

Are ecosystem services stabilized by differences among species? A test using crop pollination

Rachael Winfree and Claire Kremen

Proc. R. Soc. B 2009 **276**, 229-237

doi: 10.1098/rsjb.2008.0709

Supplementary data

["Data Supplement"](#)

<http://rsjb.royalsocietypublishing.org/content/suppl/2009/02/20/276.1655.229.DC1.html>

References

[This article cites 52 articles, 8 of which can be accessed free](#)

<http://rsjb.royalsocietypublishing.org/content/276/1655/229.full.html#ref-list-1>

[Article cited in:](#)

<http://rsjb.royalsocietypublishing.org/content/276/1655/229.full.html#related-urls>

Subject collections

Articles on similar topics can be found in the following collections

[ecology](#) (2519 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Proc. R. Soc. B* go to: <http://rsjb.royalsocietypublishing.org/subscriptions>

Are ecosystem services stabilized by differences among species? A test using crop pollination

Rachael Winfree^{1,2,*} and Claire Kremen²

¹Department of Entomology, Rutgers, The State University, 119 Blake Hall, New Brunswick, NJ 08901, USA

²Department of Environmental Science, Policy and Management, 137 Mulford Hall, University of California, Berkeley, CA 94720, USA

Biological diversity could enhance ecosystem service provision by increasing the mean level of services provided, and/or by providing more consistent (stable) services over space and time. Ecological theory predicts that when an ecosystem service is provided by many species, it will be stabilized against disturbance by a variety of ‘stabilizing mechanisms.’ However, few studies have investigated whether stabilizing mechanisms occur in real landscapes affected by human disturbance. We used two datasets on crop pollination by wild native bees to screen for and differentiate among three stabilizing mechanisms: density compensation (negative co-variance among species’ abundances); response diversity (differential response to environmental variables among species); and cross-scale resilience (response to the same environmental variable at different scales by different species). In both datasets, we found response diversity and cross-scale resilience, but not density compensation. We conclude that stabilizing mechanisms may contribute to the stability of pollination services in our study areas, emphasizing the insurance value of seemingly ‘redundant’ species. Furthermore, the absence of density compensation that we found at the landscape scale contrasts with findings of previous small-scale experimental and modelling work, suggesting that we should not assume that density compensation will stabilize ecosystem services in real landscapes.

Keywords: biodiversity–ecosystem function; cross-scale resilience; density compensation; numerical compensation; response diversity; redundancy

1. INTRODUCTION

Most ecosystem services that have been studied are being degraded by human activity (Millennium Ecosystem Assessment 2005), and there is widespread interest among ecologists in the relationships between human disturbance, biodiversity loss and the loss of ecosystem functioning or services (we use these last two terms synonymously; Hooper *et al.* 2005; Kremen 2005). A guiding principle of biodiversity–ecosystem function research is the biological insurance hypothesis, which states that ecosystem functioning is more stable in more species-rich communities, where the redundancy of species contributing to the same function reduces fluctuations in that function over space or time (Lawton & Brown 1993; Naeem 1998). Both theoretical and empirical work supports this hypothesis (Lehman & Tilman 2000; Balvanera *et al.* 2006; Tilman *et al.* 2006; Ives & Carpenter 2007).

The actual mechanisms through which biodiversity would stabilize ecosystem services (i.e. stabilizing mechanisms) have been less frequently investigated, although several have been proposed (Tilman 1999). One potential stabilizing mechanism is density (or numerical) compensation that occurs when the abundance of one species providing the service increases as a result of decreases in the abundance of another species

(e.g. Naeem & Li 1997; Klug *et al.* 2000; Solan *et al.* 2004). A second proposed stabilizing mechanism is response diversity that occurs when populations of some species are increased and others decreased by the same environmental change (Walker *et al.* 1999; Elmquist *et al.* 2003). A third is cross-scale resilience that occurs when species’ abundances are affected by environmental change at different spatial and/or temporal scales (Holling 1988, 1992; Roland & Taylor 1997; Peterson *et al.* 1998; Steffan-Dewenter *et al.* 2002; Elmquist *et al.* 2003). Models that simulate the loss of ecosystem services under various scenarios of biodiversity loss predict that outcomes can be starkly different depending on the strength of stabilizing mechanisms (Ives & Cardinale 2004; Larsen *et al.* 2005; McIntyre *et al.* 2007). But as yet, there are few empirical studies investigating whether stabilizing mechanisms actually occur in nature (Hooper *et al.* 2005; Kremen 2005).

Pollination is an important ecosystem service because most of the world’s plant species, including 75 per cent of the leading global crop plants, require animal-mediated pollination to some degree (Axelrod 1960; Klein *et al.* 2007). Most of this pollination is provided by bees (Hymenoptera: Apiformes), either managed species (primarily *Apis mellifera*) or a diverse fauna of wild species (Aizen & Feinsinger 2003; Klein *et al.* 2007). Here we consider the contributions of wild bees to crop pollination as an ecosystem service (Kremen & Chaplin-Kramer 2007; Kremen *et al.* 2007). Wild bee species contribute substantially to the pollination of many crops including coffee (e.g. Klein *et al.* 2003), watermelon (Kremen *et al.* 2002, 2004;

* Author and address for correspondence: Department of Entomology, Rutgers, The State University, 119 Blake Hall, New Brunswick, NJ 08901, USA (rwinfree@rci.rutgers.edu).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2008.0709> or via <http://journals.royalsociety.org>.

Winfree *et al.* 2007), sunflower (Greenleaf & Kremen 2006b), tomato (Greenleaf & Kremen 2006a), macadamia (Heard & Exley 1994) and canola (Morandin & Winston 2005). Most studies of crop pollination by wild bees suggest that this ecosystem service is negatively affected by human activities such as agricultural intensification (Kremen & Chaplin-Kramer 2007; Ricketts *et al.* 2008).

We used two datasets on the pollination services provided by wild bees to watermelon (*Citrullus lanatus*; Cucurbitaceae), one from New Jersey/Pennsylvania (Winfree *et al.* 2007, 2008) and the other from California's Central Valley, USA (Kremen *et al.* 2002, 2004). These two systems contrast with one another in terms of native ecosystem type, human land use intensity, and the extent to which pollinators and pollination services are affected by human land use. However, our goal is not to compare these two systems. Rather, we attempt to detect any stabilizing mechanisms that might be operating in each. Stabilizing mechanisms could in principle occur either where ecosystem services are relatively robust to human land use (as in New Jersey/Pennsylvania; Winfree *et al.* 2007, 2008), or where ecosystem services decrease sharply with increasing human land use (as in California; Kremen *et al.* 2002, 2004). In the latter case, due to stabilizing mechanisms, the observed decrease could be less than it would be otherwise.

2. MATERIAL AND METHODS

(a) Study systems and data collection

Our study plant, watermelon, requires insect vectors for pollination because it has separate male and female flowers on the same plant (Delaplane & Mayer 2000). An individual flower is active for only one day, opening at daybreak and closing by early afternoon. The number of visits from bees occurring during the day is a good predictor of whether a female flower will be fully pollinated in watermelon (Stanghellini *et al.* 1998) as in other plants (Vázquez *et al.* 2005).

Our pollinator dataset consisted of all native wild bee species found visiting watermelon flowers. We excluded the non-native European honeybee from our study because it is primarily a managed species in both study systems, and we did not observe any other non-native species.

In both study systems, study farms were arrayed along a gradient of decreasing native vegetation cover in the larger landscape surrounding the farm. Farms were located at least 1 km apart, which is beyond the typical movement distance of all but the largest bees in our study systems (Greenleaf *et al.* 2007). Data were collected only on days that were sunny, partly cloudy or bright overcast, with wind speeds of below 2.5 m s^{-1} . Data collection transects consisted of 50 m segments of crop row, and began within 5 m of the farm field edge to minimize edge effects.

(i) New Jersey/Pennsylvania

We worked in a $90 \times 60 \text{ km}$ area of central New Jersey and eastern Pennsylvania, USA, which is a temperate, mixed oak forest ecosystem. Data were collected in July–August 2005 at 21 watermelon farms. We visited each farm on two different days and netted bees from watermelon flowers for 30 min at standard times of day, for a total of 60 min collecting time per farm. In order to reduce collector bias, each farm was netted by at least three of the five persons collecting data. Specimens

were then pinned and identified to the species level. At each farm, we also measured bee visitation rate to flowers throughout the day using standardized scans (Winfree *et al.* 2007), and wild bee visitation rate was highly correlated with the number of bee specimens collected (Pearson's $r=0.80$, $p=0.000$). In further analyses, we used the collected specimen data for the 11 most abundant bee species, each of which was represented by at least 20 specimens and was found at three or more farms ($N=973$ specimens used in the analysis, or 88 per cent of the total specimens collected; for species names see the electronic supplementary material, table 1).

(ii) California

We worked in a $54 \times 45 \text{ km}$ area of northern central California, USA (Yolo County), where the native vegetation is Mediterranean oak woodland, chaparral and riparian forest. Data were collected in June–August 2001 at 14 watermelon farms (Kremen *et al.* 2002). One fieldworker visited each farm on a single day and observed bees visiting watermelon flowers for 10 min of each half hour during 12 study periods between 07.30 and 14.30 for a total of 120 min of collecting per farm (see Kremen *et al.* 2002 for further details). Bees were classified visually to 12 groups, each of which included 1–6 species (Kremen *et al.* 2002; see the electronic supplementary material, table 2 for species groups). In subsequent analysis, we used data for the nine most abundant bee species groups, each of which was represented by at least 20 observations and was found at three or more farms ($N=1944$ visits in total; electronic supplementary material, table 2).

In both study systems, the design included both organically and conventionally managed farms, but previous analyses determined that farm management was not a significant predictor of bee abundance (Kremen *et al.* 2002, 2004; Winfree *et al.* 2008), so we did not include this variable in our analyses.

(b) Measuring the land use gradient

In both study systems, we used land cover by native vegetation as our measure of human disturbance. We mapped the centre of each data collection transect with a Trimble GeoExplorer Global Positioning System (GPS; Trimble Navigation, Sunnyvale, CA, USA) corrected to $\pm 10 \text{ m}$ accuracy with GPS PATHFINDER OFFICE v. 2.9 (Touch Vision, Cypress, CA, USA). Geographical Information Systems (GIS) land cover data for New Jersey were provided by the New Jersey State Department of Environmental Protection, and were based on aerial photographs taken in 2002 and subsequently classified to 61 land cover types. GIS data for Pennsylvania were provided by the Delaware Valley Regional Planning Commission, and were based on aerial photographs taken in 2000 and subsequently classified to 27 land cover types. In California, GIS land cover data were classified from Landsat 7 Thematic Mapper imagery (1997) using a maximum-likelihood supervised classification, followed by ground truthing and correction of the areas within 5 km of each farm site. The resulting classification is estimated to be 96 per cent accurate in distinguishing between native vegetation and agriculture (see Kremen *et al.* (2004) for further details).

We used ARCGIS v. 9.0 (Environmental Systems Research Institute, Redlands, CA, USA) to determine the proportion of the area surrounding each farm that consisted of the native vegetation type (mixed deciduous woodland in

New Jersey/Pennsylvania; Mediterranean chaparral, oak woodland and riparian forest in California), as well as the linear distance to the nearest block of native habitat greater than or equal to 1 ha. As these two measures of native vegetation cover were highly correlated (in New Jersey/Pennsylvania Spearman's $\rho = -0.60$, $p < 0.0001$, and in California Spearman's $\rho = -0.79$, $p < 0.0001$), we used only the proportional area of native vegetation in analyses, because it has the larger range of variation and is consistent with our previous analyses of these datasets.

(c) Analyses

(i) Preliminary statistical analyses

Previous analyses showed that there was little or no spatial autocorrelation in our datasets (Kremen *et al.* 2004; Winfree *et al.* 2007). To identify the most explanatory scale of analysis for each bee species or species group relative to native vegetation cover, we related the response variable bee abundance to the predictor variable proportion of native vegetation cover surrounding study sites at radii of 200, 500, 1000, 1500, 2000, 2500 and 3000 m. Because the data were counts with frequent zero values, but were overdispersed for a Poisson distribution, we used a generalized linear model (the SAS v. 9.1.3 PROC GEN MOD procedure) with a negative binomial error distribution and a log link function. We then compared the resulting χ^2 values and used the scale with the highest χ^2 value in subsequent analyses (Holland *et al.* 2004). These same results were also used for our analysis of cross-scale resilience (see below).

(ii) Analysis of density compensation

We defined density compensation as negative co-variances among the abundances of species contributing to the same ecosystem service (i.e. the different bee species pollinating watermelon). Co-variance was measured across space (i.e. across the study farms that were arrayed along a gradient of increasing human disturbance). To look for density compensation using a data visualization technique, we plotted the frequency distribution of all pairwise correlation coefficients (Pearson's r) between species' abundances (transformed as $\ln(N+1)$). In this plot, density compensation would be indicated by a distribution shifted to the left of zero. Because a species might respond to the combined densities of other species in its functional group rather than to pairwise densities, we also examined the correlations between the density of each species and the densities of all other species in combination.

To assess the statistical significance of correlations among species' abundances, we used a variance ratio test (Schluter 1984; Klug *et al.* 2000). This test is based on the ratio

$$\frac{\text{var} \sum_i S_i}{\sum_i (\text{var } S_i)},$$

where S_i is the abundance of the i th bee species considered across all study sites, and the summation is taken over all species in the community. The variance ratio test uses the fact that

$$\text{var} \left(\sum_i S_i \right) = \left[\sum_i (\text{var } S_i) \right] + \left[2 \sum_i \sum_j \text{cov}(S_i S_j) \right].$$

A variance ratio less than 1 indicates that species' abundances co-vary negatively (density compensation). A variance ratio

near 1 indicates that species vary independently, and a variance ratio greater than 1 indicates that species co-vary positively. We assessed the significance of the variance ratio with a Monte Carlo simulation that calculates a null variance ratio after randomizing the abundances of each species across sites. The p -value of the observed variance ratio was calculated as the fraction of 10 000 null variance ratios that were of the same sign, but more extreme in magnitude, when compared with the observed value.

Our data for California were identified to species groups, each of which included 1–6 species (see the electronic supplementary material). This could lead to an underestimate of true density compensation if some of the species that compensated for each other were morphologically similar and therefore analysed within the same group. As a check on this possibility we used an additional, specimen-based, fully identified dataset ($N = 3811$ specimens) collected in the same study system. These data were collected by blue, white and yellow pan traps (six of each colour arrayed on two 50 m transects per site) and one-metre-high PVC pipes (three per site) during a single 24 h period in 1999. Data were collected at 19 sites arrayed across the same land use gradient as for the primary dataset from California, although the actual sites overlapped only partially. As for the other two datasets, species represented by at least 20 specimens and found at three or more farms were included in the analysis ($N = 10$ species).

(iii) Analysis of response diversity

As far as we are aware, no statistical method for identifying response diversity has been published. To test for the presence and significance of response diversity, we used the species–native vegetation interaction term from a generalized linear model. Specifically, we used bee abundance as the response variable, and examined the interaction between the categorical predictor variable 'bee species' and the continuous predictor variable 'native vegetation cover.' The interaction term indicates whether the response to native vegetation loss varies by bee species, and is analogous to the species–environment interaction term from other areas of ecology.

For both datasets, the predictor variables in the generalized linear model were bee species (or species group), native vegetation cover at the most explanatory radius for each species, and the bee species–native vegetation interaction. Other variables that were initially included, but dropped from the final models as unexplanatory, were crop flower density, weedy flower density in the farm field and their interactions with bee species. The response variables were the number of individual bees collected per species (for New Jersey/Pennsylvania) or the number of flower visits per species group (for California). Because response variables were counts related to bee arrivals at flowers and contained many zero values, but the variances were greater than would be predicted for Poisson distributions, we used negative binomial error distributions with a log link function. The deviance/d.f. for the final negative binomial models was 1.17 for the New Jersey/Pennsylvania dataset and 1.07 for the California dataset. Analyses were done in SAS v. 9.1.3 using the PROC GEN MOD procedure (SAS Institute, Cary, NC, USA). Significance was assessed using Type 3 least-square means.

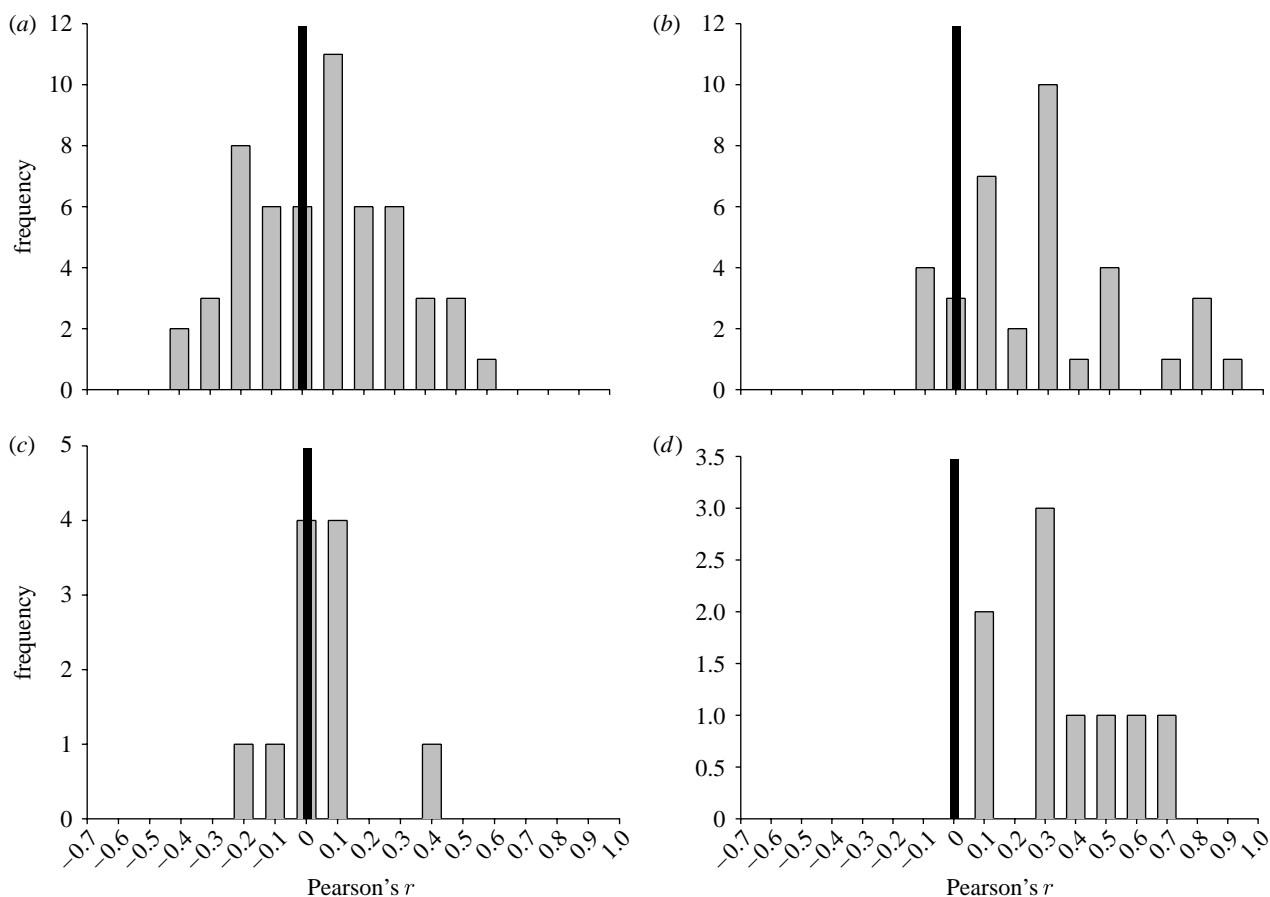


Figure 1. Frequency distributions of correlation coefficients calculated from species' abundances across study sites. A distribution shifted to the left of the solid line at zero would indicate density compensation. Observed distributions are shifted to the right of zero, indicating mostly positive correlations among bee species. (a) All pairwise values of Pearson's r for the 11 bee species in the New Jersey/Pennsylvania dataset. (b) All pairwise values of Pearson's r for the nine bee species groups in the California dataset. (c) Values of Pearson's r calculated between the abundance of each bee species and the summed abundances of all other species, for the New Jersey/Pennsylvania dataset. (d) Values of Pearson's r calculated between the abundance of each bee species group and the summed abundances of all other species groups, for the California dataset.

(iv) Analyses of cross-scale resilience

We define cross-scale resilience here as differences in the spatial scales at which watermelon pollinators respond to habitat loss. We considered only the bee species that were negatively associated with the loss of native vegetation in the surrounding landscape, because pollination services could be lost more gradually with the loss of native vegetation cover if such species are affected at different scales. For each of these species, we examined the relationship between abundance and native vegetation cover at all seven spatial scales (see §2*c*(i), above), to identify the scale at which each species or species group responded most strongly.

3. RESULTS

(a) Density compensation

We found no evidence of density compensation (negative co-variance in abundance among species) in either dataset. Instead, the abundances of different bee species tended to be positively correlated, as indicated visually by the distributions of pairwise correlation coefficients (figure 1*a,b*). Correlations between the abundance of a particular species and the summed abundances of all other species were also mostly positive (figure 1*c,d*). Variance ratio tests confirmed these results statistically. For the New Jersey/Pennsylvania data, the variance ratio was 1.04 ($p=0.40$), indicating little correlation among species.

For the California dataset, the variance ratio was 1.47 ($p=0.04$), indicating significant positive correlations among species. The additional, species-level dataset from the California system showed even stronger positive associations (variance ratio = 1.65, $p=0.002$).

(b) Response diversity

We assessed response diversity using the significance of the species–native vegetation cover interaction in a generalized linear model. In the New Jersey/Pennsylvania dataset, some bee species were positively, and others negatively, associated with native vegetation loss (figure 2*a*) such that the variable 'proportion native vegetation' itself was only marginally significantly associated with overall bee abundance (a negative association with $\chi^2=3.65$, $p=0.056$; table 1). There was a highly significant interaction between bee species and the proportion native vegetation in the surrounding landscape ($\chi^2=34.62$, $p=0.0001$; table 1; figure 2*a*), which is the signal of response diversity.

In the California dataset, the interaction between bee species and the proportion native vegetation in the surrounding landscape was also highly significant ($\chi^2=33.93$, $p<0.0001$; table 2; figure 2*b*). However, native vegetation cover was positively associated with bee abundance for all bee species, not just some of them, such that the variable

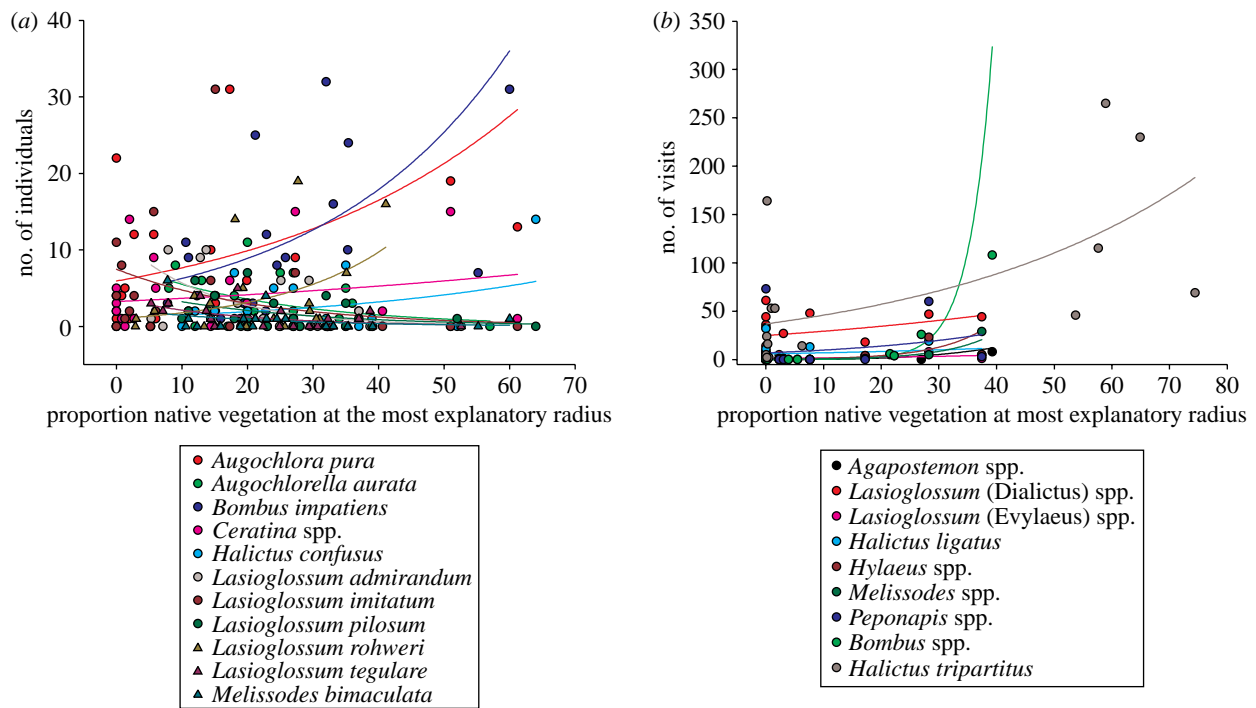


Figure 2. Response diversity, represented as changes in each bee species' abundance with increasing proportion of native vegetation in the surrounding landscape. Curves are predicted values from generalized linear models, plotted in the same colour as the data points for each species. (a) New Jersey/Pennsylvania, where species were both negatively and positively associated with native vegetation. (b) California, where all species were positively associated with native vegetation, but to varying degrees. The range of x-axis values differs by species because land cover was assessed at the most explanatory scale for each species, and the maximum and minimum values differed across scales. For complete species lists see tables S1 and S2 in the electronic supplementary material.

Table 1. Generalized linear model results for the analysis of response diversity in New Jersey/Pennsylvania. (The outcome variable was the number of individual bees collected from crop flowers for each of the 11 bee species.)

source of variation	d.f.	χ^2	p-value
proportion native vegetation in surrounding landscape ^a	1	3.65	0.056
bee species	10	16.99	0.075
proportion native vegetation × bee species interaction	10	34.62	0.0001
overall model	21	99.18	<0.001

^aCalculated at the most explanatory radius for each bee species.

itself was highly significant ($\chi^2 = 49.71$, $p < 0.0001$; table 2). The significant interaction term was driven by variation in the strength of the positive slopes (figure 2b).

(c) Cross-scale resilience

In the New Jersey/Pennsylvania dataset, two species (18%) were significantly negatively associated with the loss of native vegetation, and in the California dataset this was true of five species groups (56%). In both datasets, different species showed their strongest response to native vegetation loss at different scales, ranging from a 200 m radius around the study site (or 13 ha) to a 3000 m radius (or 2827 ha; figure 3). This is the signal for occurrence of cross-scale resilience.

4. DISCUSSION

There is long-standing interest within ecology in whether a greater number of species contributing to the same ecosystem function can stabilize the function (Lawton & Brown 1993; McGrady-Steed *et al.* 1997; Naem & Li 1997; Naem 1998; Yachi & Loreau 1999; Loreau 2000;

Ives & Carpenter 2007). Several mechanisms have been proposed for stabilization, but these have rarely been tested empirically (Ives & Carpenter 2007). Proposed mechanisms include: the 'portfolio effect', or the reduction in total variance that occurs when N individuals of one species are replaced with N/x individuals of x species (Doak *et al.* 1998; Tilman *et al.* 1998; Tilman 1999; Lehman & Tilman 2000); density compensation (e.g. Fischer *et al.* 2001); response diversity (Elmqvist *et al.* 2003); and cross-scale resilience (Peterson *et al.* 1998). Our study design did not allow us to explore the portfolio effect, which would require time-series data from multiple sites differing in species richness. Here, we show that density compensation was not found in either study system, whereas response diversity and cross-scale resilience were found in both systems.

In contrast to the expectation for density compensation that would result in negative associations among species' abundances, we found mostly positive associations between species (figure 1). We speculate that these positive associations occur because resource availability decreases with increasing human disturbance. In this

Table 2. Generalized linear model results for the analysis of response diversity in California. (The outcome variable was the number of bee visits to crop flowers for each bee species group (termed 'species' below).)

source of variation	d.f.	χ^2	<i>p</i> -value
proportion native vegetation in surrounding landscape ^a	1	49.71	<0.0001
bee species	8	90.98	<0.0001
proportion native vegetation × bee species interaction	8	33.93	<0.0001
overall model	17	113.46	<0.0001

^aCalculated at the most explanatory radius for each bee species.

case, sub-dominant species would benefit less from competitive release, because total resource availability is decreasing along with the dominant competitor. In contrast to our results here, density compensation has been found in previous experimental studies where resource availability was experimentally fixed (McGrady-Steed & Morin 2000) or standardized to some extent across plots (Tilman 1999). Similarly, fixed abundance of a limiting resource has been assumed by some models finding density compensation (Lehman & Tilman 2000), and density compensation itself has been assumed by others (Bunker *et al.* 2005). We conclude that density compensation may be less likely to occur across actual human disturbance gradients, where resource availability may co-vary with the disturbance, than in controlled experiments where resource availability is fixed. Our findings suggest that caution is warranted when using the results of controlled experiments and simulations to predict the loss of ecosystem services in real landscapes, and that models should be run with and without the assumption of density compensation (Solan *et al.* 2004).

We found highly significant response diversity in both systems. In New Jersey/Pennsylvania, the directionality of pollinators' response to native vegetation loss varied, with some species showing negative and some positive associations (figure 2*a*). This response diversity may contribute to the stability of pollination services across space in this system, where pollination of watermelon by all wild bees in combination shows no detectable association with native vegetation cover (Winfree *et al.* 2007). In California, while all species showed negative associations with native vegetation loss, the associations differed in degree, leading to response diversity (figure 2*b*). The shared directionality in response among species is consistent with the fact that aggregate pollination services from wild bees drop off sharply with native vegetation loss in the California system (Kremen *et al.* 2002, 2004; Larsen *et al.* 2005).

The land use gradient is more extreme in California and this may underlie the correlated response among bee species. In California, the most isolated sites have as little as 0.01 per cent native vegetation remaining within a 2 km radius compared with a minimum of 8 per cent in New Jersey/Pennsylvania. Alternatively, the native vegetation type in California (chaparral and oak woodland) may be a preferred habitat type for most bee species, whereas the native vegetation type in New Jersey/Pennsylvania (deciduous woodland) is less optimal bee habitat.

It is intriguing that we found significant response diversity in both systems despite the fact that we only considered a few environmental variables, meaning that our study must underestimate true response diversity. Response diversity could potentially occur with regard to many variables. For example, pollinator species are known

to differ in their diurnal activity patterns (Herrera 1990) and their thermal biology (Herrera 1997; Bishop & Armbruster 1999), and this could mitigate the impacts of climate change on pollination services to some degree.

Although we here propose a statistical test to better separate density compensation and response diversity, identifying the biological mechanism behind the two forms of compensation remains beyond the scope of associational data. The main mechanism behind density compensation is thought to be competitive release (Tilman 1996, 1999; Doak *et al.* 1998). However, a species apparently benefiting from competitive release could simply be less sensitive to the original disturbance, as recognized by other researchers (Tilman 1996; Doak *et al.* 1998; Fischer *et al.* 2001); this would be response diversity. Indeed, most previous studies have not attempted to explicitly separate response diversity and density compensation, for example in whole-lake acidification experiments (Fischer *et al.* 2001 and references therein), grassland plant communities exposed to drought (McNaughton 1977; Tilman 1996, 1999) and grazing pressure (McNaughton 1977; Walker *et al.* 1999), or arctic plants responding to climate change (Dormann & Woodin 2002). What is novel in our study is that we propose a new test for response diversity *per se*, and that we found response diversity without density compensation. While our statistical differentiation of density compensation and response diversity does not reveal mechanism, it does allow the detection of response diversity even in cases where density compensation is not occurring.

Lastly, we found evidence of cross-scale resilience in both systems: the species that were negatively associated with the loss of native vegetation showed these associations most strongly at different scales. Cross-scale resilience may increase the stability of the ecosystem service under some scenarios. For example, habitat loss relatively far from a farm should affect the species operating at the larger but not the smaller scales (as could occur in New Jersey/Pennsylvania; figure 3*a,b*). We would expect cross-scale resilience to be less of a stabilizing force in California, where all species show significant negative associations with habitat loss at multiple scales, and several species show parallel patterns with scale (figure 3*c-g*). Nonetheless, the California system should still be more stable than would be the case if all species showed identical patterns with respect to scale.

An important goal for future work is to assess the extent to which stabilizing mechanisms stabilize actual function, as opposed to the abundance of the organisms providing the function, as we examined here. For example, in both the New Jersey/Pennsylvania and the California systems, bumblebees (*Bombus* spp.) are among the most effective pollinators on a per-visit basis (Kremen *et al.* 2002;

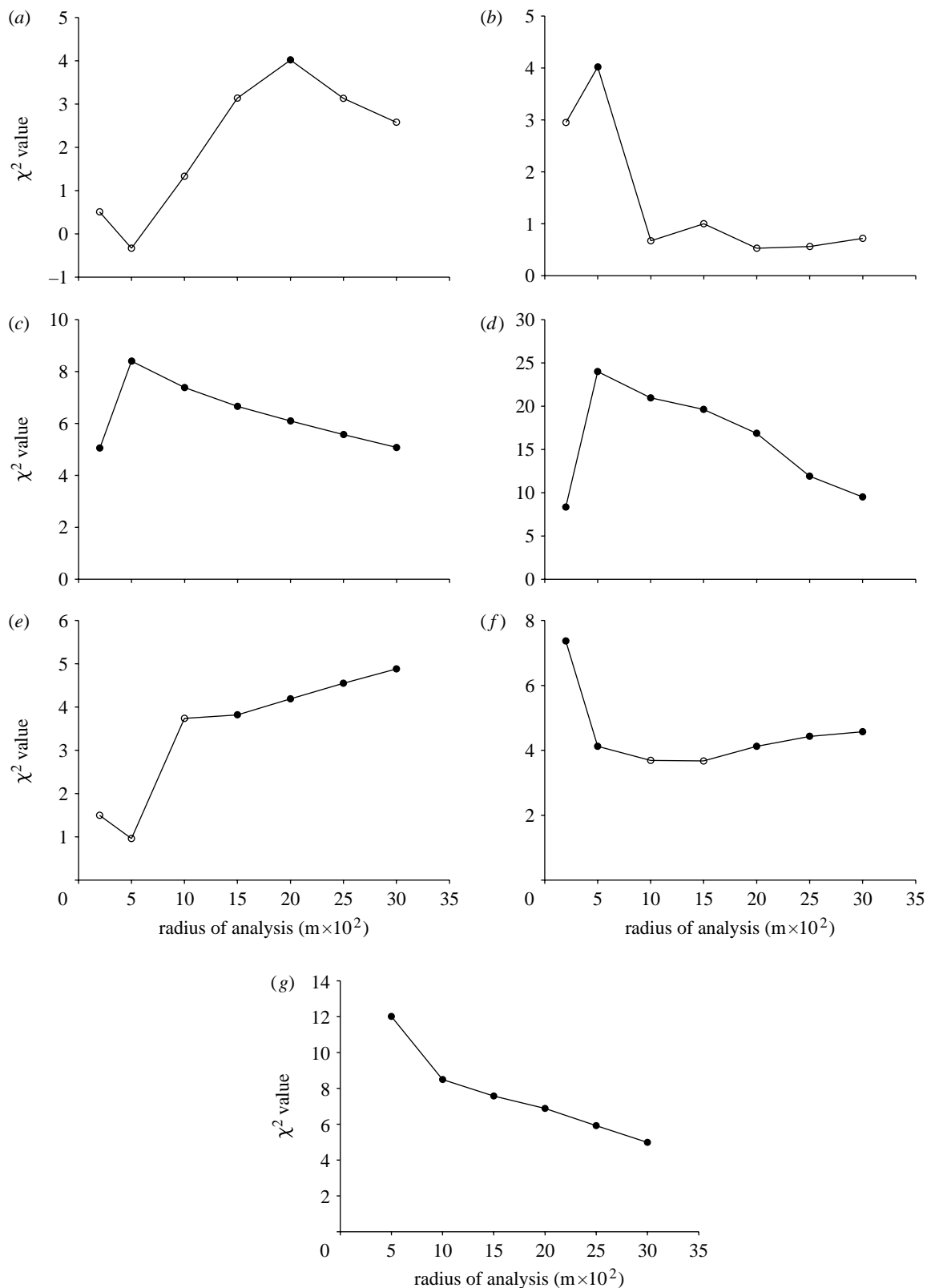


Figure 3. Cross-scale resilience in (a,b) the New Jersey/Pennsylvania system (*Bombus impatiens* and *Lasioglossum rohweri*, respectively) and (c–g) the California system (*Agapostemon texanus*, *Bombus* spp., *Halictus tripartitus*, *Hylaesus* spp. and *Melissodes* spp., respectively). Each figure shows the χ^2 value from a generalized linear model regressing a species' abundance against the proportion of native vegetation in the surrounding landscape at a given radius. Filled circles represent significant relationships. Only the species having significant negative associations with native vegetation loss are shown. These species respond most strongly at different scales, demonstrating cross-scale resilience.

Winfree *et al.* 2007), and are also the species most negatively affected by the loss of native vegetation. The compensatory responses of other species, which are less effective pollinators, may only partially compensate for the

loss of bumblebees. Another important goal for future work is investigating the role of stabilizing mechanisms over time, in addition to across a spatial disturbance gradient as we do here.

As far as we are aware, this study is the first investigation of stabilizing mechanisms for an ecosystem service provided by terrestrial animals, and the first at the landscape scale, a relevant scale for biodiversity conservation and ecosystem services. In contrast to smaller-scale experimental studies and modelling work, we failed to find density compensation in either system. We propose that this is because resources may vary across sites, weakening the effects of competition. Our two datasets were consistent in showing response diversity and cross-scale resilience. These little-studied mechanisms may be important stabilizing forces in nature, allowing apparently redundant species contributing to the same function to respond differently across space and time to future environmental shifts such as climate change.

We thank the many landowners who participated in the field studies; N. Williams for assistance with implementing these studies; J. Ascher, S. Droege and R. Thorp for bee species identification; J. Dushoff and J. Hooker for statistical advice; H. Gaines, C. Locke, R. Malfi, D. Miteva, N. Nicola and B. Tonietto for field and laboratory work; and Princeton University and the Harry H. Laidlaw Jr Honey Bee Research Facility at University of California, Davis for providing space and facilities. S. Barrett and several anonymous reviewers improved an earlier version of the manuscript with their comments. Funding was provided by the National Fish and Wildlife Foundation (to C.K. and N. Williams), a McDonnell Foundation Award (to C.K.) and an NSF collaborative grant no. DEB-05-54790/ no. DEB-05-16205 (to C.K., N. Williams and R.W.).

REFERENCES

- Aizen, M. A. & Feinsinger, P. 2003 Bees not to be? Responses of insect pollinator faunas and flower pollination to habitat fragmentation. In *How landscapes change*. Ecological Studies, no. 162, (eds G. A. Bradshaw & P. A. Marquet), pp. 111–129. Berlin/Heidelberg, Germany; New York, NY: Springer.
- Axelrod, D. I. 1960 The evolution of flowering plants. In *The evolution of life* (ed. S. Tax). Evolution after Darwin, vol. 1, pp. 227–305. Chicago, IL: University of Chicago Press.
- Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J. S., Nakashizuka, T., Raffaelli, D. & Schmid, B. 2006 Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* **9**, 1146–1156. (doi:10.1111/j.1461-0248.2006.00963.x)
- Bishop, J. A. & Armbruster, W. S. 1999 Thermoregulatory abilities of Alaskan bees: effects of size, phylogeny and ecology. *Funct. Ecol.* **13**, 711–724. (doi:10.1046/j.1365-2435.1999.00351.x)
- Bunker, D. E., DeClerck, F., Bradford, J. C., Colwell, R. K., Perfecto, I., Phillips, O., Sankaran, M. & Naem, S. 2005 Species loss and aboveground carbon storage in a tropical forest. *Science* **310**, 1029–1031. (doi:10.1126/science.1117682)
- Delaplane, K. S. & Mayer, D. F. 2000 *Crop pollination by bees*. New York, NY: CABI Publishing.
- Doak, D. F., Bigger, D., Harding, E. K., Marvier, M. A., O'Malley, R. E. & Thomson, D. 1998 The statistical inevitability of stability–diversity relationships in community ecology. *Am. Nat.* **151**, 264–276. (doi:10.1086/286117)
- Dormann, C. F. & Woodin, S. J. 2002 Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. *Funct. Ecol.* **16**, 4–17. (doi:10.1046/j.0269-8463.2001.00596.x)
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. & Norberg, J. 2003 Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* **1**, 488–494. (doi:10.2307/3868116)
- Fischer, J., Frost, T. M. & Ives, A. R. 2001 Compensatory dynamics in zooplankton community responses to acidification: measurement and mechanisms. *Ecol. Appl.* **11**, 1060–1072. (doi:10.1890/1051-0761(2001)011[1060:CDIZCR]2.0.CO;2)
- Greenleaf, S. S. & Kremen, C. 2006a Wild bee species increase tomato production but respond differently to surrounding land use in Northern California. *Biol. Conserv.* **133**, 81–87. (doi:10.1016/j.biocon.2006.05.025)
- Greenleaf, S. S. & Kremen, C. 2006b Wild bees enhance honey bees' pollination of hybrid sunflower. *Proc. Natl Acad. Sci. USA* **103**, 13 890–13 895. (doi:10.1073/pnas.0600929103)
- Greenleaf, S. S., Williams, N., Winfree, R. & Kremen, C. 2007 Bee foraging ranges and their relationship to body size. *Oecologia* **153**, 589–596. (doi:10.1007/s00442-007-0752-9)
- Heard, T. A. & Exley, E. M. 1994 Diversity, abundance, and distribution of insect visitors to macadamia flowers. *Environ. Entomol.* **23**, 91–100.
- Herrera, C. M. 1990 Daily patterns of pollinator activity, differential pollinating effectiveness, and floral resource availability, in a summer-flowering Mediterranean shrub. *Oikos* **58**, 277–288. (doi:10.2307/3545218)
- Herrera, C. M. 1997 Thermal biology and foraging responses of insect pollinators to the forest floor irradiance mosaic. *Oikos* **78**, 601–611. (doi:10.2307/3545623)
- Holland, J. D., Bert, D. G. & Fahrig, L. 2004 Determining the spatial scale of species' response to habitat. *Bioscience* **54**, 227–233. (doi:10.1641/0006-3568(2004)054[0227:DTSSOS]2.0.CO;2)
- Holling, C. S. 1988 Temperate forest outbreaks, tropical deforestation, and migratory birds. *Mem. Entomol. Soc. Can.* **146**, 21–32.
- Holling, C. S. 1992 Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol. Monogr.* **62**, 447–502. (doi:10.2307/2937313)
- Hooper, D. U. *et al.* 2005 Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* **75**, 3–35. (doi:10.1890/04-0922)
- Ives, A. R. & Cardinale, B. J. 2004 Food-web interactions govern the resistance of communities after non-random extinctions. *Nature* **429**, 174–177. (doi:10.1038/nature02515)
- Ives, A. R. & Carpenter, S. R. 2007 Stability and diversity of ecosystems. *Science* **317**, 58–62. (doi:10.1126/science.1133258)
- Klein, A.-M., Steffan-Dewenter, I. & Tscharntke, T. 2003 Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. R. Soc. B* **270**, 955–961. (doi:10.1098/rspb.2002.2306)
- Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C. & Tscharntke, T. 2007 Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B* **274**, 303–313. (doi:10.1098/rspb.2006.3721)
- Klug, J. L., Fischer, J. M., Ives, A. R. & Dennis, B. 2000 Compensatory dynamics in planktonic community responses to pH perturbations. *Ecology* **81**, 387–398. (doi:10.2307/177435)
- Kremen, C. 2005 Managing ecosystem services: what do we need to know? *Ecol. Lett.* **8**, 468–479. (doi:10.1111/j.1461-0248.2005.00751.x)
- Kremen, C. & Chaplin-Kramer, R. 2007 Insects as providers of ecosystem services: crop pollination and pest control. In *Insect conservation biology: Proc. Royal Entomological*

- Society's 23rd Symp.* (eds A. J. A. Stewart, T. R. New & O. T. Lewis), pp. 349–382. Wallingford, UK: CABI Publishing.
- Kremen, C., Williams, N. M. & Thorp, R. W. 2002 Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl Acad. Sci. USA* **99**, 16 812–16 816. (doi:10.1073/pnas.262413599)
- Kremen, C., Williams, N. M., Bugg, R. L., Fay, J. P. & Thorp, R. W. 2004 The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol. Lett.* **7**, 1109–1119. (doi:10.1111/j.1461-0248.2004.00662.x)
- Kremen, C. *et al.* 2007 Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land use change. *Ecol. Lett.* **10**, 299–314. (doi:10.1111/j.1461-0248.2007.01018.x)
- Larsen, T. H., Williams, N. W. & Kremen, C. 2005 Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecol. Lett.* **8**, 538–547. (doi:10.1111/j.1461-0248.2005.00749.x)
- Lawton, J. H. & Brown, V. K. 1993 Redundancy in ecosystems. In *Biodiversity and ecosystem function* (eds E. D. Schulze & H. A. Mooney), pp. 225–270. New York, NY: Springer.
- Lehman, C. L. & Tilman, D. 2000 Biodiversity, stability and productivity in competitive communities. *Am. Nat.* **156**, 534–552. (doi:10.1086/303402)
- Loreau, M. 2000 Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**, 3–17. (doi:10.1034/j.1600-0706.2000.910101.x)
- McGrady-Steed, J. & Morin, P. J. 2000 Biodiversity, density compensation, and the dynamics of populations and functional groups. *Ecology* **81**, 361–373. (doi:10.2307/177433)
- McGrady-Steed, J., Harris, P. M. & Morin, P. 1997 Biodiversity regulates ecosystem predictability. *Nature* **390**, 162–165. (doi:10.1038/36561)
- McIntyre, P. B., Jones, L. E., Flecker, A. S. & Vanni, M. J. 2007 Fish extinctions and nutrient cycling in tropical freshwaters. *Proc. Natl Acad. Sci. USA* **104**, 4461–4466. (doi:10.1073/pnas.0608148104)
- McNaughton, S. J. 1977 Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *Am. Nat.* **111**, 515–525. (doi:10.1086/283181)
- Millennium Ecosystem Assessment 2005 *Ecosystems and human well-being: synthesis*. Washington, DC: Island Press.
- Morandin, L. A. & Winston, M. L. 2005 Wild bee abundance and seed production in conventional, organic, and genetically modified canola. *Ecol. Appl.* **15**, 871–881. (doi:10.1890/03-5271)
- Naeem, S. 1998 Species redundancy and ecosystem reliability. *Conserv. Biol.* **12**, 39–45. (doi:10.1046/j.1523-1739.1998.96379.x)
- Naeem, S. & Li, S. 1997 Biodiversity enhances ecosystem reliability. *Nature* **390**, 507–509. (doi:10.1038/37348)
- Peterson, G., Allen, C. R. & Holling, C. S. 1998 Ecological resilience, biodiversity, and scale. *Ecosystems* **1**, 6–18. (doi:10.1007/s100219900002)
- Ricketts, T. H. *et al.* 2008 Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.* **11**, 499–515. (doi:10.1111/j.1461-0248.2008.01157.x)
- Roland, J. & Taylor, P. D. 1997 Insect parasitoid species respond to forest structure at different spatial scales. *Nature* **386**, 710–713. (doi:10.1038/386710a0)
- Schluter, D. 1984 A variance ratio test for detecting species associations, with some applications. *Ecology* **65**, 998–1005. (doi:10.2307/1938071)
- Solan, M., Cardinale, G. J., Downing, A. L., Engelhardt, K. A. M., Ruesink, J. L. & Srivastava, D. S. 2004 Extinction and ecosystem function in the marine benthos. *Science* **306**, 1177–1180. (doi:10.1126/science.1103960)
- Stanghellini, M. S., Ambrose, J. T. & Schultheis, J. R. 1998 Seed production in watermelon: a comparison between two commercially available pollinators. *HortScience* **33**, 28–30.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C. & Tscharntke, T. 2002 Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* **83**, 1421–1432. (doi:10.2307/3071954)
- Tilman, D. 1996 Biodiversity: population versus ecosystem stability. *Ecology* **77**, 350–363. (doi:10.2307/2265614)
- Tilman, D. 1999 The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**, 1455–1474. (doi:10.2307/176540)
- Tilman, D., Lehman, C. L. & Bristow, C. E. 1998 Diversity–stability relationships: statistical inevitability or ecological consequence? *Am. Nat.* **151**, 277–282. (doi:10.1086/286118)
- Tilman, D., Reich, P. B. & Knops, J. M. H. 2006 Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**, 629–632. (doi:10.1038/nature04742)
- Vázquez, D. P., Morris, W. F. & Jordano, P. 2005 Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecol. Lett.* **8**, 1088–1094. (doi:10.1111/j.1461-0248.2005.00810.x)
- Walker, B., Kinzig, A. & Langridge, J. 1999 Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* **2**, 95–113. (doi:10.1007/s100219900062)
- Winfree, R., Williams, N. M., Dushoff, J. & Kremen, C. 2007 Native bees provide insurance against ongoing honey bee losses. *Ecol. Lett.* **10**, 1105–1113. (doi:10.1111/j.1461-0248.2007.01110.x)
- Winfree, R., Williams, N. M., Gaines, H., Ascher, J. S. & Kremen, C. 2008 Wild bee pollinators provide the majority of crop visitation across land use gradients in New Jersey and Pennsylvania. *J. Appl. Ecol.* **45**, 793–802. (doi:10.1111/j.1365-2664.2007.01418.x)
- Yachi, S. & Loreau, M. 1999 Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl Acad. Sci. USA* **96**, 1463–1468. (doi:10.1073/pnas.96.4.1463)