LETTER

A novel application of the Price equation reveals that landscape diversity promotes the response of bees to regionally rare plant species

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Abstract

Bees are ecosystem service providers that are globally threatened by losses of plant diversity. However, effects of multi-species floral displays on bees in agro-ecosystems with variable landscape context remain poorly understood, hindering pollinator conservation tactics. We addressed this knowledge gap through a novel application of the modified Price equation to evaluate responses of bees to diverse floral communities on 36 farms in Washington, USA, over 3 years. We found that floral richness, not floral identity, was the best predictor of floral visits by bees. However, the benefits of regionally rare floral species (i.e. plants found at relatively few sites) were only fully realised when farms were embedded in diverse landscapes. Our analysis used the modified Price equation to demonstrate that plant diversity, rather than specific plant species, promotes pollinator visitation, and that diverse landscapes promote the response of pollinators to regionally rare plant species.

Keywords

Bees, complementarity, composition, landscape diversity, Price equation, regionally rare species.

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INTRODUCTION

Bees provide billions of dollars in pollination services worldwide each year (Kleijn *et al.* 2015) and support reproduction of many angiosperms (Biesmeijer *et al.* 2006). Many bees, however, are threatened by losses of plant diversity, which reduces floral resources and nest sites (Goulson *et al.* 2015; Newbold *et al.* 2015). Conservation of diverse plant communities is thus a key tactic to promote bee populations (Goulson *et al.* 2015). However, it is difficult to assess the effects of multi-species floral displays on bees outside of controlled conditions (Fründ *et al.* 2013). In particular, it is often unknown whether bee conservation should focus on preserving rich plant communities or rather on promoting particular plants that support many bee species.

Specialist bees often benefit from plant communities containing particular, often rare, plant species (Fründ *et al.* 2010). Generalists, however, may not benefit from plant diversity unless synergies occur across species, such as improved nutrition with diet mixing (Waser *et al.* 1996; Ghazoul 2006). With such 'species complementarity effects', where benefits of plant diversity accrue from synergies between plants, conserving diverse plant communities may be most beneficial for bees (Hooper *et al.* 2005). However, plant diversity benefits can be confounded by 'species identity' effects when diverse communities are more likely to contain particular species that benefit many bee taxa (Hooper *et al.* 2005). In this case, conserving only plant species that benefit many bee taxa could provide the greatest benefits. These effects are difficult to assess outside of manipulative experiments, however. Studies that fail to account for complementarity and species identity effects are likely misleading (Hooper *et al.* 2005) and may hinder bee conservation because they do not define patterns of plant richness that promotes bees. The modified Price equation has been used to separate complementarity and species identity effects in field settings (Winfree *et al.* 2015), yielding practical insights for the management of bees. Using a similar approach to evaluate the benefits of plant diversity for bee pollinators might thus yield insights into effectiveness of conservation strategies that would otherwise be difficult to describe by simply relating the response of bees to metrics of plant richness.

While species complementarity and identity are often treated as dichotomous mechanisms underlying biodiversity effects (Loreau & Hector 2001), the distinction becomes less clear when considering community assembly (Zavaleta & Hulvey 2004). Species with low regional densities are often lost first from communities while common species persist. However, species depending on particularly rare habitats may thrive at sites containing that habitat but be sparse at regional scales (Mouillot *et al.* 2013). Rare species often fill unique niches that complement more common species, and the benefits of rare species may not be directly proportional to abundance or site occupancy (Zavaleta & Hulvey 2004; Mouillot

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et al. 2013). Thus, the order that species are lost can strongly influence ecosystem function. However, whether rare or vulnerable species provide critical services, or whether they are redundant with common species, is debatable (Kleijn et al. 2015; Winfree et al. 2015), and the mechanism by which these ecosystem services are provided (complementarity, species identity effects or both) remains largely unknown (Hooper et al. 2005). Moreover, the identity and function of regionally rare plant species (plants found at relatively few sites across a region) can be affected by environmental conditions and landscapes around study systems (Rabinowitz 1981; Tscharntke et al. 2005), and plants that are highly attractive to pollinators at one site may attract few at another (Bannar-Martin et al. 2018). Thus, assessing benefits of regionally common and rare plants for pollinators across sites with variable landscape contexts is critical for efficacious pollinator conservation (Kleijn et al. 2015).

Here, we use a novel application of the Price equation (Fox & Kerr 2012; Winfree et al. 2015; Bannar-Martin et al. 2018) to assess the effects of multi-species floral displays on wild bee and honey bee visitation to plants on 36 diversified production farms in Washington, USA, over 3 years. Our study tested whether complementarity between flowering plants, or the presence of particular flowering plant species, was more important for supporting bee pollinator visitation on farms, and whether trends were mediated by farming practices and landscape context. Our study demonstrates a novel application of the Price equation, showing that floral complementarity, rather than species identity, promotes bee visitation, and that diverse landscapes promote the response of bees to regionally rare plant species.

MATERIALS AND METHODS

Study sites

Our study was conducted from 2014 to 2016 on 36 farm sites in western WA, USA (Fig. 1a; Table S1). This urbanised region is typified by small, diversified farms (Kirby & Granatstein 2013). Each farm had more than five different flowering crop plants and between 0.5 and 13 ha under organic management (Fig. 1b, c). Farms were located along a landscape diversity gradient and were at least 1 km apart for spatial independence. Not all farms were surveyed each year, with 10 sampled in 2014, 35 in 2015 and 22 in 2016 (Table S1).

Floral biodiversity and pollinator surveys

We measured flowering plant species richness and abundance at sites three times per year in spring, summer and fall (67 sites × 3 = 201 site visits) (Appendix S1). Plants with flowers in anthesis were recorded in 1 h surveys of each site. Beginning 5 m from the field edge, we placed a portable 1×1 m plot in a production row and recorded all plants with open flowers. We repeated this every 5 m down the production row until reaching the row end. We then moved over 5 m and repeated this measure down the nearest production row in the opposite direction, moving in a serpentine fashion up and down rows. All transects were approximately 800 m long. We

were unable to identify ≈6% of plants, which were excluded from analyses.

Bee visitation was measured twice during site visits. To quantify the frequency of bee–plant interactions, we walked two 1 h serpentine transects starting 5 m from the field margin, stopping every 5 m for 30 s to record bee visits to the reproductive organs of each flowering plant in the field; these observations were made visually within 1 m^2 of the observer. Portable plots were not used to avoid disturbing bees, and permanent plots were not established because sites were active farms. Visits were recorded if bees made contact with sexual parts of the flower for over 0.5 s. Transects were performed from 09:00 to 11:00 and 14:00 to 16:00. Sampling was conducted on days above 10°C, with no precipitation, and minimal cloud cover. Bees were classified as honey bees (Apis mellifera L.) or wild bees (all other bees, see Table S2). This resulted in six frequency matrices, one for each bee group (honey bees or wild bees) across each of 3 years. Each cell recorded the frequency of the bee group's visits to each plant species at that site across the year.

We also measured wild bee and honey bee abundance during each site visit. In all, 15 bee bowls (5 white, 5 yellow and 5 blue) and three blue vane traps (SpringStar LLC, Washington, DC, USA) were placed evenly along a 50 m transect beginning 5 m from the edge into the interior of each site from 08:00 to 17:00 (Droege 2015). Netting was performed in two 15-min serpentine transects from 09:00 to 11:00 and 14:00 to 16:00, beginning 5 m from the field margin and along a serpentine 1 m^2 transect. If the researcher exhausted the farm area before the end of 15 min, they restarted walking the transect until 15 min elapsed. Specimens were placed in ethanol and later identified as either wild bees or honey bees.

Plants measured in our floral diversity survey could be absent from our evaluation of plant–pollinator interactions because some plants with flowers in anthesis were not observed to have floral visitors. Thus, all analysis involving plant–pollinator interactions only included plants that were observed to have floral visitors. Conversely, measures of plant richness and abundance were used to evaluate the response of bee abundance to plant populations. This analysis was performed to separate effects of plant diversity on bee behaviour from bee abundance. This has important practical implications, since plant diversity could increase the efficiency of pollinator populations by altering pollinator behaviour without increasing pollinator abundance.

Measuring landscape context and production practices

To determine the effects of landscape context on wild and honey bee visitation and abundance, we collected Cropland Data Layers (USDA-NASS 2017). From these, we extracted Simpson's diversity index for habitat classes within 1 km of each site as follows: $1 - \sum_{i=1}^{m} P_i^2$, where P_i is the proportion of the landscape occupied by habitat class i. Each habitat class was treated as a unique component of landscape diversity because each class might represent a unique niche for bees. Increasing landscape diversity was negatively correlated with urbanisation (Pearson's correlation, $t_{62} = -7.41$, $P < 0.0001$). However, we focused on landscape diversity in
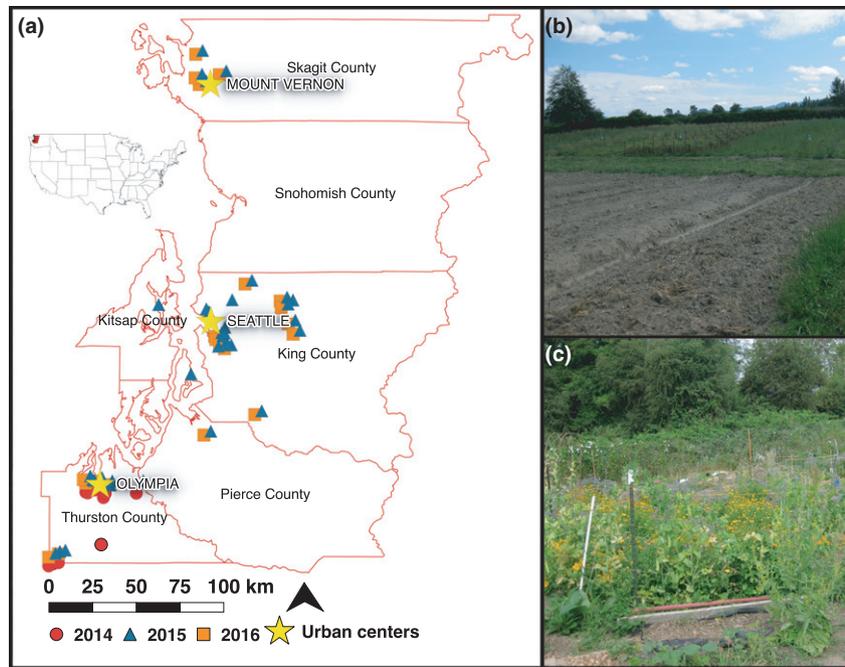
Figure 1 Farm sites in the study. (a) Farms were located across three urban areas (Olympia, Seattle and Mount Vernon), and six counties in western Washington, USA. (b) Example of reduced and (c) increased floral diversity that may cause loss or gains in bee visitation, respectively.

models as urbanisation affects bees by homogenising the landscape and reducing habitat, and thus is a largely redundant measure with landscape diversity (Winfree *et al.* 2009).

To determine the effects of agronomic variables on plant–pollinator interactions, we gathered data from site operators on certification status (certified organic or using organic practices) and the number of years each farm had used organic techniques. Farms that 'used organic practices' were not certified. However, we assumed certification status may be important because organic practices are regulated, while uncertified farms have the flexibility to use conventional products that may be more or less toxic to pollinators compared to certified organic production. Moreover, we measured the number of years each farm had used organic techniques because older farms may often have more stable plant communities.

Evaluating floral diversity effects with the modified Price equation

To measure the effects of floral richness on total bee visitation, we first used a generalised linear mixed model with a negative binomial distribution. Separate models were used to evaluate the response of each bee group (wild bees and honey bees). We used an identity, rather than log-link function, due to an improvement in model fit with the linear model (Venables & Ripley 2002). Importantly, we assumed that the relationship between adding plant diversity and gaining pollinator visitation is linear, and modelling confirmed this (Fig. 2a, b).

Next, we evaluated the relationship between floral richness and bee visitation using the modified Price equation (Fox & Kerr 2012), which uses a pairwise approach, with differences in total visitation (ΔT) from a 'baseline' to a 'comparison' site parsed into five terms:
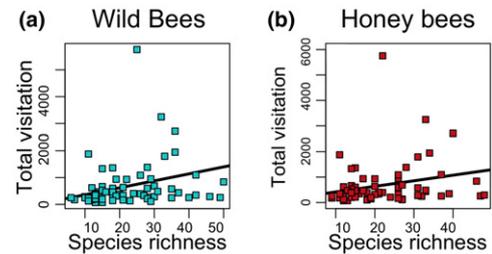

Figure 2 Effects of plant species richness (s') on total visitation (T') of wild bees (a) and honey bees (b) at comparison sites ($n = 128$). Both wild bees and honey bees were found to increase visitation in farms with more plant species, indicating the benefit of plant diversity for bee visitation on farms. Farms with mean unique richness values from 10 to 25 and species richness from 25 to 35 (see Figs S1 and S2) had high total visitation. Further analysis indicates that regionally rare plant species were more attractive to pollinators in diverse landscapes.

$$\Delta T = T' - T = \underbrace{(s_c - s)\overline{z}}_{\nu} + \underbrace{(s\prime - s_c)\overline{z'}}_{\nu'} + \underbrace{s_c(\overline{z}_c - \overline{z})}_{\theta} \\ + \underbrace{\left[-s_c(\overline{z'}_c - \overline{z'}) \right]}_{\theta\prime} + \underbrace{\left[s_c(\overline{z'}_c - \overline{z}_c) \right]}_{\kappa}, \tag{1}$$

T and T' are the total bee visitation across all plants in the community for baseline and comparison sites, and s and s' are the numbers of flowering plant species at baseline and comparison sites, respectively (Fox & Kerr 2012). The mean visitation rates averaged across all plants are represented by $\overline{z}$ and $\overline{z'}$, for the baseline and comparison sites, respectively (Fox & Kerr 2012). A critical component of the Price equation is a comparison of the average visitation for all plants

found at one site (s and s') with the average visitation to a subset of plants shared with a second site. The number of plant species shared across both sites is s_c, and the mean visitation averaged across those plant species is $\bar{z}_c$ and $\bar{z}'_c$ for the baseline and comparison sites, respectively (Fox & Kerr 2012).

The first two terms of the Price equation describe complementarity as defined by changes in ecosystem function due to species lost from the baseline site compared to the comparison site (v) and species gained due to new species found at the comparison site (v') (Fox & Kerr 2012). These terms represent the negative (v) or positive (v') product of the number of species unique to one site, multiplied by the mean visitation at the site (eqn 1). The magnitude of these terms is maximised when large numbers of plant species are unique to each site and high visitation rates occur at each site. We infer that complementarity (niche partitioning and/or facilitation) is an important biodiversity ecosystem function driver if differences in function are largely explained by differences in species richness, independently of per-species function. Other processes such as non-linear increases in visitation with increases in plant species could produce a similar pattern (Pillai & Gouhier 2019), but we found no evidence of such nonlinearities (Fig. 2).

Two additional terms describe changes in species-specific visitation rates associated with species lost from the baseline (θ) or gained at the comparison (θ') sites. These terms are the positive (θ) or negative (θ') product of the number of species shared between the two sites, and difference in visitation rates averaged across the entire community and across just the shared species (eqn 1). These terms incorporate the identity of species being compared and relate to species identity effects (Fox & Kerr 2012). The magnitude of these terms is greatest when the sites share a large number of species (large s_c) and the visitation rates for these shared species are high relative to other plant species in each site. We infer that species identity effects (defined as variation in visitation simply due to the presence or absence of particular plant species) are an important biodiversity ecosystem function driver if differences in function are largely explained by losing (or gaining) disproportionally high- (or low-) functioning species. We acknowledge that complementarity effects can depend on the identity of species in the community and thus assessed the effects of landscape characteristics on complementarity, including effects that may be mediated by community composition.

In addition to community compositional effects on visitation, visitation rates can depend directly on the environmental conditions, and here site-specific visitation rates are estimated by comparing visitation rates across the shared species at both sites in the context-dependent effect (κ) term (Fox & Kerr 2012). This focus on shared species holds community composition constant in an attempt to focus solely on the site-specific variation in visitation.

Evaluating Price equation components

Since the Price equation is a pairwise analysis, we needed to select a baseline site to compare each site to. We selected the six farms with the most visitation from each bee group in each year as baseline sites (two bee groups × 3 years) and 128 other sites (67 sites × 2 bee groups – 6 baseline sites) as comparison sites (denoted by primes in eqn 1) (as in Winfree *et al.* 2015). We then standardised across all terms (v, v', θ, θ', κ) for every pairwise combination. Standardisation was performed by scaling the values for each term in eqn 1 by dividing it by the absolute value of the most extreme value across all terms for the particular site combination, year and bee group, resulting in values that ranged from −1 to 1 (Winfree *et al.* 2015). Standardisation made each term's relative strength comparable among pairs of sites with different total pollinator visitation.

Selecting a single baseline site constrains inference to comparisons with a single site for each year and bee group, which is useful for assessing context dependency of terms describing effects of species loss on the comparison sites (v', θ'). However, evaluations of the effects of species gain on the baseline sites (v, θ) put undue emphasis on a single baseline and may bias the results. To remove this bias, we performed an additional analysis using pairwise comparisons across all sites for each bee group. We then standardised each term as described previously. For each pairwise comparison, we selected the site with the higher visitation rate as the 'baseline' and the other site as the comparison to parallel previous studies using a single baseline (Winfree *et al.* 2015). For comparison, we present both the evaluation of each term with a single baseline for each year and bee group as well as the summary of all pairwise comparisons.

Evaluating the benefits of regionally rare flowering plants for bees

Terms attributed to complementarity, v and v', are linearly correlated with the number of species lost or gained in the comparison, or the number of species unique to that site. To better understand how these terms reflected our data set, we calculated the mean number of unique species for a given site as compared to each other site: $\frac{1}{n-1}\sum_{i \neq j}\left(s_i - s_j\right)$, where s_i and s_j represent plant richness at site i and j, respectively. We evaluated the relationship between the average number of unique species on a particular site to visitation at that site using a general linear model with a negative binomial error distribution and an identity link function. We then evaluated separate models for each bee group (honey bees and wild bees) using the MASS package in R (Venables & Ripley 2002). This averaging across all sites to characterise a site by the mean number of unique species ignores species identity and does not allow estimation of identity effects. Nonetheless, it allows a graphical representation of the relationship between regionally rare plants and bee visitation, providing context to the complementarity terms in the Price equation. Previous studies refer to species that are unique to a few sites as regionally rare (Mouillot *et al.*, 2013). This differs from local rarity which refers to low densities within a site, whereas regional rarity refers to species found at relatively few sites across a broad region.

Evaluating context dependency in complementarity using the Price equation

Local and landscape factors can mediate biodiversity effects on ecosystems, and variation in the Price equation terms allow for evaluation of these effects (Fox & Kerr 2012). We assessed

whether landscape and agronomic factors affected the Price equation terms using general linear mixed effect models in R (Bates *et al.* 2015). Models were based on a general structure:

$$\text{Estimate} = \beta_0 + \beta_1 X_1 + \ldots + B_N X_N,$$

where 'Estimate' is the value of the Price equation term being modelled, X_i are covariates, B_i are partial regression coefficients for each covariate and B_0 is the intercept. Each model included farm as a random effect. Model stability was improved by standardising continuous fixed effects using a scale function (R Core Team 2017) that calculated the mean and standard deviation of the entire vector for the effect and subtracted each element of the effect by the mean and then divided by the standard deviation. We focused on the characteristics of each site and their effect on visitation at comparison sites relative to a baseline. The ν and θ terms are each a product of the mean visitation at the baseline site (only for shared species for θ), and the number of unique (ν) or shared species (θ). Therefore, they do not depend on visitation at comparison sites, and variation in these terms across the data set only depends on the differences in species composition between the baseline and comparison site. Because we were interested in variations in complementarity, rather than species composition across different landscape characteristics, the ν and θ terms were not included in our context dependency analyses.

Our model set included four variables: (1) bee group (wild or honey bee), (2) landscape diversity, (3) organic status (certified or not) and (4) time in organic production, and all two-way interactions (Table S3). Our model set was balanced, so each covariate appeared in the same number of models. We ranked models based on AIC$_c$, and identified top models based on a criteria of $\Delta \text{AIC}_c < 2.0$ from the best model (Kennedy *et al.* 2013). We also calculated Akaike weights (ω) and model-averaged partial regression coefficients for each covariate based on the 95% confidence set (Burnham & Anderson 2002), with 1 being the most important (present in all models with weight) and 0 the least. We considered covariates as important drivers of the Price terms if they appeared in top models ($\Delta \text{AIC}_c < 2$), had a high weight ($\omega \geq 0.6$) and unconditional 95% confidence interval did not overlap zero (Kennedy *et al.* 2013). All analyses were performed in R (R Core Team 2017) with packages 'MASS' (Venables & Ripley 2002), 'LME4' (Bates *et al.* 2015) and 'MuMIn' (Bartoń 2018).

Independent of the modified Price equation, we assessed the response of bee abundance to Simpson's farm diversity (plant diversity on farms), bee group (wild or honey bee) and the interaction between the variables. This isolated whether floral diversity effects on bee visitation (the modified Price equation terms) might be confounded by differences in bee abundance across farms with varying floral diversity; greater visitation to plants might be expected if bees are more abundant at particular sites due to greater floral diversity on farms.

RESULTS

Effects of plant richness and unique species on bee visitation

From 201 site visits, we recorded 134 658 flowering plants from 192 species and 23 720 bee visits to flowers, capturing 2798 honey bees and 4167 wild bees. Bee visitation increased in more plant-rich communities (Fig. 2). This response was similar for wild (Estimate = 25.99; SE = 7.46; Z = 3.48; P < 0.001) and honey bees (Estimate = 21.99; SE = 8.56; Z = 2.57; P = 0.010). Visitation did not increase by wild or honey bees when more regionally rare plant species were present (Fig. S1). However, some sites with moderate numbers of regionally rare plant species and floral richness had high visitation (Figs S1 and S2), indicating that bee visits to regionally rare plant species may depend on local-level production practices and the diversity of landscape-level resources.

Effects of floral complementarity and composition on bee visitation rates

The loss of floral complementarity (ν) reduced visitation rates for wild and honey bees, while gains in floral complementarity (ν′) increased visitation rates (Fig. 3a). However, the loss or gain of particular plant species (θ and θ′), and context-dependent effects (κ), had little effect on visitation rates for wild or honey bees (Fig. 3a). Regionally rare plant species, as measured by ν′, promoted visitation by wild and honey bees, while benefits of regionally common plant species, as measured by θ′, were limited. Using a single site as a baseline (Fig. 3a) can potentially limit insights from the Price equation, and we thus used a pairwise approach (Fig. 3b) to calculate each Price equation term for each site pair across our study network. This approach underscored the benefits of regionally rare plant species for pollinator visitation due to the high positive value for ν′.

Covariance with local and landscape factors and independence from abundance

Increasing landscape diversity strengthened benefits of ν′ (ω = 0.54; Tables 1 and 2), suggesting regionally rare plant species increased visitation on farms in more diverse landscapes. Wild bees benefited similarly to honey bees from gains in floral complementarity (Fig. 3c; Tables 1 and 2), indicating that regionally rare plant species may be beneficial to both wild bee and honey bees. The agronomic factors we assessed moderately influenced ν′ (ω = 0.45; Tables 1 and 2), suggesting bees respond more strongly to regionally rare plant species on certified organic farms than uncertified farms (Tables 1 and 2). No factors we assessed affected θ′ (Tables S4 and S5), indicating that benefits of regionally common plant species for bees were not dependent upon landscape context or farming practices. Wild bees and honey bees had similar abundance that was not affected by floral diversity (Table S6), suggesting that responses of bee visitation to floral diversity were behaviourally mediated and not due to a correlation between bee abundance and bee visitation rates.

DISCUSSION

Farming systems with high floral diversity often promote the abundance and diversity of pollinator communities (Kennedy *et al.* 2013; Shackelford *et al.* 2013). However, it is difficult to assess the benefits of multi-species floral displays for bees outside of controlled environments (Fründ *et al.* 2013), hindering
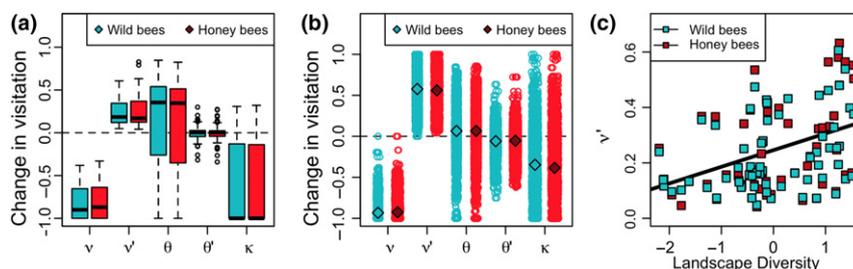
Figure 3 Mechanisms mediating the plant diversity–bee visitation relationship. (a, b) Change in bee visits due to complementarity (ν, ν′) identity (θ, θ′) and context-dependent (κ) effects. Using a single site as a baseline (a) can potentially limit the insight gained from the Price equation. Therefore, we use a pairwise approach, calculating each Price equation terms for each site pair within our study network (b). This pairwise approach (b) further underscores the benefits of regionally rare plant species for pollinator visitation as seen by the strong positive value for ν′. The values for the Price equation terms have been rescaled by the largest value in each set of comparison sites. (c) Effects of landscape diversity on strengthening the positive effects of gains in floral complementarity (ν′) and promoting bee interactions with regionally rare species. Panel shows the best-fit regression line based on model-averaged terms (Tables 1 and 2).

development of conservation practices that promote pollinators (Kleijn *et al.* 2015). We showed that while restoring key plant species may promote pollinators, increases in plant richness *per se* may prove most beneficial for enhancing managed and wild bee visitation on farms, with consistent benefits of diversity for both wild and honey bees. In contrast, sites with moderate numbers of regionally rare plant species were quite variable in their visitation rates, suggesting that effects of conserving these rare species depended on environmental context. Evaluation of the modified Price equation helped explain this context dependency and separated context dependency in complementarity from identity effects.

Application of the Price equation suggested that regionally rare plant species provide complementary benefits to pollinator communities, which exhibited greater visitation rates on farms with greater floral diversity. These results suggest that increased floral diversity decreased niche overlap and competition for floral resources, leading to greater bee visitation and more complete use of floral resources. Facilitation (collective attraction) may have also contributed to our results (Hooper *et al.* 2005; Ghazoul 2006), as co-flowering plant species may be mutually beneficial when more diverse floral displays attract more pollinators (Ghazoul 2006). This means more florally diverse farms should receive more visitation, with the same number of bees, than less diverse farms. This implies that farmers who manage honey bee colonies, or use practices to conserve wild bees, may receive greater pollination by also promoting floral diversity.

Floral diversity benefitted wild bees and honey bees similarly, although potentially not via the same mechanism. Honey bees may benefit from increased floral diversity through increased nutritional availability across space and time (Girard *et al.* 2012; Donkersley *et al.* 2014). While wild bees may benefit from such factors, increased floral diversity could promote wild bees that have co-evolved mutualisms with particular plants (May 1982). Increasing floral diversity may thus promote greater niche partitioning, and reduced competition among bees, including between generalists and specialists. For example, squash bees (*Peponapis pruinose*) are co-evolved with squash plants, and likely benefit from diversity only when squash is grown (López-Uribe *et al.* 2016). However, many other species of bees visit squash, including

Table 1 Model-averaged partial regression coefficients (β), unconditional 95% CIs, Z-statistics and P values from models of ν′ in relation to bee, landscape and agronomic variables (see Table S3)

Covariate	ω	β	95% CI	Z	P
Group	0.01	−0.031	−0.083 to 0.019	1.23	0.21
Landscape	**0.54**	**0.057**	**0.024 to 0.091**	**3.38**	**0.00072**
Time	< 0.01	−0.014	−0.053 to 0.025	0.69	0.48
Status	**0.45**	**−0.11**	**−0.18 to −0.037**	**2.98**	**0.0028**
Group × landscape	< 0.01	−0.024	−0.072 to 0.023	1.01	0.31
Group × time	< 0.01	−0.0012	−0.049 to 0.046	0.05	0.95
Group × status	< 0.01	0.049	−0.045 to 0.14	1.02	0.31
Landscape × time	< 0.01	0.0096	−0.028 to 0.047	0.51	0.61
Landscape × status	< 0.01	−0.043	−0.12 to 0.031	1.13	0.25

Akaike weights (ω) indicate relative importance of each covariate based on summing weights across models where the covariate occurs. Coefficients are in bold if CIs do not include 0 or if ω ≥ 0.6. Variables are described in Table S3.

Table 2 AIC$_c$ and ΔAIC$_c$ values for models assessing ν′ in relation to bee, landscape, and agronomic variables (see Table S3)

Model	Factor(s)	AIC$_c$	ΔAIC$_c$
2	**Landscape**	**−105.6**	**0**
4	**Status**	**−105.2**	**0.4**
1	Group	−97.6	8.0
9	Landscape × status	−96.3	9.3
3	Time	−96.2	9.4
7	Group × status	−93.6	12
5	Group × landscape	−92.6	13
10	Time × status	−91.1	14.5
8	Landscape × time	−89.2	16.4
6	Group × time	−82.1	23.5

Models with a ΔAIC$_c$ < 2.0 are bolded.

honey bees. Promoting floral diversity and conserving vulnerable species may thus reduce niche overlap and competition for particular plant species, leading to visitation of other plants in the community.

Our results show farms in diverse landscapes benefitted more from conserving regionally rare plant species than previously realised (Tscharntke *et al.* 2005; Kennedy *et al.* 2013). Price equation terms associated with complementarity (ν and ν′) were each linearly correlated with regionally rare plant

species at the baseline (v) or comparison (v′) sites, suggesting they were affected by species gains. As in our more simplified evaluation of the importance of regionally rare species on bee visitation, the v′ term describing complementarity at the comparison site was quite variable across sites. By evaluating the drivers of this variation, we demonstrated that landscape diversity enhances the response of bees to regionally rare plant species. In contrast, landscape diversity had little effect on θ′, the term associated with species identity effects at the comparison sites. In theory, agri-environment schemes are generally thought to have limited benefits in particularly diverse landscapes, where spillover of pollinators from the surrounding landscape mitigates effects of local species loss on ecosystem function (Tscharntke *et al.* 2005). In contrast, sites embedded in landscapes with lower levels of diversity may be more influenced by changes in biodiversity (Tscharntke *et al.* 2005). Because this negative relationship between landscape diversity and local biodiversity benefits on ecosystem function relies on spillover effects, it most likely occurs where landscape diversity is relatively high, such that habitats are great enough to drive spillover (Fig. 4). In contrast, along the urbanisation gradient we studied we found a positive relationship between landscape diversity and benefits from local plant richness. Sites embedded in landscapes with relatively low diversity received the fewest benefits from changes in local diversity, presumably because improvements in ecosystem services were constrained at the landscape level by factors such as habitat availability outside farms. It was only when these landscape-level constraints are relieved at higher levels of landscape diversity that ecosystem function can benefit from local biodiversity. We propose a convex relationship may exist between landscape diversity and the benefits of local diversity on ecosystem function (Fig. 4), whereby low levels of landscape diversity may override changes in local biodiversity by constraining improvements in ecosystem function, whereas high levels of landscape diversity may induce spillover effects that mitigate local species loss. These results indicate that farms may have the greatest incentive to promote plant diversity to enhance pollination services when landscape diversity is not low enough to constrain ecosystem function or high enough to overcome local changes in diversity.

Using our results, farmers and policy-makers may be better equipped to assess conservation tactics for wild and managed bees (Potts *et al.* 2010; Goulson *et al.* 2015; Kleijn *et al.* 2015). For example, farmers in diverse landscapes who conserve regionally rare plant species should enhance bee visitation, while those that use a single 'pollinator plant' species may fail to realise such gains. Increasing landscape diversity may also be more important than adopting sustainable farming practices in promoting floral visitation. This is likely due to strong pollinator limitations imposed by lack of habitat, rather than weak effects of management. Indeed, management practices on farms that are not certified organic could be detrimental to bees (Kennedy *et al.* 2013). As wild bees and honey bees benefitted equally from regionally rare plant species, conserving such species will likely enhance both wild and honey bee visitation on farms.

Globally, decreased plant diversity is a threat to food production and the maintenance of healthy pollinator
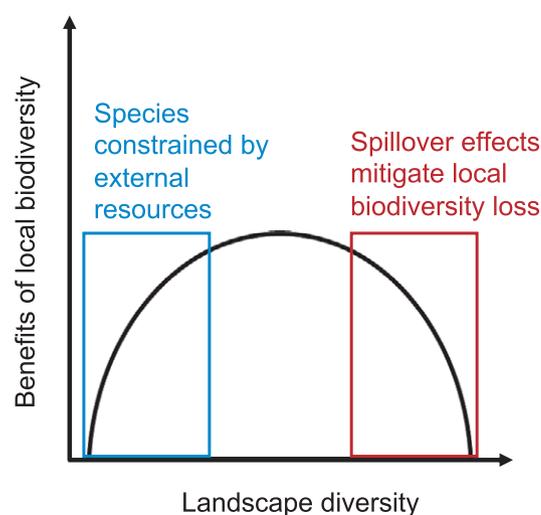

Figure 4 Proposed convex relationship between landscape diversity and local biodiversity benefits for ecosystem function. Previous research (e.g. Tscharntke et al. 2005) identified a negative relationship between landscape diversity and the benefits of local plant biodiversity where biodiversity is great enough at the landscape scale to induce spillover effects which mitigate biodiversity loss. In the figure, this part of the relationship is highlighted in red. In contrast, the current study observed a positive relationship between landscape diversity and the benefits of local plant diversity on pollinator visitation. This is likely due to other limiting factors such as habitat availability in the area surrounding farms that limits the ability of pollinators to respond to local plant diversity in areas with low landscape diversity. This portion of the curve is highlighted in blue.

communities (Biesmeijer *et al.* 2006; Potts *et al.* 2010; Goulson *et al.* 2015). Both conservation biologists and farmers have a need for more comprehensive conservation efforts. Our results indicate that complementary use of diverse floral resources by bees (niche partitioning or facilitation) is the strongest contributor to plant–pollinator interactions in farming systems (Hooper *et al.* 2005). Future pollinator conservation programmes and pollinator policy should thus focus on increasing floral richness and conserving rare plant species to promote visitation from wild and honey bees. More broadly, landscape diversity appears to mediate the benefits of plant species gains for bees (Winfree *et al.* 2009; Kennedy *et al.* 2013; Koh *et al.* 2016), underscoring the need to consider landscape-level factors when developing and deploying pollinator conservation strategies.

AUTHORSHIP

EB and DC conceived the study. EB and TN performed the analyses. All authors wrote and edited the manuscript.

DATA AVAILABILITY STATEMENT

Data associate with the manuscript are deposited in the Figshare Repository: https://doi.org/10.6084/m9.figshare.9902378.

CONFLICT OF INTERESTS

None declared.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.