultural cover at one radius was not correlated with the other ($R^2 = 0.11$) (Fig. 1). Within each study farm, we established a single transect consisting of two 50-m sections of crop row. Transect locations

Fig. 1. Images of four farms used in our study, representing low and high percentages of agricultural cover at each scale. Inner circles represent the field scale (300 m), while outer circles represent the landscape scale (1500 m). Sites that are either high agricultural intensity or low agricultural intensity at both scales (top row) are relatively common. Our study design is novel in that we also included farms where the agricultural intensities were different at different scales (bottom row), such that across all farms in our study, agricultural cover at the field and landscape scales were uncorrelated ($R^2 = 0.11$). (All images copyright Google Inc. 2013).



were chosen to span a gradient of surrounding agricultural land cover at both 300 m (field scale) and 1500 m (landscape scale). Our field-scale radius, 300 m, represents the typical flight distance for small bees (Gathmann & Tscharrntke 2002); the landscape scale, 1500 m, represents the typical flight distance for large bees, especially bumblebees *Bombus* spp. (Greenleaf *et al.* 2007; Osborne *et al.* 2008; Concepción & Díaz 2011). Agricultural cover at 300 m ranged from 37% to 98% across sites and at 1500 m ranged from 14% to 82%. All transects were located at least 1000 m from all other transects (see Table S1, Supporting Information for further information on inter-site distance). These scales were chosen a priori; although the literature indicated that they were appropriate for our study design, we had to select our scales before site selection could be completed, without knowing which radius would be most explanatory for our region. A *post hoc* test using the means of log-abundance for large and small bees showed that for large bees, 1500 m was the most explanatory radius, while for small bees, R^2 was small across scales. (See Fig. S1, Supporting Information for details).

LAND COVER ANALYSES

The centre point of each 50-m transect was used to calculate land cover at the 300-m and 1500-m radii. Our land-cover data came from the New Jersey Department of Environmental Protection Geographic Information System (<http://www.state.nj.us/dep/gis/>) and were based on aerial photo imagery taken in 2002 at a 1-foot pixel resolution, which had been previously classified into nine land-cover classes with a one-acre minimum mapping unit. Maps of each site showing vegetation at the 300-m scale were then hand checked against more recent satellite photographs and ground observations and were corrected using ArcGIS to map vegetation

at a smaller scale with a 100-m² minimum mapping unit to check for any changes in land use since 2002. These corrections also accounted for small land-use features that may potentially benefit pollinator populations, such as weedy ditches, which were not reliably detected in the above land-cover classes. Analysis for field-scale agricultural cover was run with both the original land-cover data and with the hand-corrected maps; results were similar for both analyses. Hand-digitized local agricultural area was used for the final analysis.

We conducted land-cover analyses with respect to the proportion of agricultural land surrounding each transect. In our study region, the two dominant land-cover types are agriculture and forest, which together account for an average of 85% of the land use at all spatial scales (from 200 to 5000 m). When fallow fields and wetlands, the two other natural or semi-natural land-use types in our region, are combined with forest, the total land cover is strongly and inversely correlated at all scales (R^2 range: 0.89–0.95) (Table S2, Supporting Information). Since agriculture is the dominant human-modified landscape type in our system and it has a strong inverse correlation with natural and/or semi-natural vegetation, we used percentage agricultural cover to measure land use at each scale.

POLLINATOR ABUNDANCE

In each of the 3 years of the study (2010, 2011, 2012), each site was visited on three separate days during the bloom period, which occurred between 13 April and 15 May in all years. Within each year, data collectors were rotated among sites. To minimize variation due to weather, all data were collected between 09:30 and 17:00 h, on days that were favourable for bee activity (temperature above 14°C by 10:00 h and above 17°C by 12:00 h, clear

to partly cloudy skies). On each day, data were collected three times, in temporally stratified sampling periods. During each sample, observers walked along the transect at a standard pace for 20 min, recording identities of all insects observed visiting flowers. Bees were the majority of native wild pollinators observed. Bees were recorded to one of seven species groups: *Bombus*, *Colletes*, *Habropoda*, *Xylocopa*, large *Andrena*, medium *Andrena* and other small bees. Each of these groups comprised 1–14 species of similar size, shape, and behaviour (Table 1). All field technicians were trained to identify bees to these groups before bloom and were evaluated with post-season testing (mean error rate <2%).

After each of the three observation periods, a second 20-min transect walk was carried out and all pollinators observed visiting flowers in the transect were collected by hand net, with time stopped to allow processing of specimens. In all subsequent analyses, we combine the data for the observations of bees visiting flowers with the data on bees netted while visiting flowers as our measure of the total abundance of flower-visiting bees. All netted specimens were identified to species by Dr. John Ascher (National University of Singapore) or Dr. Jason Gibbs (Michigan State University).

Data on several covariates were collected during each site visit. Temperature and average and gusting wind speed were recorded before and after each sampling period. Relative blueberry flower

density and stage of bloom were recorded by counting the number of buds, open flowers and senescent flowers on a haphazardly selected branch on each of 10 randomly selected bushes within the transect.

ESTIMATES OF SINGLE-VISIT POLLEN DEPOSITION

The day before each site visit, we haphazardly chose 18 clusters of flowers and enclosed them with pollinator exclusion mesh bags. All open flowers on the cluster were removed before bagging to ensure that only virgin flowers remained. To measure pollen deposition in a single bee visit, a cluster was cut from the bush and presented to bees foraging on blueberry flowers in the field. Only the first flower visited by a given bee was used for analysis because subsequent flowers visited by the same bee would not be an independent measure of pollen deposition. Immediately after the insect concluded its visit to the flower, the corolla and sepals of the visited flower were marked with red ink and the following data were recorded: the species group of the insect (Table 1); the duration of the visit; and whether the insect appeared to be nectar foraging, pollen foraging or nectar robbing. Flowers were again covered with pollinator exclusion mesh and were maintained in water in the laboratory for 48 h to allow

Table 1. Pollinator species groups used in analysis. Bees were assigned to species groups on the wing during the observation portion of the protocol. Netted specimens were identified to species. Totals given for 'Observed' and 'Netted' are for the species group

Size class	Species group	Species included	Observed	Netted
Large	<i>Bombus</i>	<i>Bombus bimaculatus</i> Cresson	204	272
		<i>Bombus griseocollis</i> DeGeer		
		<i>Bombus impatiens</i> Cresson		
		<i>Bombus perplexus</i> Cresson		
	<i>Xylocopa</i>	<i>Xylocopa virginica</i> L.	200	162
		<i>Habropoda</i>	<i>Habropoda laboriosa</i> Fabricius	126
	<i>Colletes</i>	<i>Colletes inaequalis</i> Say	216	218
		<i>Colletes thoracicus</i> Smith		
		<i>Colletes validus</i> Cresson		
		Large <i>Andrena</i>		
Small	Medium <i>Andrena</i>	<i>Andrena vicina</i> Smith	277	218
		<i>Andrena banksi</i> Malloch		
		<i>Andrena barbara</i> Bouseman & Laberge		
		<i>Andrena bradeyi</i> Viereck		
		<i>Andrena carolina</i> Viereck		
		<i>Andrena cressonii</i> Robertson		
		<i>Andrena fenningeri</i> Viereck		
		<i>Andrena ilicis</i> Mitchell		
		<i>Andrena imitatrix</i> Cresson		
		<i>Andrena mandibularis</i> Robertson		
		<i>Andrena morrisonella</i> Viereck		
		<i>Andrena scrypteropsis</i>		
	Small Bees	<i>Augochlora pura</i> Say	24	41
		<i>Augochlorella aurata</i> Smith		
		<i>Ceratina calcarata</i> Robertson		
		<i>Lasioglossum acuminatum</i> McGinley		
		<i>Lasioglossum coeruleum</i> Robertson		
		<i>Lasioglossum fuscipenne</i> Smith		
		<i>Lasioglossum leucocomum</i> Lovell		
<i>Lasioglossum oblongum</i> Lovell				
<i>Lasioglossum pilosum</i> Smith				
<i>Lasioglossum versatum</i> Robertson				
<i>Lasioglossum weemsi</i> Mitchell				
<i>Lasioglossum zephyrum</i> Smith				

pollen tubes sufficient time to grow (Dogterom, Winston & Mukai 2000; Mayer *et al.* 2011). After 48 h, stigmas from the visited flower and four control flowers from the same cluster were harvested into 70% ethanol for storage.

To make microscope slides for pollen scoring, stigmas were removed from ethanol and softened for 24 h in 1 M NaOH solution, then stained for 48 h in 0.01% aniline blue solution buffered in 1 M K_3PO_4 (modified from Kearns & Inouye 1993). Pollen grains that had initiated pollen tubes, indicating pollen viability and potential contribution to fruit production, were scored at 100 \times magnification.

STATISTICAL ANALYSES

We performed three separate analyses to determine the effect of land cover on three different outcomes: overall pollinator abundance, pollinator abundance by body size and aggregate pollination services delivered by native bees. Overall, pollinator abundance was measured as the sum of the individuals observed and netted while visiting flowers, as described above. Abundance data were log-transformed prior to analysis to meet the assumption of normality of residuals. To investigate the effect of body size, pollinator species were categorized as large (intertegular span ≥ 2.25 mm) or small (intertegular span < 2.25 mm) (Table 1, Fig. S2, Supporting information). Intertegular span is a commonly used metric of bee body size because it is a strong predictor of body mass and thoracic wing musculature (Cane 1987) and is therefore correlated with average foraging distance (Greenleaf *et al.* 2007; Ricketts *et al.* 2008; Garibaldi *et al.* 2011). For comparison, honeybees have an intertegular span of $2.8 \text{ mm} \pm 0.14$ SD. Pollination services were calculated for each of our seven bee identification groups as the product of abundance on flowers \times mean pollen grains with pollen tubes per flower visit; these products were then summed for a measure of aggregate pollination function. Sensitivity analysis was performed by using the values for the 25% and 75% quantiles from the distributions of pollen tubes per flower visit, in place of the mean, and repeating the analysis.

For each of the three separate analyses, models were generated and analysed using the following parallel approach. Four candidate models, plus a null model with no fixed effects, were compared. Each model represents a different hypothesis about which scale had the greatest effect on bee abundance and included the following fixed effects: model 1: field-scale agricultural cover alone; model 2: landscape-scale agricultural cover alone; model 3: both field- and landscape-scale agriculture separately; and model 4: both field- and landscape-scale agriculture and their interaction term. All models included the random factors of farm, observer and data collection round. Fixed-effects model inputs were standardized to a mean of 0 and standard deviation of 0.5 to allow comparison of coefficients between analyses (Peterson, Allen & Holling 1998; Swift, Izac & van Noordwijk 2004; Grueber *et al.* 2011). Blueberry bloom density, average temperature and average wind speed were also analysed, but none of these covariates had a significant effect on bee abundance and were excluded from the final analysis. We then used AICc model selection to choose the best model or models for each analysis. Models were chosen that differed from the AICc of the best-fitting model by < 2 ; if more than one model was retained, we used model averaging to determine the relative importance of each fixed effect to bee abundance or pollination function. All analyses were performed in R (R Development Core Team 2011) using the lme4 package (Bates, Maechler & Bolker 2011) and the MuMIn package (Bartoń 2012).

Results

Our three-year data set includes 1217 observed and 1088 collected flower-visiting bees. Of these, 1681 were classified as large bees and 624 were classified as small bees. We collected pollen deposition data on 281 single visits to virgin flowers from seven species groups (Fig. 2). Median pollen deposition by native bees ranged from 7.0 grains (interquartile range: 0.8–15.3) per visit for small bees to 27.5 grains (interquartile range: 10.0–38.5) per visit for

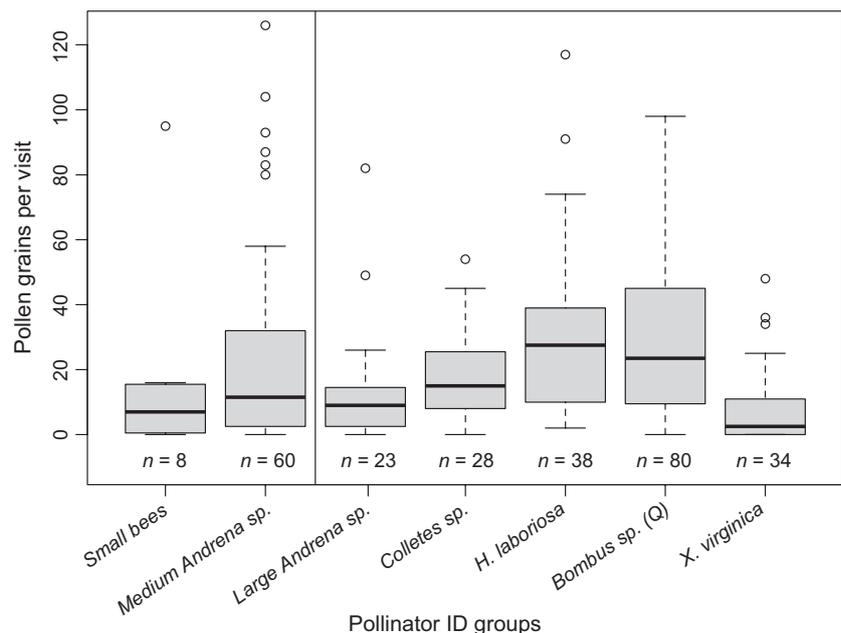


Fig. 2. Pollen deposition (pollen grains with pollen tubes per stigma) by species group. Black bars represent median value, boxes are first and third quartiles, and whiskers are 95% confidence intervals. Numbers below boxes are sample sizes. Species groups are arranged along x-axis in order of increasing intertegular distance from smallest to largest, and the vertical line divides small bees (left) from large bees (right). Seven data points above 125 pollen grains per visit are not shown for clarity but were included in all analyses.

Habropoda laboriosa Fabricius. An additional 734 control stigmas were collected; the median number of pollen grains with pollen tubes per control stigma was 0.0 (interquartile range: 0.0–1.0).

Overall, bee abundance was negatively related to increasing agricultural cover at both the local and landscape scales (Fig. 3a, b). Three models were retained for model averaging with $\Delta AICc$ s of <2 . All three models included the percentage of agricultural cover at the field (300 m) scale (hereafter, 'field ag'); two of the three retained models also included percentage agricultural cover at the landscape (1500 m) scale (hereafter, 'landscape ag') and one included the interaction term (Table 2a). The model-averaged coefficients for both field ag and landscape ag were negative (Table 3a). In all graphs in Fig. 3, the equation for the line on each graph used model-average coefficients in the following formula:

$$Y = \text{intercept} + [\text{predictor variable}] * \text{model coefficient} \\ + [\text{average value of alternate scale}] * \text{model coefficient} \\ + \text{interaction coefficient} * [\text{average value of} \\ \text{alternate scale}] * [\text{predictor variable}]$$

For example, for total bee abundance at the field scale, field scale is the predictor variable, landscape ag is the 'alternate' scale, and the equation we used was as follows:

$$Y = \text{intercept} + \text{field ag} * \text{model coefficient} \\ + \text{average landscape ag} * \text{model coefficient} \\ + \text{interaction coefficient} * \text{average landscape ag} \\ * \text{field ag}$$

This method better represents the simultaneous effects of both local and landscape agriculture on the outcome variable.

Bee response to field ag and landscape ag varied by body size. Large bees responded to agricultural cover at both the field and landscape scales, with a larger negative slope at the landscape scale (Tables 2b and 3b, Fig. 3c, d). The interaction term, retained in some models, indicates that the response to land use at one scale is dependent on land use at the other scale. For small bees, only one model was retained and it included both field ag and landscape ag, but not their interaction term (Tables 2c and 3d, Fig. 3e, f). The coefficient for landscape ag was positive, while field ag was negative. This indicates a different directional response to landscape-scale agricultural cover by small bees as compared with large bees, which responded negatively to increasing agricultural land use at both scales.

Lastly, when pollination function by all bees combined was used as the outcome, model selection retained only two models, with field ag and landscape ag as the only variables (Tables 2d and 3c, Fig. 3g, h). The model-averaged coefficients were negative for both field ag and landscape ag.

Discussion

Although it is well-established that the presence and abundance of natural habitat affects pollinator abundance and pollination function, most studies cannot rigorously distinguish the spatial scale at which land cover exerts its strongest effects because land cover tends to be positively correlated across scales (Steffan-Dewenter *et al.* 2002). In contrast, our study design allowed us to determine that bumblebees and other large bees respond to agricultural cover at a larger scale than small-bodied bees, but that blueberry flower visits from bees of all body sizes decrease strongly with increasing agricultural cover immediately around the farm field itself. We found that pollination services delivered by native pollinators to blueberry flowers were more strongly influenced by agricultural land cover at the field scale (300 m radius), although agricultural land use at the landscape scale (1500 m radius) was also important. These results for pollination services were paralleled by the results for native bee abundance, for which both the field scale and landscape scale were retained in model selection, but the stronger effect was exerted by the field scale. These strong aggregate effects emerged despite the fact that bee responses varied by body size: large bees were strongly affected by land use at the landscape scale, while both large and small bees were affected by land use at the field scale (Fig. 3).

Large bees responded strongly and negatively to increasing agricultural land cover at both scales (Fig. 3c–d). Additionally, for large bees, the interaction term of field x landscape scales was retained in several cases, suggesting that variation in large bee abundance at each scale was dependent on the extent of land use at the other scale. Sites that were on the low end for landscape agricultural cover, regardless of field-scale land use, had abundant large bees. However, for sites with highly agricultural landscapes, the field scale had a stronger effect on bee abundance. This effect may be conceptually similar to the 'hump-shaped curve' describing the effectiveness of agri-environment schemes in Tschardtke *et al.* (2005), in which the response to restoration in agricultural landscapes varies depending on intensity of land use. Interactions of this type are common: response to habitat modification at the local scale, such as changes in farming practice (from conventional to organic) or use of agri-environment management schemes, is often dependent on the greater landscape context in which the changes occur (Batáry *et al.* 2011; Kennedy *et al.* 2013). For example, bumblebee abundance in cereal fields and field margins increased with organic farming practice, but only when the site was in a homogeneous, highly agricultural landscape (Rundlöf, Nilsson & Smith 2008; Mayer *et al.* 2011; Balmford, Green & Phalan 2012). Interactions between field and landscape scales have been observed for other taxa in addition to bees, including plants, spiders, flies and birds (Kleijn & Van Langevelde 2006; Chaplin-Kramer *et al.* 2011; Concepción *et al.* 2012). However, our study differs from much of the pub-

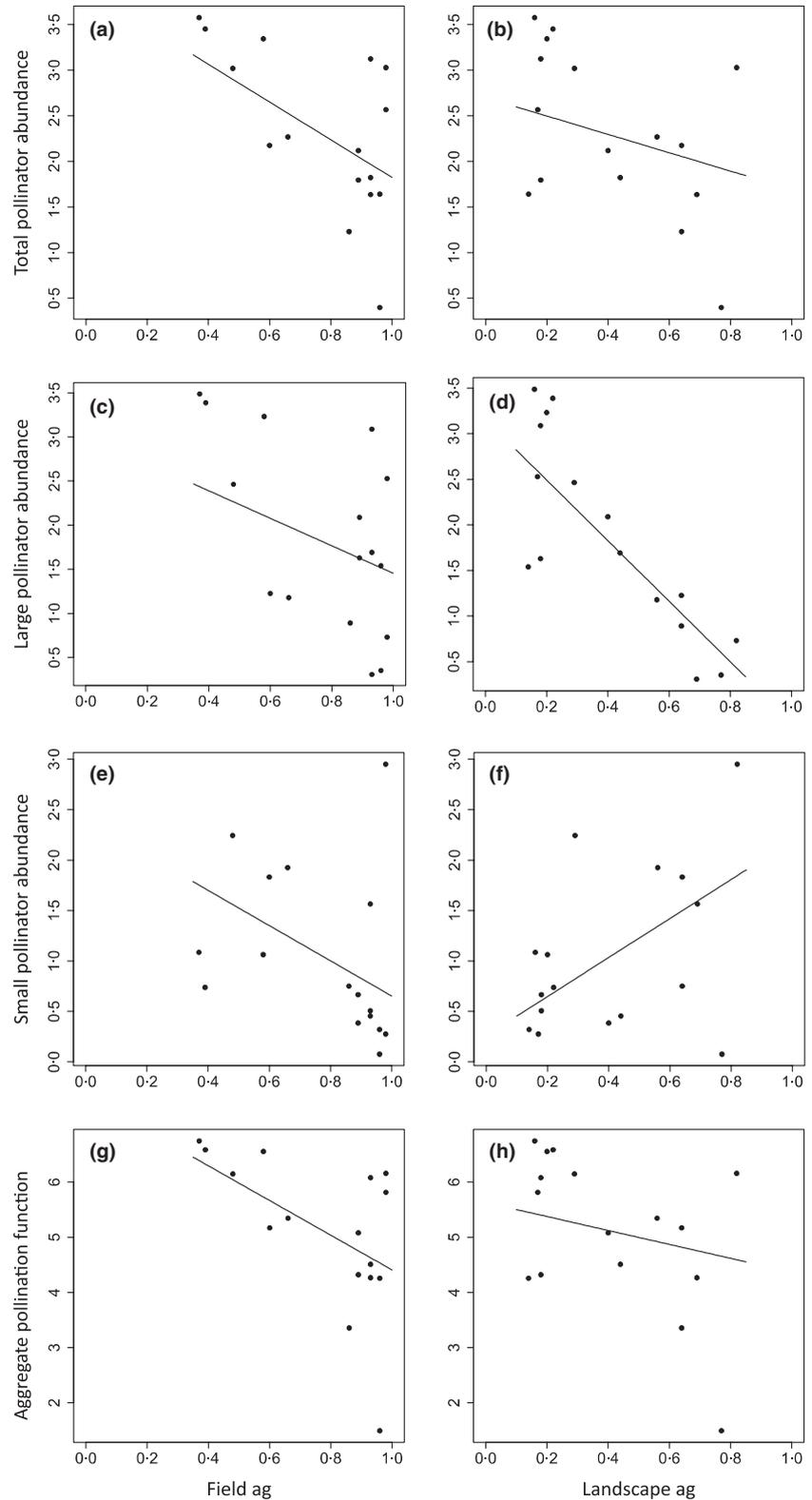


Fig. 3. The relationship between bee abundance or pollination function and field (left column) and landscape (right column) agricultural cover, for total abundance (a and b), large bee abundance (c and d), small bee abundance (e and f) and aggregate pollination function (g and h). Each data point represents the mean value across all site visits. All y-axis values are log-transformed. Lines are model-predicted values using the intercept calculated by model selection and slopes based on the two predictors (field ag, or the percentage agricultural cover at field scale (300 m), and landscape ag, the percentage agricultural cover at landscape scale (1500 m)).

lished literature; although our study system falls within the category considered ‘complex’ in previous work (only one of our sites had more than 80% agriculture at the landscape scale), we still found strong negative effects of increasing agricultural cover at the field scale. In general, habitat restorations that mitigate agricultural intensity in

complex systems are thought to be less effective than they are in simple landscapes (Batáry *et al.* 2011; Scheper *et al.* 2013).

Small bees showed weaker responses to land use, as compared with large bees. Although small bees responded negatively to agricultural land cover at the local scale,

Table 2. Model selection statistics for (a) total bee abundance, (b) large bee abundance, (c) small bee abundance, and (d) aggregate pollination function. Models in bold were used in model averaging. 'Field ag' and 'Landscape ag' are the percentage agricultural cover at 300 m and 1500 m radii, respectively; 'Interaction' is the interaction term of Field ag and Landscape ag

	d.f.	AICc	Δ AICc	Cum.Wt	Field ag	Landscape ag	Interaction
(a) Total bee abundance							
Model 3	7	345.17	0.00	0.43	+	+	
Model 1	6	346.13	0.96	0.6	+		
Model 4	8	346.31	1.15	0.93	+	+	+
Model 2	6	349.24	4.07	0.98		+	
Null model	5	351.80	6.63	1.00			
(b) Large bee abundance							
Model 3	7	322.01	0.00	0.49	+	+	
Model 4	8	322.02	0.01	0.98	+	+	+
Model 2	6	328.28	6.27	1.00		+	
Model 1	6	340.14	18.13	1.00	+		
Null model	5	344.91	22.90	1.00			
(c) Small bee abundance							
Model 3	7	320.57	0.00	0.51	+	+	
Model 4	8	322.73	2.16	0.69	+	+	+
Model 2	6	322.93	2.36	0.85		+	
Null model	5	324.05	3.48	0.94			
Model 1	6	324.77	4.19	1.00	+		
(d) Aggregate pollination function							
Model 3	7	513.29	0.00	0.42	+	+	
Model 1	6	514.18	0.89	0.70	+		
Model 4	8	515.45	2.16	0.84	+	+	+
Model 2	6	515.75	2.46	0.96		+	
Null model	5	518.23	4.95	1.00			

Table 3. Model-averaged coefficients and relative variable importance for (a) all bees, (b) large bees, and (d) aggregate pollination function, as well as (c) single-model estimates for coefficients for small bees, for which only one model was retained. All estimates are based on standardized values for the fixed-effect variable input. 'Estimate' is the model-based estimate for the coefficient for each parameter without weighting; 'Model-avg coeff' is the model-averaged coefficient, with shrinkage, for each variable. 'Rel. variable importance' is the relative importance of each parameter in the average model, calculated by summing the AICc for each model included in model averaging that includes the parameter.

	Estimate	Std. Error	z value	Pr (> z)	Model-avg coeff.	Rel. variable importance
(a) All bees						
(Intercept)	2.2894	0.1747	13.108	<2e-16 ***	2.289	
Field ag	-0.8927	0.3681	2.425	0.0153 *	-0.893	1.00
Landscape ag	-0.6672	0.3442	1.939	0.0528.	-0.478	0.72
Interaction	0.8300	0.7785	1.066	0.2863	0.214	0.26
(b) Large bees						
(Intercept)	1.8063	0.1291	13.991	<2e-16 ***	1.80631	
Field ag	-0.6724	0.2656	2.532	0.0114 *	-0.67240	1.00
Landscape ag	-1.5790	0.2554	6.183	<2e-16 ***	-1.57897	1.00
Interaction	0.8391	0.5419	1.548	0.1215	0.41826	0.5
(c) Small bees						
(Intercept)	1.0465	0.1583	6.612			
Field ag	-0.7533	0.3275	-2.300			
Landscape ag	0.9191	0.3275	2.807			
(d) Pollination function						
(Intercept)	5.1158	0.2689	19.022	<2e-16 ***	5.11581	
Field ag	-1.3569	0.5616	2.416	0.0157*	-1.35689	1.00
Landscape ag	-0.9854	0.5317	1.853	0.0638.	-0.60184	0.61

Significance codes: 0 ***0.001; ** 0.01; *0.05; '.' 0.1; ''1.

their response was positive at the landscape scale (Fig. 3e–f). This response may be an identity effect (sensu Bell *et al.* 2009). One species (*Andrena bradleyi* Viereck) in the local species pool is dominant within the small bees

group and therefore has a strong influence on the analysis. Based on netted specimens, we estimate that of the 560 small bee flower visits used in this analysis, 78% were *A. bradleyi*. This species is an oligolectic *Vaccinium* spe-

cialist with a short flight season timed to overlap with the bloom period of wild blueberry and other ericaceous shrubs native to our study region. Thus, unlike other bees that experience negative effects of increased agriculture, it is possible that *A. bradleyi* responds positively to increasing blueberry agriculture because it increases floral resources for this specialist species.

Our study is of considerable interest in applied ecology because we have demonstrated that field-scale habitat management may successfully support both small- and large-bodied pollinators in agricultural landscapes. The strong negative effect of field-scale agricultural intensity on large-bodied bees is particularly interesting, given their large foraging ranges (Greenleaf *et al.* 2007) and their importance for pollination function. The opposite result would seem more likely, given the findings by Jauker *et al.* (2012) that small bees require larger patches of natural habitat than large bees. The long distance flight capacity of large bees suggests that they could travel farther into intensive agriculture, while small bees would be trapped near the edges, but this does not seem to be the case in our study system. Further, our study is conservative in its estimate of the impact of non-agricultural land. Our analysis assumes that all non-agricultural land is suitable habitat for wild bees, but this may not be the case for all of the natural or semi-natural areas in our study region. However, despite the potential unsuitability of the forest-dominated natural landscape in our study region, the available natural vegetation was still necessary to support larger populations of bees, especially large-bodied bees. Land set-asides or agri-environment schemes that specifically target pollinator habitat needs, even if they occupy <1% of the landscape, may have greater positive effects than we have shown here, since our non-crop habitat included a wide variety of habitat types, not all of which are attractive to pollinators. Thus, increasing land set-asides with the specific motive of increasing pollinator habitat could have greater impacts than suggested here for both wild pollinators and pollinator-dependent crops.

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Data accessibility

Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.d0f3b> (Benjamin, Reilly & Winfree 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. R^2 values from regressions of mean log-abundance for large bees and small bees against agricultural cover at ten scales.

Fig. S2. Intertegular spans for bees collected on blueberry.

Table S1. Inter-site distance matrix for all sites.

Table S2. R^2 values from natural/semi-natural vegetation vs. agricultural cover at ten scales.

Figure S1. Graph of R^2 values from regressions of mean log-abundance for large bees and small bees against agricultural cover at ten scales. Each data point represents the R^2 value from one linear regression. Points in red represent the scales chosen a priori for our study design. For large bees, our chosen scale of 1500 m had the highest R^2 value of the ten scales tested. For small bees, the 300 m scale is a local maximum in a weakly bimodal distribution, but all R^2 values are relatively low.

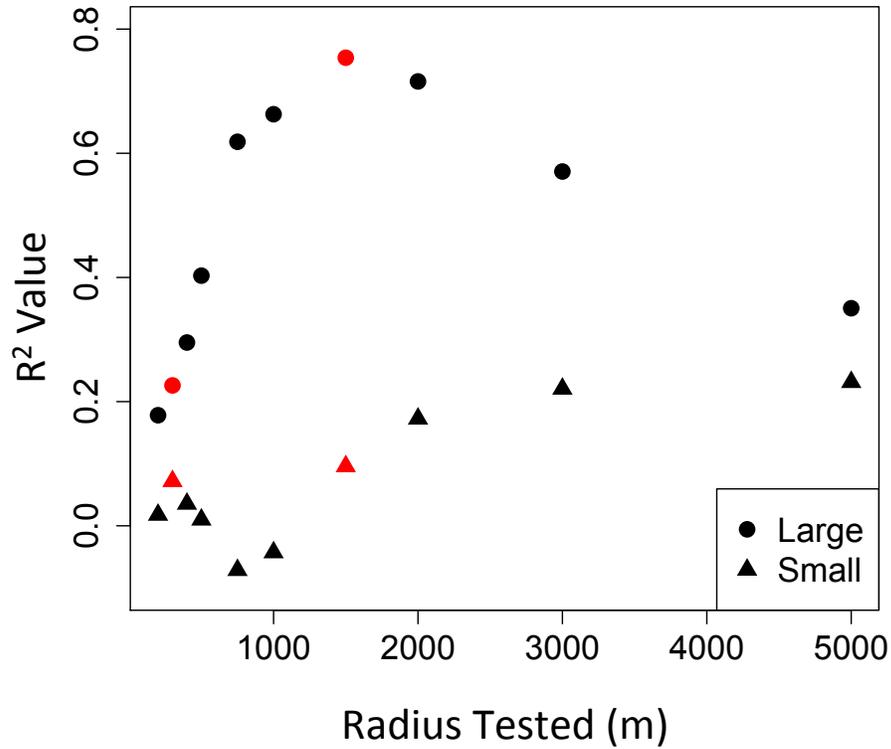


Figure S2. Histogram of intertegular (IT) spans for bees collected on blueberry showing the dividing point between small and large size classes. All bees with an IT span > 2.0 mm were grouped as “large” bees for this study, while all bees with IT span ≤ 2.0 were considered “small” bees. The red line indicates the dividing point between these two groups.

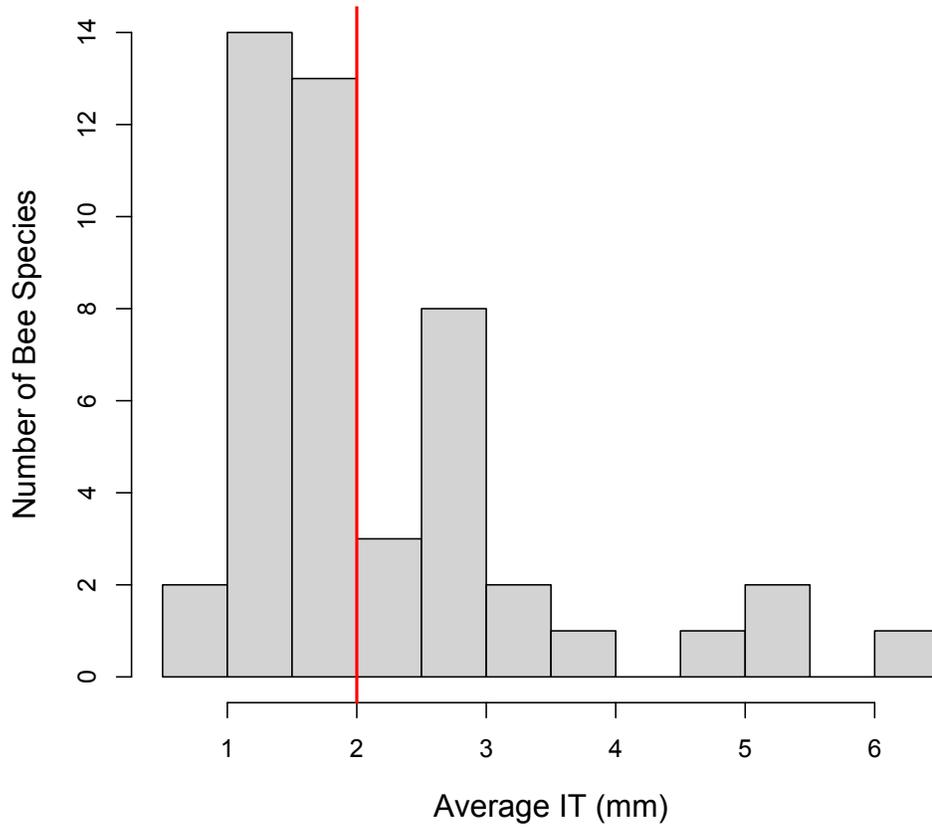


Table S2. The percent land cover of agriculture and natural/semi-natural cover at ten scales, and the Pearson’s product-moment correlation of these two land types. Natural/semi-natural cover includes forest, fallow fields, and wetlands. At all scales, agriculture and natural vegetation were inversely correlated.

Radius (m)	Percent Agricultural Land Cover	Percent Natural/Semi-natural Land Cover	Total Agriculture + Natural/Semi-natural	Correlation of Agriculture vs. Natural/Semi-Natural
200	0.79	0.18	0.97	-0.97
300	0.77	0.20	0.97	-0.98
400	0.73	0.23	0.96	-0.97
500	0.68	0.27	0.95	-0.97
750	0.60	0.34	0.93	-0.96
1000	0.53	0.38	0.91	-0.95
1500	0.42	0.47	0.89	-0.95
2000	0.36	0.52	0.88	-0.94
3000	0.27	0.60	0.87	-0.93
5000	0.18	0.68	0.86	-0.93