

LETTER

Response diversity to land use occurs but does not consistently stabilise ecosystem services provided by native pollinators

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Abstract

More diverse biological communities may provide ecosystem services that are less variable over space or time. However, the mechanisms underlying this relationship are rarely investigated empirically in real-world ecosystems. Here, we investigate how a potentially important stabilising mechanism, response diversity, the differential response to environmental change among species, stabilises pollination services against land-use change. We measured crop pollination services provided by native bees across land-use gradients in three crop systems. We found that bee species responded differentially to increasing agricultural land cover in all three systems, demonstrating that response diversity occurs. Similarly, we found response diversity in pollination services in two of the systems. However, there was no evidence that response diversity, in general, stabilised ecosystem services. Our results suggest that either response diversity is not the primary stabilising mechanism in our system, or that new measures of response diversity are needed that better capture the stabilising effects it provides.

Keywords

Bees, biodiversity, crop pollination, ecosystem function, land-use change, pollination, stabilising mechanisms.

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INTRODUCTION

Concerns over declines in biological diversity and a growing recognition of the importance of ecosystem services for human well-being have generated a large body of work exploring the relationship between biodiversity and ecosystem services (Hooper *et al.* 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2012). Biodiversity may influence ecosystem services in two ways. First, higher diversity generally leads to an increase in the overall quantity of the service being provided (Balvanera *et al.* 2006). Second, increased biodiversity can stabilise services by reducing the variance across space and/or time (Tilman 1999; Yachi & Loreau 1999). The positive relationship between diversity and stability has been found across a number of ecosystem services including biomass production (Tilman *et al.* 2006; Isbell *et al.* 2009), parasitism (Vedder *et al.* 2010), and pollination (Klein *et al.* 2003; Garibaldi *et al.* 2011), and across multiple levels of ecosystem organisation (Proulx *et al.* 2010).

A number of mechanisms have been proposed to explain the observed positive relationship between diversity and the stability of ecosystem services, including density compensation (Solan *et al.* 2004), cross-scale resilience (Holling 1992) and portfolio effects (Lehman & Tilman 2000). In this study, we focus on a stabilising mechanism termed response diversity, which occurs when multiple species contributing to the same service exhibit differential responses to the same environmental perturbation (Walker *et al.* 1999; Elmqvist *et al.* 2003). Such differential responses have been proposed to stabilise the aggregate ecosystem service against environmental change (McNaughton 1977; Walker *et al.* 1999; Leary &

Petchey 2009; Winfree & Kremen 2009; Laliberté *et al.* 2010; Romanuk *et al.* 2010). In particular, if some species increase in abundance with a disturbance while others decrease, the aggregate ecosystem service could be buffered against the disturbance.

One limitation of biodiversity–ecosystem service research to date is that most studies have been conducted in small-scale and highly controlled communities that may have little relevance to real-world ecosystems (Kremen 2005; Srivastava & Vellend 2005). Those studies that do investigate real-world systems have used the abundance or biomass of the organisms providing the service as a proxy for ecosystem service, rather than measuring the service itself (Winfree & Kremen 2009; Laliberté *et al.* 2010; Karp *et al.* 2011). However, the abundance of organisms does not necessarily translate into ecosystem services, because species can vary widely in their per-individual contribution to the service (Larsen *et al.* 2005; Peltzer *et al.* 2009). To fully understand the importance of response diversity in stabilising ecosystem services, it is important to measure the service provided by each species within natural communities (Luck *et al.* 2009).

While it has been suggested that response diversity could be critical to stabilising real-world ecosystem services against global environmental change (Elmqvist *et al.* 2003), empirical studies that could confirm or refute this expectation are scarce. Among the few studies that have assessed response diversity, methodologies vary widely and include simply noting differing responses among species (Elmqvist *et al.* 2003; Sanford *et al.* 2009), explicitly testing for differences among species in their response to disturbance (Leary & Petchey 2009; Winfree & Kremen 2009; Karp *et al.* 2011), and

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measuring within-group dispersion of pre-assigned response traits (Laliberté *et al.* 2010). More importantly, to our knowledge no study has explicitly examined whether response diversity actually stabilises ecosystem services (Mori *et al.* 2013).

Here, we use crop pollination by native, wild bees to investigate whether response diversity stabilises ecosystem services against land-use change in real-world landscapes. We focus on conversion of natural habitat to agriculture as our environmental perturbation because it is the leading cause of biodiversity loss worldwide (Pereira *et al.* 2010). As we do not have multi-decadal data on how changes in agriculture intensity influence pollinators and pollination services, we use space-for-time substitution and measure both outcomes across a contemporary land-use gradient. We focus on crop pollination as an ecosystem service because 75% of the leading global food crop species are pollinated by animals (Klein *et al.* 2007), with native pollinators making a substantial contribution (Garibaldi *et al.* 2013). We used three landscape-scale data sets on native bee pollination of three crops – highbush blueberry *Vaccinium corymbosum* L., cranberry *Vaccinium macrocarpon* Aiton and watermelon *Citrullus lanatus* (Thunb.) Matsum. & Nakai – to answer the following questions: (1) Does response diversity occur, in terms of both pollinator abundance and pollination services? and (2) Does response diversity lead to stability of ecosystem services? Here, we define stability as the ability of the community of ecosystem service providers to maintain consistent services in the event of a permanent disturbance (Ives & Carpenter 2007). We found significant response diversity to agricultural land use in all three study systems in terms the abundance of the different bee species, and in two systems we found significant response diversity of pollination services. However, we found that response diversity did not, in a general sense, lead to stability of pollination services.

METHODS AND MATERIALS

Study species and systems

The study sites for two of our systems, blueberry and cranberry, were located on farms within a 35 × 55 km area in southern New Jersey, USA. The primary native land cover in this region is temperate forest dominated by pitch pine (*Pinus rigida* Mill.), various oak species (*Quercus* spp.) and an understory of ericaceous shrubs. Within this system, the two crop plants shared similar study designs in that 16 study sites were arrayed along a land-cover gradient with regard to the proportion of surrounding land cover devoted to agricultural production (proportion agricultural land cover within a 1.5 km radius, blueberry 14–82%; cranberry 5–48%). All sites were separated by a minimum of 1.0 km (range, blueberry: 1.0–38.0 km; cranberry 1.0–32.0 km) to ensure sampling of independent bee communities across sites. We minimised intersite variation in insecticide use, which can affect native bee communities (Tuell & Isaacs 2010) by selecting sites that practice conventional agricultural management but have low pesticide inputs due to carefully managed Integrated Pest Management (IPM) programmes.

Our third crop plant, watermelon, was studied on farms within a 38 × 48 km area of the Central Valley region of California, USA. The native land cover in this part of California is a mosaic of mixed-oak savannah, chaparral and remnant riparian grassland. The 12 watermelon sites were arrayed along a gradient of land cover with respect to surrounding area in agricultural production (within a

1.5 km radius, 11–99% agriculture). All watermelon sites were separated by a minimum of 1 km (range, 1.1–41.5 km). To standardise the effect of farm management and pesticide use, all watermelon sites were managed using organic techniques.

Our three focal study plants all require animal-mediated (primarily bee) pollination for the production of marketable fruits (Mackenzie 1997; Cane & Schiffhauer 2003; Brown & McNeil 2006; Klein *et al.* 2007). Our focal pollinators were the native, wild bee species that provide crop pollination as an ecosystem service. We did not include honey bees because nearly all honey bee visits to these crops are from managed hives with farmers placing up to 18 hives per acre. These hives remain at the farms only during bloom. Thus, honey bee abundance is not likely to be influenced by landscape factors. In our study systems, wild bees provided 14%, (blueberry), 25%, (cranberry) and 22% (watermelon) of the flower visits, with the remainder of the visits being provided by honey bees (FEB, DPC, NMW unpublished data).

Data collection

At each of our 44 study sites, we measured bee species abundance by netting all individual bees observed visiting crop flowers within standardised transects at standard times of day. In the blueberry and watermelon systems, where native bees are less abundant, we supplemented our net-collected data with visual observations for which we did on-the-wing identification. For the visual observations and for measuring pollen deposition (see below), we combined species into morphologically similar species groups when necessary. Hereafter, for brevity we use the term ‘species’ to refer to both species and species groups. Similarly, if based on our net-collected samples >90% of the individuals in a species group belong to a single species, we refer to that group throughout by the name of that dominant species. Species composition of each species group is listed in Table 1.

Details of data collection for each study system are as follows. The 16 blueberry sites were each sampled on three different days in each of 2010 and 2011, for a total of 96 data collection days. One 200 m transect was placed in the same location in each year. On each sample date, observers first walked along the transect for 20 min and recorded all bees visiting blueberry flowers. After observations, bees visiting blueberry flowers were collected for 20 min. Both observations and netting were repeated at three standardised times each day for a total of 120 min of data collection per day.

The 16 cranberry sites were sampled on two different days in each of 2009 and 2010 for a total of 64 data collection days. Two 60-m transects were delineated at each cranberry site with one paralleling the edge of a bog and near natural habitat and a second situated in an interior of the bog. On each sample date following observations, any bees visiting flowers were collected for 30 min in the morning and 30 min in the afternoon for a total of 60 min of data collection per day.

Our 12 watermelon sites were sampled on three dates in 2010 for a total of 36 data collection days. One 50 metre transect was established in the crop row bordering the edge of the field. On each sample date, observers recorded visitation by bees to watermelon flowers for 17 min along the transect. Following the observation, bees visiting watermelon flowers were collected from the transect for 10 min. Observations and netting were repeated at four different times throughout the sample date for a total of 108 min of data collection per day.

Table 1 Species groups, abundance of constituent species and the radius used for analysis by for all three study systems

Crop	Bee group	Species included	Abundance	Single visit number	Radius
Blueberry	<i>Andrena bradleyi</i>	<i>A. bradleyi</i> Viereck (90%), eight other <i>Andrena</i> species (10%)	371	25	3000
	<i>Xylocopa virginica</i>	<i>X. virginica</i> L. (100%)	334	16	1500
	<i>Habropoda laboriosa</i>	<i>H. laboriosa</i> F. (100%)	157	17	500
	<i>Andrena vicina</i>	<i>A. vicina</i> Smith (93%), <i>A. carlini</i> Cockerrell (7%)	155	8	1000
Cranberry	<i>Bombus impatiens</i>	<i>B. impatiens</i> Cresson (100%)	779	53	1000
	<i>Bombus bimaculatus</i>	<i>B. bimaculatus</i> Cresson (100%)	554	22	1500
	<i>Bombus griseocollis</i>	<i>B. griseocollis</i> DeGeer (100%)	524	35	500
	<i>Melitta americana</i>	<i>M. americana</i> Smith (100%)	252	10	3000
	<i>X. virginica</i>	<i>X. virginica</i> (100%)	91	13	1500
Watermelon	<i>Bombus vosnesenskii</i>	<i>B. vosnesenskii</i> Radoszkowki (100%)	41	44	500
	<i>Dialictus spp</i>	<i>L. incompletum</i> Crawford (60.5%), <i>L. tegulariforme</i> Crawford (11.5%), <i>L. morphospecies B</i> (3%), Undetermined (25%)	882	65	3000
	<i>Erylaeus spp</i>	<i>Erylaeus spp</i>	68	5	500
	<i>Halictus ligatus</i>	<i>H. ligatus</i> Say (100%)	135	30	500
	<i>Halictus tripartitus</i>	<i>H. tripartitus</i> Cockerell (100%)	460	61	500
	<i>Melissodes spp</i>	<i>M. lupine</i> Cresson (50%), <i>M. tepida</i> Cresson (23%), <i>M. agilis</i> Cresson (18%), <i>M. robustior</i> Cockerell (4.5%), <i>M. stearnsi</i> Cockerell (4.5%)	54	54	3000
	<i>Peponapis pruinosa</i>	<i>P. pruinosa</i> Say (100%)	264	39	1000

In all three study systems, we estimated the pollination service provided per flower visit by counting pollen grains deposited by individual bees in single visits to virgin flowers. Prior to data collection, we placed pollinator exclosures around unopened flower buds. Once flowers were open, we offered them individually to bees foraging on crop flowers. An individual bee was allowed to visit the flower, after which the flower was protected from further visitation. Flowers were allowed to sit at room temperature for 24 h (watermelon) or 48 h (blueberry and cranberry) to permit pollen tube growth. At the end of this period, stigmas were removed and placed in 70% EtOH until processing. For the ericaceous plants, processing consisted of softening stigmas in 1 M NaOH solution for 24 h and subsequently staining with 0.01% aniline blue. Each stigma was then squashed on a slide and scored for pollen at 100 \times using a compound fluorescent microscope. Ericaceous plants such as cranberry and blueberry package pollen in tetrads (groups of four pollen grains), but it is rare that all four grains develop pollen tubes. For both plants, we scored only the tetrads with at least one germinating pollen tube; we hereafter refer to these as 'pollen grains' for simplicity. For watermelon, stigmas were stained with fuchsin dye, and the number of pollen grains was counted as in Kremen *et al.* (2002). For all three crop plants, stigmas that were pollinator-excluded but not visited were also processed for use as controls.

Estimating pollination service per bee species

For each study system, we selected species and species groups for use in the analyses according to three criteria: (1) We were able to identify all individuals to the species or the species group, (2) The species was sufficiently abundant (minimum 25 specimens or observations per year) and widespread (minimum four sites in each year) for statistical analysis and (3) We were able to obtain at least five measures of single visit pollen deposition for the species.

To determine the pollination services provided by each bee species, we multiplied the mean number of pollen grains deposited per flower visit by that species, by the abundance of that species at each site in each year. We explored the sensitivity of this analysis to our use of the mean of the pollen deposition distribution by repeating

all analyses using the median, and \pm 40 and 60% quantiles. Results of these sensitivity analysis were qualitatively similar to those obtained using the mean (Table S1 in Supporting Information).

Land-cover analysis

To assess land-cover surrounding sites, ArcGIS v9.2 (Environmental Systems Research Institute, Redlands, CA, USA) was used to calculate the proportion of land area in agricultural production at radii of 500 m, 1000 m, 1500 m, 2000 m and 3000 m around the transect where data were collected. In New Jersey, land cover surrounding a site was assessed using land-cover data layers provided by the New Jersey Department of Environmental Protection (NJDEP). Sixty-one land cover types were delineated by NJDEP from aerial photographs taken in 2002. To create our analysis category 'agriculture,' we combined the original categories Agricultural Wetlands, Croplands and Pasture Lands, Orchards, and Other Agriculture. In California, we used a GIS land-cover data set created by Kremen *et al.* (2004) using Landsat 7 Thematic Mapper imagery (1997) and used a maximum-likelihood supervised classification. The resulting data layer was ground-truthed and updated to reflect land-use changes using hand digitisation in 2003. The resulting data layer differentiates agriculture from native vegetation to an accuracy of 96% (see Kremen *et al.* 2004 for further details).

Preliminary spatial analyses

To determine the most appropriate scale at which to assess response to land cover for each species, we first determined the scale at which each species responded most strongly to surrounding land cover (Holland *et al.* 2005). General linear mixed models were fit for each species using the nlme package in R (Pinehero *et al.* 2013). The response variable was abundance of each species; abundance was log-transformed to stabilise variance and meet assumptions of normality. The proportion of land cover in agriculture, and year (for blueberry and cranberry, for which we had 2 years of data), were fixed effects, and site was a random effect. Five models, one for each radius, were conducted for each species. The radius from the model with the

lowest AICc value was designated as the most explanatory radius and was used for each species in subsequent analyses (Table S2).

To determine whether spatial autocorrelation was present in the data, Mantel tests were conducted for each species using the *vegan* package (Oksanen *et al.* 2013) in R (R Development Core Team 2012). Because we tested 18 different species, we used a Bonferroni correction to account for multiple testing. One species group (*Colletes spp* in blueberry) exhibited spatial autocorrelation after correcting for multiple tests ($P < 0.003$) and was removed from further analyses, because spatial autocorrelation could violate the assumptions of independence among sites in our analyses involving land cover. This removal did not qualitatively affect the results (data not shown).

Data analyses

Does response diversity occur, in terms of pollinator abundance and pollination services?

Our definition of response diversity was that the response to surrounding land cover, in terms of a species' abundance or the pollination service it provides, differs by bee species. Our statistical test for response diversity was a significant interaction between the factors bee species and land cover in a general linear mixed model, when either abundance or pollination service is used as the outcome variable (Winfree & Kremen 2009). To test this as well as all subsequent analyses and simulations, we performed GLMMs using R v.2.15 (R Development Core Team 2012). Except where noted, all GLMMs were conducted using the *nlme* package. In all models, the proportion of surrounding agricultural land cover at the most explanatory radius for each species (see *Spatial analyses* above), bee species and year (for blueberry and cranberry only, since watermelon had a single year) were fixed effects, and site was a random effect. Response variables were pollinator abundance (one set of models) and pollination services (another set of models). Response variables were log-transformed ($x + 1$) as necessary prior to analysis to meet assumptions of normality and homoscedasticity.

We used AIC model selection to identify the best model for each data set. For blueberry and cranberry, we compared the following candidate models: (1) Species respond to the land-cover gradient differently in different years (species \times land cover \times year interaction), (2) Species respond differently to land cover (species \times land-cover interaction), (3) Species differ in abundance among years (species \times year interaction), (4) Species differ in abundance among years and species respond differently to land cover (both the species \times year, and the species \times land cover interactions) and (5) No interactions among fixed effects. This led to a total of five candidate models for blueberry and cranberry. For watermelon, for which data were collected in 1 year only, we tested only two candidate models: one with a species \times land cover interaction, and a second with no interaction. For the watermelon data set only, the models for pollination service indicated over-dispersion (overdispersion parameter = 4.6; all other analyses had overdispersion parameters < 2); thus, we used a Poisson error distribution with an observation-level random effect that assumes a log-normal distribution for individual observations (Elston *et al.* 2001). In all cases, we used AICc to select the best-fit models. Models with $\Delta\text{AICc} < 2$ were retained, and within this group, model averaging was used to estimate parameter values (R package MuMIN). If the final model set contained the interaction between species and land cover, this was evidence of response diversity.

Does response diversity lead to stability of ecosystem services?

To assess whether the presence of response diversity indicates increased stability of ecosystem services across the land-use gradient, we conducted a simulation that generated many different sets of pollinator species by randomly sampling from our complete data set. The strength of response diversity, and the stability of pollination services across the land-use gradient, was then calculated for each of these communities. This approach allowed us to assess the relationship between response diversity and stability using many data points, whereas if we used only the complete empirical communities, we would have had three data points (one per study system). The simulation was performed separately for each crop system, and reported results are based on 1000 iterations per crop system.

Each iteration of the simulation proceeds as follows. First, we generated a set of N species, ranging from 2 to the total number of species in the data set, by randomly sampling from the complete species pool. The strength of response diversity in pollination services is then calculated for the species set using the method described above (*Does response diversity lead to stability of ecosystem services?*), with one difference. In the previous models, we tested whether response diversity was present and therefore tested only whether the species by land-cover interaction was present in the best-fit models. However, to relate response diversity to stability, we sought to determine the likelihood of response diversity across all species subsets. To do this, we calculated the relative importance of the interaction term for each set of candidate models for every species subset, as the relative importance of the interaction term provided a continuous metric to compare across multiple species sets. The relative importance value is the sum of Akaike weights of the models that include the interaction term and thus reflects the integrated likelihood of the interaction term (Burnham & Anderson 2002).

Second, to quantify the stability of the aggregate pollination services provided by each randomly chosen set of species, we assessed the slope of aggregate pollination across the land-use gradient. The slope of the land-cover term is our metric of stability with slopes closer to zero indicating greater stability (with the exception of a few simulated cases in the cranberry and watermelon systems in which slopes were slightly positive; we considered these to indicate stability of function with land-use change, since pollination actually increased across the land-use gradient). This metric of stability indicates that the pollinator community is maintaining consistent pollination services with increasing proportion of area in agricultural land use.

We calculated our metric of stability as follows. For each species set, the aggregate pollination service was summed for each farm and date. We used a general linear mixed model with $\log(\text{aggregate pollination} + 1)$ as the response variable, proportion of surrounding area in agriculture at 1500 m and year as a fixed effects, and farm as a random variable. Year and farm were not included in the watermelon models because that data set was collected in only 1 year. We used a 1500 m radius to measure land cover as it was approximately the average of all species-specific radii used for the main analysis of response diversity (mean = 1406 ± 255 SE).

To determine whether greater response diversity predicted greater stability of pollination services, we plotted the stability of pollination services across the land-use gradient against response diversity,

using each species set as a data point. Because these data are subsets of the actual data and not independent, we do not perform statistics on this relationship (Isbell *et al.* 2009). We expected a positive relationship between response diversity and stability, which would indicate that as response diversity increases, aggregate pollination services are increasingly stabilised against land-use change.

RESULTS

We recorded 1017 individual visits of four species in the blueberry study; 2200 individual visits of five species in the cranberry study; and 1917 individual visits of seven species in the watermelon study (Table 1). Pollen deposition estimates were based on 70 single visit pollen deposition records for blueberry, 133 for cranberry, and 299 for watermelon. The amount of pollen delivered in a single flower visit varied widely among species in all three study systems (Fig. 1).

Does response diversity occur, in terms of pollinator abundance and pollination services?

We found significant response diversity among bee species to land-use intensity in all three study systems. In blueberry, the best model for pollinator abundance retained the interaction between land cover and species group indicating that species groups exhibited different responses to land cover (Table S3A). One species, *Andrena bradleyi*

Viereck, increased with area in agricultural production while the three other species groups decreased (Fig. 2a). In cranberry, the single-selected model included the interaction between land cover and species (Table S3B). Abundance of two species (*Bombus griseocollis* DeGeer and *Bombus bimaculatus* Cresson) decreased as surrounding area in agriculture increased, whereas abundance of three other species (*Bombus impatiens* Cresson, *Melitta americana* Smith and *Xylocopa virginica* L.) increased with agricultural land cover (Fig. 2b). There was also an interaction between species group and year. This was largely driven by *B. impatiens*, which was more abundant in 2010 compared to 2009. There was no three-way interaction, however, indicating that *B. impatiens* responded similarly to land use regardless of abundance level. In watermelon, one of the two best-fit models retained the interaction between species group and land cover (Table S3C). Two of the seven species (*Peponapis pruinosa* Say and *Melissodes spp.*) decreased with increasing agriculture while the other five increased (Fig. 2c). We also tested whether radii used affected our results and found the results being qualitatively similar (Table S4).

We found significant response diversity in terms of the pollination services provided by different bee species in two of the three study systems. The interaction between land cover and species was retained in the best-fit models in both blueberry and cranberry (Tables S3A & S3B, Fig. 3a and b). Unlike the other two crops, the best-fit model for watermelon did not contain the interaction between land cover and species (Table S3C). However, the lack of

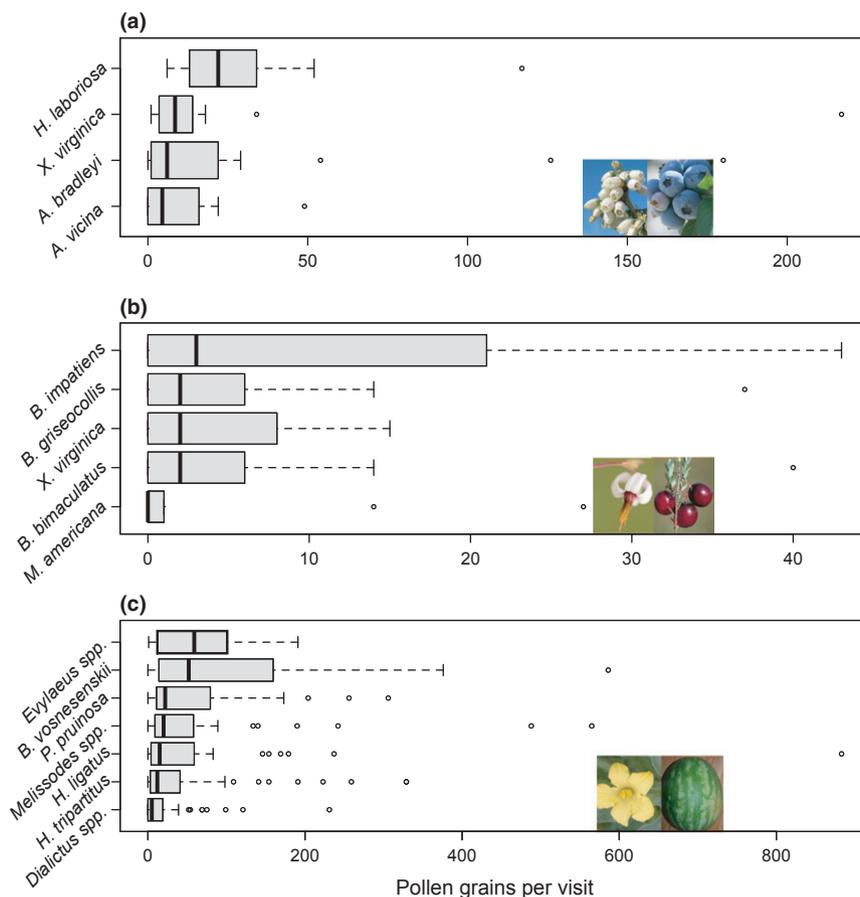


Figure 1 Pollen deposition for single flower visits for each bee species or species group for (a) blueberry, (b) cranberry and (c) watermelon. Centre lines represent median pollen deposition, boxes are interquartile range, and whiskers are 90%/10% quantiles.

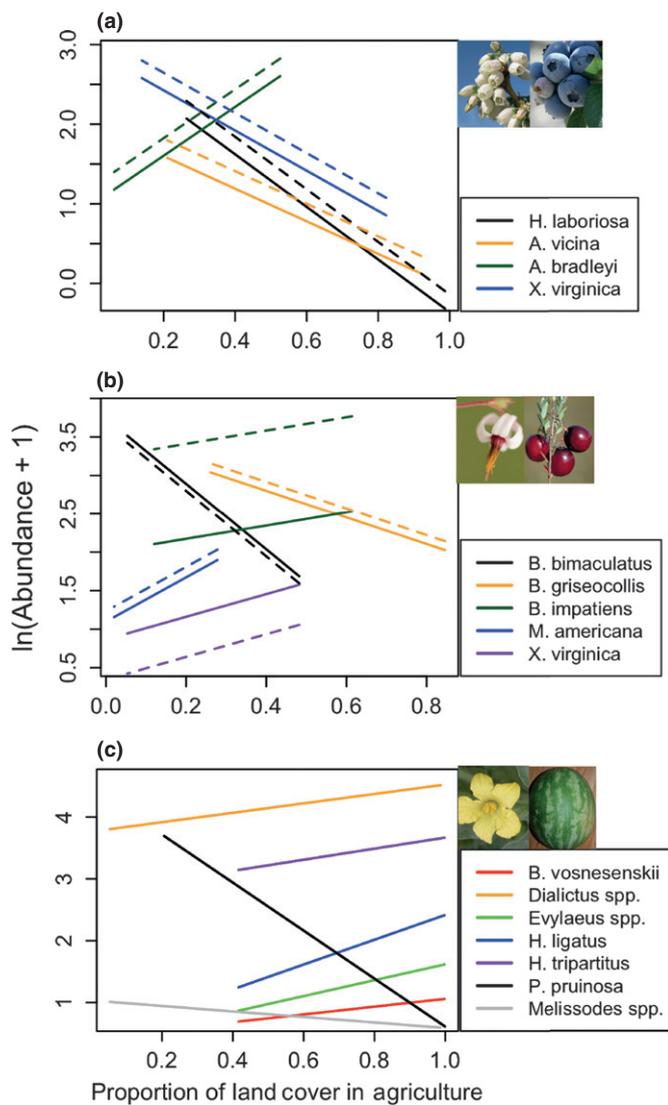


Figure 2 The relationship between bee species abundance and proportion of surrounding land cover in agricultural production for (a) blueberry, (b) cranberry and (c) watermelon. Solid lines represent the first year of the study while dashed lines represent the second year. Plotted lines were calculated using model averaging from the top models in the candidate set. The range of variation in the x -axis differs among species because land cover was assessed at the most explanatory radius for each species, and radii varied in maximum and minimum values.

a significant interaction is not due to a lack of differences in the mean slopes (Fig. 3c), but rather to increased uncertainty. The variance for each species group increased in the pollination service model as compared to that of abundance, because zero abundance values will remain zero when multiplied by mean pollen deposition, while positive values increase. While this occurred in the models of all three of the study systems, the effect on significance may have been strongest in the watermelon system for two reasons: First there were fewer species showing strong trends with land cover thus the variance increased greater than the mean. Second, watermelon had more zero values than the two other systems. Therefore, the error associated with each species when function was included increased dramatically and likely resulted in the inability to detect differences among species responses.

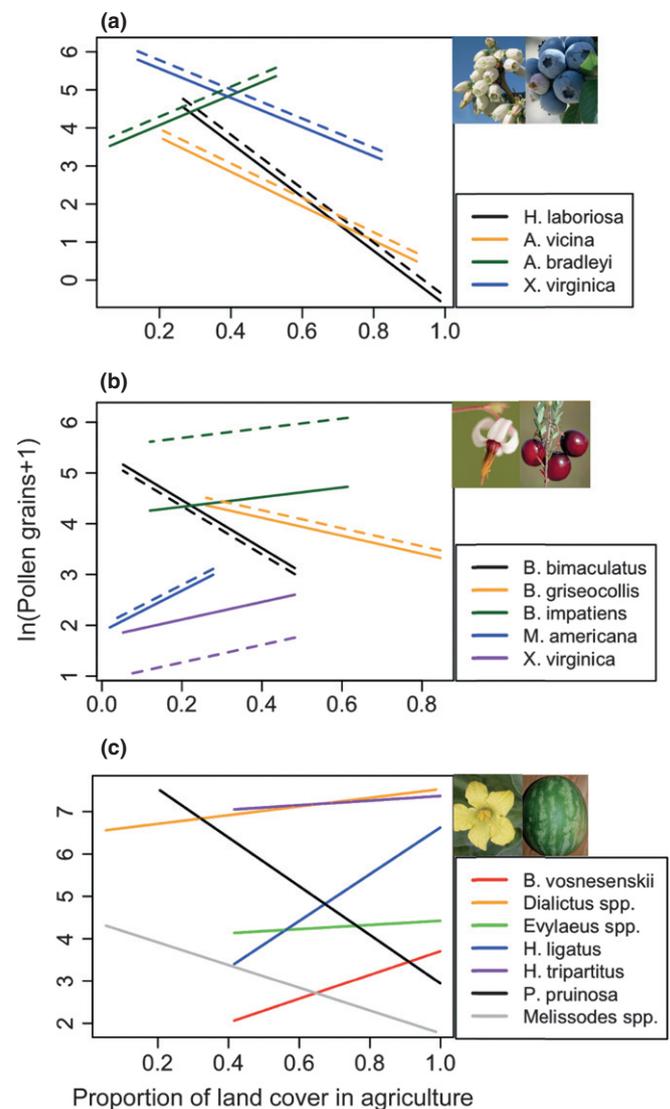


Figure 3 The relationship between the pollination service provided by each bee species, and proportion of surrounding land cover in agricultural production for (a) blueberry, (b) cranberry and (c) watermelon. For 2-year studies, solid represents year one and dashed year represents two. Plotted lines were calculated using model averaging. The range of variation in the x -axis differs among species because land cover was assessed at the most explanatory radius for each species, and radii varied in maximum and minimum values.

Does response diversity lead to stability of ecosystem services?

Stability (measured as a less negative slope of aggregate pollination as a function of land cover) increased as response diversity increased in the blueberry system (Fig. 4a). However, stability declined slightly with increasing response diversity in the other two systems (Fig. 4b and c).

DISCUSSION

Numerous theoretical and empirical studies have found a positive association between species diversity and the stability of ecosystem services (Lehman & Tilman 2000; Balvanera *et al.* 2006; Garibaldi *et al.* 2011), but the mechanisms behind this relationship remain elu-

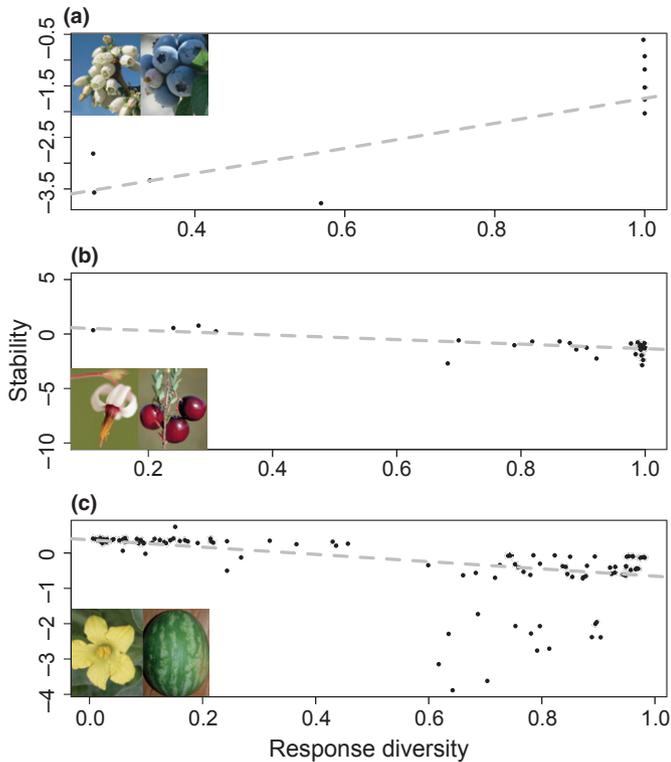


Figure 4 The association between response diversity and stability. The x -axis is response diversity (relative importance variable of the species \times land-cover interaction term for the candidate set of models) and the y -axis is stability (the slope of aggregate pollination for each set of species). Simulations were carried out separately for (a) blueberry, (b) cranberry and (c) watermelon.

sive (Ives & Carpenter 2007). Here, we investigated one rarely studied mechanism, response diversity, in a set of real-world pollination systems. We found strong differential responses to land-use change among pollinator species, in terms of both abundance and the pollination services provided. However, the strength of response diversity was associated with increased stability in pollination services across the land-use gradient in only one of the three systems. This result demonstrates that a difference in species responses to disturbance does not necessarily stabilise ecosystem services.

We found that the relationship between response diversity and stability, rather than being a general one, depended on the particular distribution of species' responses within each system. For example, in the blueberry system, there was a positive relationship between response diversity and stability. This was because one species, *A. bradleyi*, had a strong positive response to proportion to land cover while the other three species had strong negative responses. Therefore, any species set that included *A. bradleyi* exhibited strong response diversity because the response of *A. bradleyi* was markedly different from that of all other species. Furthermore, because *A. bradleyi* responded positively to agricultural land cover while the other species were negative, species sets that included *A. bradleyi* provided more stable aggregate pollination across the land-use gradient. We found the opposite pattern for cranberry and watermelon. In both of these systems, most species had weak positive responses to agricultural land cover, whereas only one or two species had strong negative responses. Thus, when these negatively responding species were included in the species set, response diversity was

higher, but stability was lower. Therefore overall, in contrast to blueberry, cranberry and watermelon exhibited a slight decline in stability as response diversity increased (Fig. 4). These results indicate that response diversity as measured here can stabilise ecosystem services but it is contingent on the distribution of species' responses within the community.

One important pattern that is clear in our data is that the pollinator species that respond positively to agricultural land use have a dramatic buffering effect on the aggregate pollination services. To see this graphically, we used parameter estimates from a mixed model to plot the aggregate pollination services, along with what those aggregate services that would have been provided in the absence of the positively responding species (Fig. 5, Table S5). The difference between these two lines measures the buffering effect provided by the species that respond positively to agricultural land use. This suggests that species that respond positively to a given disturbance may be more important for stabilising ecosystem services than response diversity *per se*. Therefore, the presence of one or a few stable, highly abundant species may lead to more stable delivery of ecosystem services in some situations, highlighting the importance of species identity.

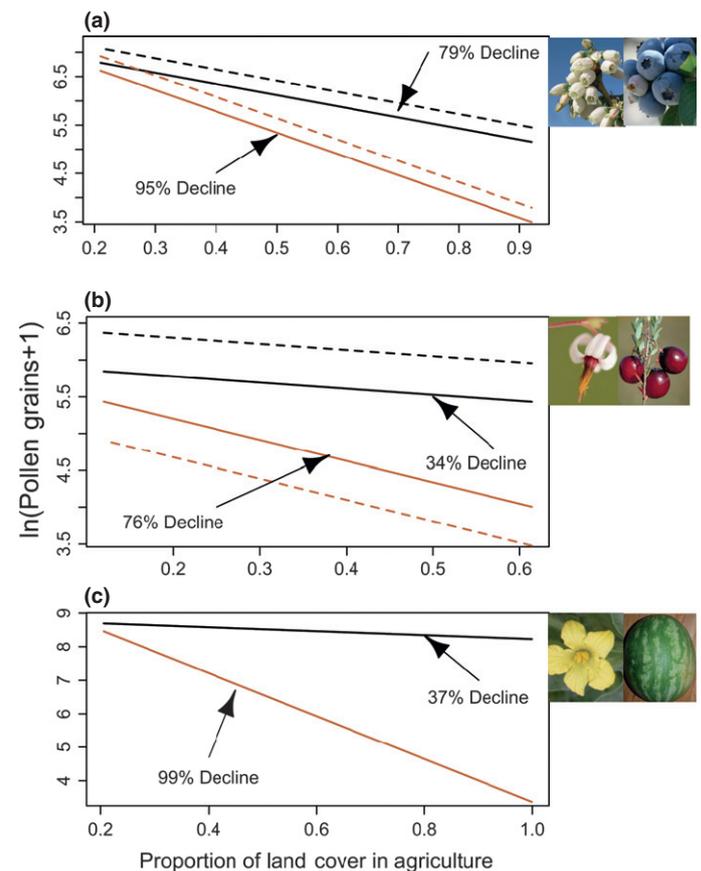


Figure 5 The relationship between aggregate service and proportion of surrounding area in agriculture for (a) blueberry, (b) cranberry and (c) watermelon. Black lines represent the aggregate pollination service when all species are considered. Brown lines represent the aggregate service provided by only the subset of negatively responding species. Thus, the difference between the two lines measures the buffering effect provided by the species that respond positively to agricultural land use. Solid lines represent the first year of the study while dashed lines represent the second year.

It is currently unknown whether other systems have similar relationships between response diversity and stability, because explicit tests of response diversity are scarce (Mori *et al.* 2012). A few large-scale, observational studies in natural systems have found response diversity (McNaughton 1977; Walker *et al.* 1999; Sanford *et al.* 2009), and furthermore, studies that compared multiple stabilising mechanisms found stronger evidence for the presence of response diversity than for other stabilising mechanisms (Winfree & Kremen 2009; Karp *et al.* 2011; Thibaut *et al.* 2012). However, no real-world studies have yet addressed how response diversity works to stabilise ecosystem services. In a microcosm experiment, Leary & Petchey (2009) found that response diversity increased stability of biomass production but only when one particular species that responded negatively to disturbance was excluded from the community. This suggests that understanding particular responses of species in the context of the community of ecosystem-service-providing organisms may be more important than simply demonstrating differential responses among species.

Our findings may underestimate the true role of response diversity in stabilising ecosystem services against environmental change, for at least two reasons. First, in this study, we assumed that single visit pollen deposition values per species were constant across sites. However, pollinators may carry or deliver more pollen per visit when the abundance of other species are reduced and more pollen is available (Thomson & Goodell 2001). This 'functional compensation' could lead to greater stabilisation of total services than response diversity alone, but it has rarely been investigated (Kremen 2005). Second, we examined only one type of environmental perturbation – the amount of surrounding land cover in agricultural production. However, species show differential responses to many forms of environmental perturbation including climate change (Bartomeus *et al.* 2011), disease (Cameron *et al.* 2011), parasite susceptibility (Keesing *et al.* 2009), and pesticide use (Tuell & Isaacs 2010). Recent work has shown that the number of species important for ecosystem services increases when multiple services and locations are considered (Isbell *et al.* 2011). Thus, the importance of biodiversity in stabilising ecosystem services via the mechanism of response diversity may likely be much greater when multiple drivers of global change are considered.

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AUTHORSHIP

DPC and RW designed the study. DPC, NMW and FEB collected data. DPC, RW and NMW designed analyses and DPC performed

the analysis. DPC and RW wrote the manuscript with substantial contributions from NW.

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