

## LETTER

# Abundance of common species, not species richness, drives delivery of a real-world ecosystem service

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### Abstract

Biodiversity-ecosystem functioning experiments have established that species richness and composition are both important determinants of ecosystem function in an experimental context. Determining whether this result holds for real-world ecosystem services has remained elusive, however, largely due to the lack of analytical methods appropriate for large-scale, associational data. Here, we use a novel analytical approach, the Price equation, to partition the contribution to ecosystem services made by species richness, composition and abundance in four large-scale data sets on crop pollination by native bees. We found that abundance fluctuations of dominant species drove ecosystem service delivery, whereas richness changes were relatively unimportant because they primarily involved rare species that contributed little to function. Thus, the mechanism behind our results was the skewed species-abundance distribution. Our finding that a few common species, not species richness, drive ecosystem service delivery could have broad generality given the ubiquity of skewed species-abundance distributions in nature.

### Keywords

Biodiversity-ecosystem functioning, biodiversity-ecosystem function, dominance, pollination, pollinator, species-abundance distribution.

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## INTRODUCTION

Several decades of biodiversity-ecosystem functioning research has shown that in experimental settings, biodiversity loss strongly reduces ecosystem functioning (Cardinale *et al.* 2012; Tilman *et al.* 2012). Across hundreds of experiments, the loss of species richness, as well as the loss of particular species (termed species composition or identity effects), both have strong effects on function (Cardinale *et al.* 2012). These findings, however, have remained largely untested in real-world, larger scale systems (Duffy 2009; Cardinale *et al.* 2012). Understanding of the role of biodiversity in maintaining real-world ecosystem services is an important goal given high rates of biodiversity loss (Pimm *et al.* 2014) and the reliance of much of the world's population on ecosystem services (Millennium Ecosystem Assessment 2005).

There are several reasons why the real-world relationship between biodiversity and ecosystem services (BES) might differ from the findings of smaller scale experiments investigating the biodiversity-ecosystem functioning (BEF) relationship. First, experimental communities typically have low numerical dominance (Dangles & Malmqvist 2004; Kirwan *et al.* 2007), whereas real-world communities universally have strong dominance (McGill *et al.* 2007). Abundance or its proxy, biomass, can be a good predictor of function for a variety of ecosystem functions and services (Grime 1998; Smith & Knapp 2003; Dangles & Malmqvist 2004; Vázquez *et al.* 2005). Thus, dominance could weaken the effect of richness, because there might be many rare species each of which contributes little to func-

tion. Second, aggregate abundance (the total number of individuals per community) is generally controlled in BEF experiments, but can vary greatly across real-world communities. Thus, abundance could be an important driver of the BES relationship, even if it has only rarely been explored in BEF experiments (Hulvey & Zavaleta 2011).

Third, in most BEF experiments communities of different richness levels are assembled randomly, whereas real-world communities disassemble non-randomly, with the most extinction-prone species being lost first. Therefore, if the most extinction-prone species also contribute disproportionately to function, function will decay rapidly with species loss. Conversely, if the more functional species are lost last, function will decay slowly. Both cases can be compared to the null expectation of linear loss of function with decreasing richness, which occurs under the random loss scenario (Larsen *et al.* 2005). As yet we know little about the species loss orders observed in real-world ecosystems (Larsen *et al.* 2005; Wardle *et al.* 2011). Lastly, there is the issue of scalability in both space and time. Delivery of real-world ES is determined across hundreds of km<sup>2</sup> and over multiple years, whereas the typical unit in a BEF experiment is the size of a 20-L bucket, and the typical duration < 1 organismal generation (Cardinale *et al.* 2009). The increase in scale has been predicted to make biodiversity both more (Duffy 2009; Cardinale *et al.* 2012) and less (Jiang *et al.* 2009) important to ecosystem services.

It has been difficult to test these hypotheses about how the BEF and BES relationships might differ because ecologists have lacked analytical tools that can separate the effects of

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the different components of biodiversity (species richness, composition, and abundance) on ecosystem services. Large-scale, real-world data are often associational, and the components of biodiversity are often strongly correlated. Few BES studies have rigorously separated the causal role of the different components of biodiversity, and perhaps for this reason, results to date are highly variable (Cardinale *et al.* 2012).

Recently, an analytical innovation based on the Price equation from evolutionary biology has made more rigorous BES analyses possible (Fox 2006; Fox & Harpole 2008; Fox & Kerr 2012). The Price equation partitions biodiversity's effect on function into five additive components: species richness losses that are random with respect to the pollination function the species provides (RICH-L), species richness gains that are random with respect to the pollination function the species provides (RICH-G), species composition effects that capture any non-randomness with respect to function of the species that were lost (COMP-L), species composition effects that capture any non-randomness with respect to function of the species that were gained (COMP-G), and changes in abundance of species that are always present (ABUN) (Fox 2006; Fox & Harpole 2008; Fox & Kerr 2012). The RICH-L corresponds conceptually to the effect of richness as measured in BEF experiments that seek to remove composition effects, through combinatorial designs and/or statistical methods. In the real-world context, the RICH-L measures the reduction in function that would occur with a given level of species loss, if species were lost randomly with respect to their functional contribution. The COMP-L corresponds conceptually to compositional and/or identity effects in BEF experiments. In the real-world context it measures the change in function attributable to the fact that species were not lost randomly with respect to function. For example, a positive COMP-L means that the lower functioning species were lost, thereby increasing function over what it would be if species loss were random. Because the five terms of the Price partition are additive, the sum of RICH-L+COMP-L represents the total change in function attributable to species loss, including both its random and non-random components. The two terms representing species gain, RICH-G and COMP-G, have parallel interpretations to those representing species loss. The ability to include species gains, not just losses, is a strength of the Price approach in a BES context because species composition is rarely nested across sites in nature (although it often is nested in experiments). Lastly, ABUN represents changes in function attributable to abundance fluctuations independent of changes in richness.

Here, we present the first Price equation analysis of the real-world BES relationship, using four large-scale data sets on crop pollination by wild bees. While our data collection and analysis methods cannot fully capture the complexity of real-world ecosystem services, they represent a significant step forward in that they are based on field measurements of pollinator visitation rates and pollen deposition as done by free-living wild bee communities in commercial crop fields. Specifically, we answer three questions: (1) What is the relative importance of changes in species richness, species composition, and abundance in explaining variation in ecosystem service delivery over space and time?, (2) Is species loss order

random with respect to function? and (3) Do skewed species-abundance distributions act as a mechanism behind differences between the BEF and the BES relationships? We found that abundance fluctuations of a few dominant species drove changes in ecosystem services across space and time. In contrast, species richness was less important, because a non-random set of rare and functionally unimportant species accounted for most species richness changes. Thus, the skewed species-abundance distribution was the mechanism that decoupled species richness from ecosystem services.

## METHODS

### Study systems and species

We used parallel study designs and data collection methods to measure crop pollination by wild bees in four study systems. Our first system was watermelon (*Citrullus lanatus*) pollination in the eastern USA, where we worked at 15 farms within a 90 × 60 km area of central New Jersey and east-central Pennsylvania over 3 years (2010–2012). Second, we studied cranberry (*Vaccinium macrocarpon*) pollination at 16 farms within a 40 × 24 km region in southern New Jersey, over 2 years (2009–2010). Third, we studied highbush blueberry (*Vaccinium corymbosum*) pollination at 16 farms within a 35 × 55 km region in southern New Jersey over 3 years (2010–2012). Fourth, we studied watermelon pollination in the western USA, at 7 farms within a 38 × 48 km area of the Central Valley region, California over 3 years (2010–2012). All of our focal study plants require animal-mediated (primarily bee) pollination for the production of marketable fruits (Klein *et al.* 2007). Our focal pollinators were the wild and predominantly native bee species that provide crop pollination as an ES. We did not include the European honey bee (*Apis mellifera*) in our analysis because it is a domesticated species in our study systems, with commercial hives stocked in crop fields by farmers.

### Data collection

At each farm, we established a transect within the crop row where the data were collected. In order to identify the pollinator species providing ecosystem services at each farm, and the relative abundance of each species, we used temporally stratified sampling with insect nets to collect bees visiting crop flowers throughout the transect during the peak bloom period of the crop. Total data collection effort was 135 days for eastern watermelon, 64 days for cranberry, 144 days for blueberry and 63 days for western watermelon. In order to measure the pollination provided by each type of bee, we performed experiments with virgin flowers in which we measured the number of pollen grains deposited in a single bee visit to a flower. In these experiments, because it is not possible to identify most native bees to the species level in the field, we grouped morphologically similar species into species groups (Table S1). Further detail on the study systems, sites and data collection methods are available for all four systems in Text S1, and in published sources specifically for the eastern watermelon (Winfree *et al.* 2007; Winfree & Kremen 2009; Rader *et al.* 2013), cranberry (Cariveau *et al.* 2013), blueberry (Benjamin

*et al.* 2014), and western watermelon (Kremen *et al.* 2002; Garibaldi *et al.* 2013) systems.

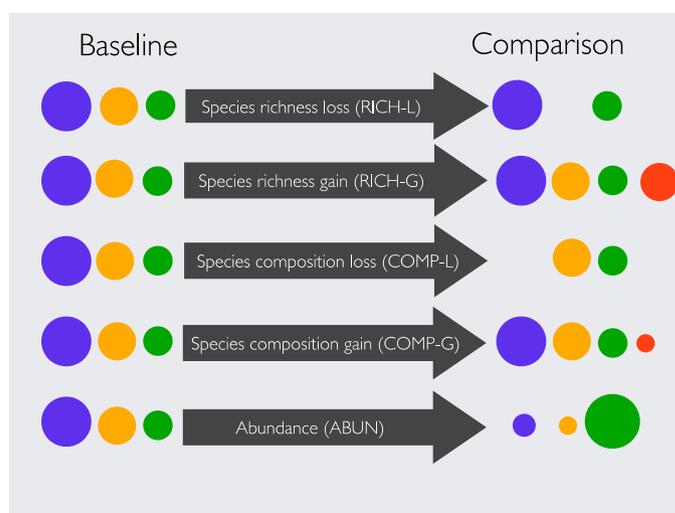
### Estimating pollination services

To estimate the pollination services provided by each bee species at each site in each year, we multiplied the number of individuals of that species collected on flowers at that site and year, by the mean number of pollen grains deposited per flower visit, as calculated for the species group to which the bee species belongs. The pollination services delivered by the entire bee community in a given site-year are then the sum of pollen grains deposited over all bee species present in that site-year. These methods have been developed and tested elsewhere (Kremen *et al.* 2002; Winfree *et al.* 2007; Cariveau *et al.* 2013; Garibaldi *et al.* 2013; Rader *et al.* 2013) and are further detailed in Text S1, along with sensitivity analysis on our use of the mean, as compared with alternative metrics from the distribution of single-visit pollen deposition values.

### Analytical methods – the price equation

The Price equation is based on the change in ecosystem function (or services) between a baseline site, which has more pollination services, and a comparison site, which has less. The total difference in pollination between the two sites is partitioned into the five terms of the Price equation: changes in function due to random species richness losses (RICH-L); random species richness gains (RICH-G); non-random species losses, i.e. a species composition effect (COMP-L); non-random species gains (COMP-G); and fluctuations in abundance for species present at both sites (ABUN) (Fox & Kerr 2012). Figure 1 shows a graphical illustration of simple hypothetical cases in which the effects occur more or less separately; in nature all five effects will generally co-occur. For instance, loss or gain of species from the baseline site changes both species richness and species composition, so that functional effects of species richness and composition necessarily accompany one another. The power of the Price equation is that it separates and quantifies all five effects into additive components even when they co-occur (Fox & Kerr 2012). Box 1 reviews the uses of the Price equation in BEF/BES studies as compared with evolutionary biology, and Appendix S1 provides more detailed background on the Price equation.

We conduct parallel analyses over space and time, using the Price equation to evaluate which aspects of community structure drive changes in function across sites within years, and across years within sites. Thus, when we make comparisons across sites within a year, we compare all other sites to the site that had the highest function in that year, and when we make comparisons across years at the same site, we compare all other years to the year that had the highest function at that site. While the use of the highest-functioning site as the baseline constrains the sum of the terms to be negative, it does not constrain the relative importance of the five terms, which is our primary question, and it makes our results more interpretable with respect to which components of biodiversity are most important in driving changes in function over space and time (see Text S1).



**Figure 1** A cartoon illustrating the five components of the Price equation as applied to the biodiversity-ecosystem function relationship. Different colours represent different species, and size represents the amount of ecosystem function each species provides. The species richness terms represent changes in richness that are random with respect to function, such that the lost or gained species provide the mean level of function. The species composition terms represent changes that are non-random with respect to function. The abundance term represents abundance fluctuations with no changes in richness or composition between sites.

We calculated the Price equation partition using the outcome variable pollination function, which we measured in units of pollen grains deposited on stigmas. However, in our presentation of the results below we normalize the output for each site-year by the largest value in that sample (i.e. the largest of the terms in a given comparison) to rescale to a  $-1$  to  $1$  range. This normalization makes the relative strength of each of the terms comparable among pairs of sites or years that had different total changes in pollination function, and also comparable across the different crop plants, which produce different amounts of pollen and have different thresholds for full pollination, thus making the unit of a ‘pollen grain’ incommensurate across plants.

### Analytical methods – species-abundance distributions

We explored the role of the underlying species-abundance distribution in determining the results of the Price equation analysis in several ways. First, to obtain a visual assessment of the degree of functional dominance in our study systems, we plotted the species-function distributions for each data set. These distributions are analogous to species-abundance distributions, but use the number of pollen grains deposited in place of the number of individuals (Balvanera *et al.* 2005). Second, to assess the role of abundance in determining function, we calculated the Pearson’s correlation between abundance and function for each study system, using species as the replicate. Third, we assessed the relative contributions of functionally dominant and functionally unimportant species to changes in species richness and abundance between sites. The functionally dominant species were defined as the

### Box 1 The use of the Price equation in biodiversity-ecosystem functioning research

The Price equation originally was developed to partition the effects of different causes of directional evolutionary change in mean phenotype in an evolving population (Price 1970, 1972). It is not itself a model of evolution, in that it makes no substantive assumptions about the evolutionary process (e.g. about population sizes, strength of selection, or other evolutionary parameters). Rather, it is a descriptive tool, showing how to calculate the effects of any and all underlying processes that might contribute to directional evolutionary change. It is now an established analytical tool in evolutionary biology (Frank 1997, 2012; Gardner 2008). Fox (2006), Kerr & Godfrey-Smith (2009), and Fox & Kerr (2012) extended the Price equation to cover a wider range of situations, and showed how the same mathematics used to describe directional evolutionary change also could be used to describe directional change in ecosystem function or services. In this Box we briefly discuss the interpretation of the Price equation in the BEF/BES as compared with the evolutionary context. We draw heavily on Fox & Kerr (2012) as well as Kerr & Godfrey-Smith (2009), and refer readers to those papers for further discussion, as well as to Appendix 1 for a mathematical derivation of the Price equation as used in our study.

As used in BEF/BES analysis, the Price equation compares the communities at two sites (or times; for simplicity we discuss sites) and the function they provide. The Price equation partitions the difference in function between the two sites into additive components attributable to differences in various components of community structure. For convenience, we refer to one site as the 'baseline' site and the second as the 'comparison' site, but the directionality is not essential to the analysis. The baseline site is analogous to the ancestral population in evolution, and the comparison site is analogous to the descendent population. The five terms of Price partition can be interpreted as follows. The RICH-L term is the amount by which total function would decline if the number of species lost from the baseline site (i.e. the number of species present at the baseline site but not the comparison site) had been lost at random with respect to the function they provide. The RICH-G term has interpretations parallel but opposite to the RICH-L. It represents the amount by which function would increase between the baseline and comparison sites if the species gained at the comparison site had been gained at random with respect to their function. The two RICH terms have no evolutionary analogue (Fox 2006; Fox & Kerr 2012).

The species composition (COMP) terms capture non-randomness with respect to function in the identity of the species lost and gained. For example, if the species lost from the baseline site were those that contributed the most to ecosystem function, then the COMP-L term would reflect this and increase the loss of function beyond the random case (RICH-L). Analogously, in evolutionary biology, if large-bodied individuals die, the mean body size of the descendant population will be reduced. The COMP-G term has the same interpretation but applies to species gain at the comparison site. The COMP-G term is analogous to non-random immigration in evolution. If the migrants into the descendant population are larger than the residents, immigration will increase mean body size in the descendant population.

The final term, ABUN, captures the between-site difference in function due to between-site variation in the abundances of species that are present at both sites. The ABUN term is analogous to biased transmission in evolution. Biased transmission in evolution refers to any factor that causes the phenotypes of descendant organisms to differ on average from the phenotypes of their ancestors. For instance, if for some reason (say, an environmental change) the offspring are smaller than their parents were, this would reduce the mean body size of the offspring population compared to the parental population. Analogously, any factor that causes species present at both sites to function differently at the two sites will contribute to between-site variation in function. In our dataset, abundance is the only such factor, because we assume that species do not exhibit between-site variation in their per-capita rates of pollen deposition.

minimum set of wild bee species that collectively provide  $\geq 50\%$  of the total wild bee pollination in that study system. Although we did not include the managed honey bee in our analyses (see Methods and Text S1), this is likely a bias against our hypothesis and findings about the importance of dominant species, because honey bees would have been an additional strongly dominant species that was present at virtually all sites and years, thus its abundance fluctuations likely have strong effects on pollination. The functionally unimportant species were defined as those that contributed  $\leq 2\%$  of the total pollination in the system. Alternative definitions obtained qualitatively similar results (data not shown).

All analyses were done in R version 2.15.3 (R\_Core\_Team 2013). Source code used to calculate the Price equation partition is available as Appendix S2.

## RESULTS

In the eastern watermelon system we collected 3483 individual bees of 56 species and 287 single-visit pollen deposition records; in the cranberry system 2992 bees of 54 species and 193 pollen deposition records; in the blueberry system 1087 bees of 43 species and 305 pollen deposition records; and in the western watermelon system 681 bees of 23 species (only three of which were also found in the eastern watermelon system) and 406 pollen deposition records (Fig. S1). Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.6qd88>

### The five price equation terms

Results for the Price equation partition were qualitatively similar across space and time, with the rank order of the five terms

being the same in 88% of comparisons between the medians obtained for the across-space vs. across-time analyses within a given system (Fig. 2). Results were also qualitatively similar across three of our four study systems (Fig. 2). We report the results of the three similar systems first, before presenting the fourth (blueberry) along with possible reasons for its difference. In the eastern watermelon, cranberry, and western watermelon systems the effect of random species loss (RICH-L) was large and negative, indicating that if species had been lost randomly with respect to their function, species loss would have strongly reduced pollination between sites and years. The effect of random species gain (RICH-G) was smaller and positive. However, both species composition effects (COMP-L and COMP-G) were opposite in sign to their corresponding richness effects, indicating that the non-random loss of low-functioning species partially cancelled the random effects. In these three systems, the abundance effect (ABUN) is strongly negative and similar in magnitude to the RICH-L, indicating that abundance losses for species present at both sites reduce pollination as strongly as would random loss of species richness (Fig. 2). The fourth system, blueberry, differs from the above pattern in two ways. First, ABUN is at most 40% as large as RICH-L, indicating that abundance losses did not reduce pollination as much as would random richness losses. Second, the SCE terms are smaller, indicating that species losses were slightly biased towards low-functioning species but not as biased as in the other three systems (Fig. 2).

#### Additive combinations of the Price equation terms

Three combinations of species-related effects are compared with the abundance effect (ABUN) in Fig. 3. Again considering the eastern watermelon, cranberry, and western watermelon systems jointly, the total effect species loss, including both its random and non-random components (RICH-L+COMP-L), is always negative but is on average only 0.27 of the RICH-L alone, and only 0.31 of the abundance effect. The net effect of species gain, including both its random and non-random components (RICH-G+COMP-G), is positive but small. Thus, overall, the sum of all species-related effects, including both random and non-random losses, and both loss and gain of species (RICH-L+RICH-G+COMP-L+COMP-G), is on average only 0.15 the effect of abundance (ABUN). The blueberry system shows a different pattern, with the RICH-L+COMP-L effect being larger than the ABUN effect, such that the sum of all species-related effects is 1.7 times the abundance effect (Fig. 3).

#### Dominance as a mechanism for the Price results

Species-function histograms for the four systems showed that in all cases, the distribution of per-species functional contribution to total pollination services was highly skewed, such that a small number of species contributed a large proportion of the total function, whereas the majority of species contributed little (Fig. 4). The species-function distribution is driven by the species-abundance distribution: values of Pearson's  $r$  between the total number of individuals collected for a bee species, and the total number of pollen grains deposited by

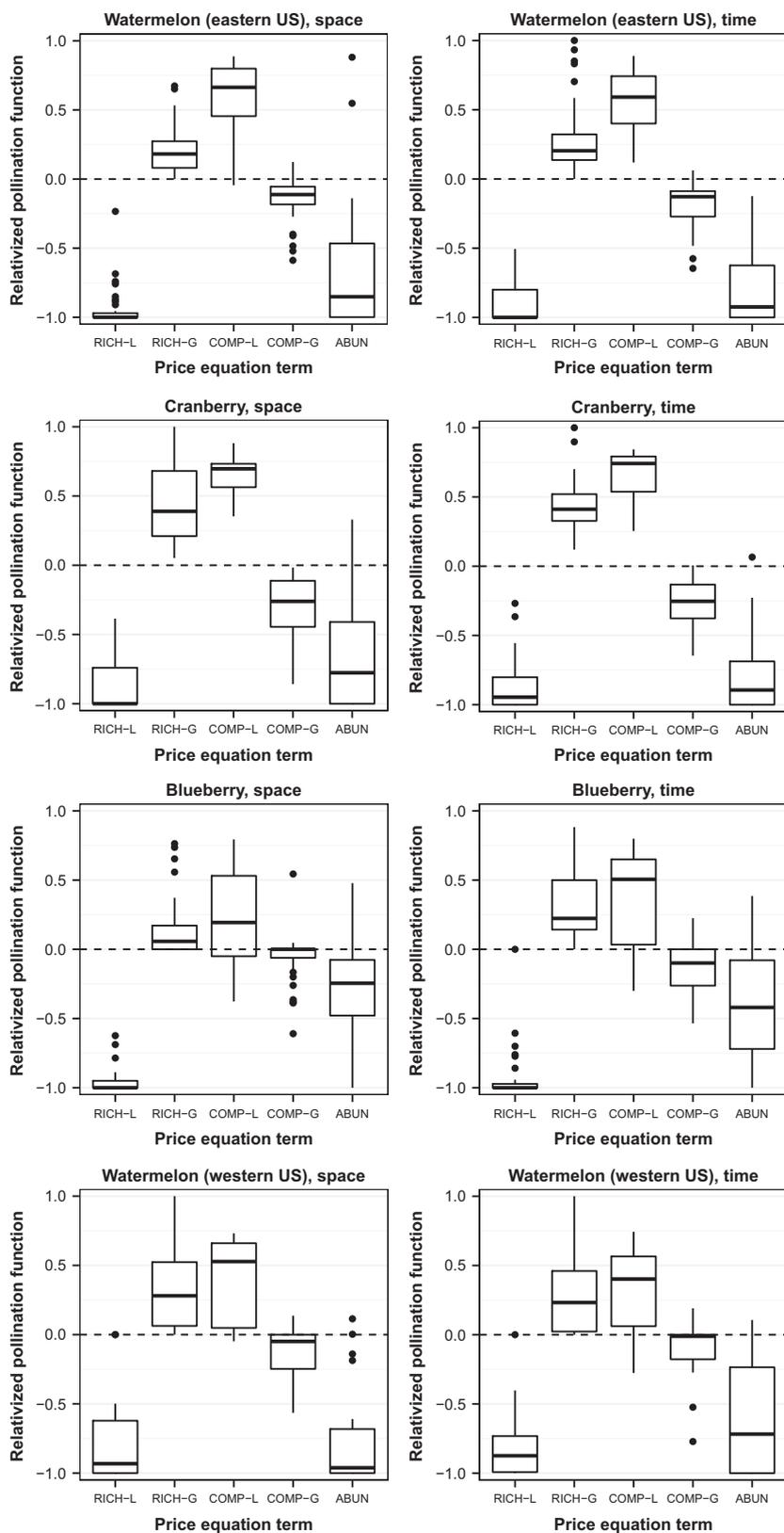
that species, were high in all four systems (eastern watermelon  $r = 0.95$ ,  $n = 56$  species; cranberry  $r = 0.92$ ,  $n = 54$  species; blueberry  $r = 0.95$ ,  $n = 43$  species; and western watermelon  $r = 0.93$ ,  $n = 23$  species). Although our methodology for estimating function as the product of individuals and function per individual makes such a correlation likely, it does not constrain it to be the case. The same expectation pertains to the per-individual function measure, which was not strongly correlated with total function in any of the four systems (eastern watermelon  $r = 0.15$ , cranberry  $r = 0.31$ ; blueberry  $r = 0.42$ ; and western watermelon  $r = -0.08$ ). The likely mechanism for the greater importance of visitation rate as compared with per-visit pollen deposition is the larger variance of the former, as found by Vázquez *et al.* (2005).

Lastly, we explored a possible mechanism through which functionally dominant species could cause both the weak richness effects observed in three study systems, and the stronger richness effects found in the blueberry system. In the first three study systems, only two dominant species collectively accounted for  $\geq 50\%$  of the total pollination function (dominant species are identified in Table S1). Because these functionally dominant species were also numerically dominant, they were present in most sites and years, and thus contributed little to changes in richness or composition between sites (eastern watermelon, functionally dominant species accounted for 4% of richness changes; cranberry 0%; western watermelon 1%). In the blueberry system, there were 4 dominant species, and they were absent from more sites and years, overall accounting for 18% of richness changes. In contrast, functionally unimportant species, defined as those contributing  $< 2\%$  of the total pollination in the system, accounted for most of the changes in richness between sites in all four systems (eastern watermelon, 82%; cranberry 88%; blueberry 56%; western watermelon 51%). Thus, richness changes were driven by rare, not dominant species in all four systems, although dominant species played a stronger role in richness changes in the blueberry system than in the other systems.

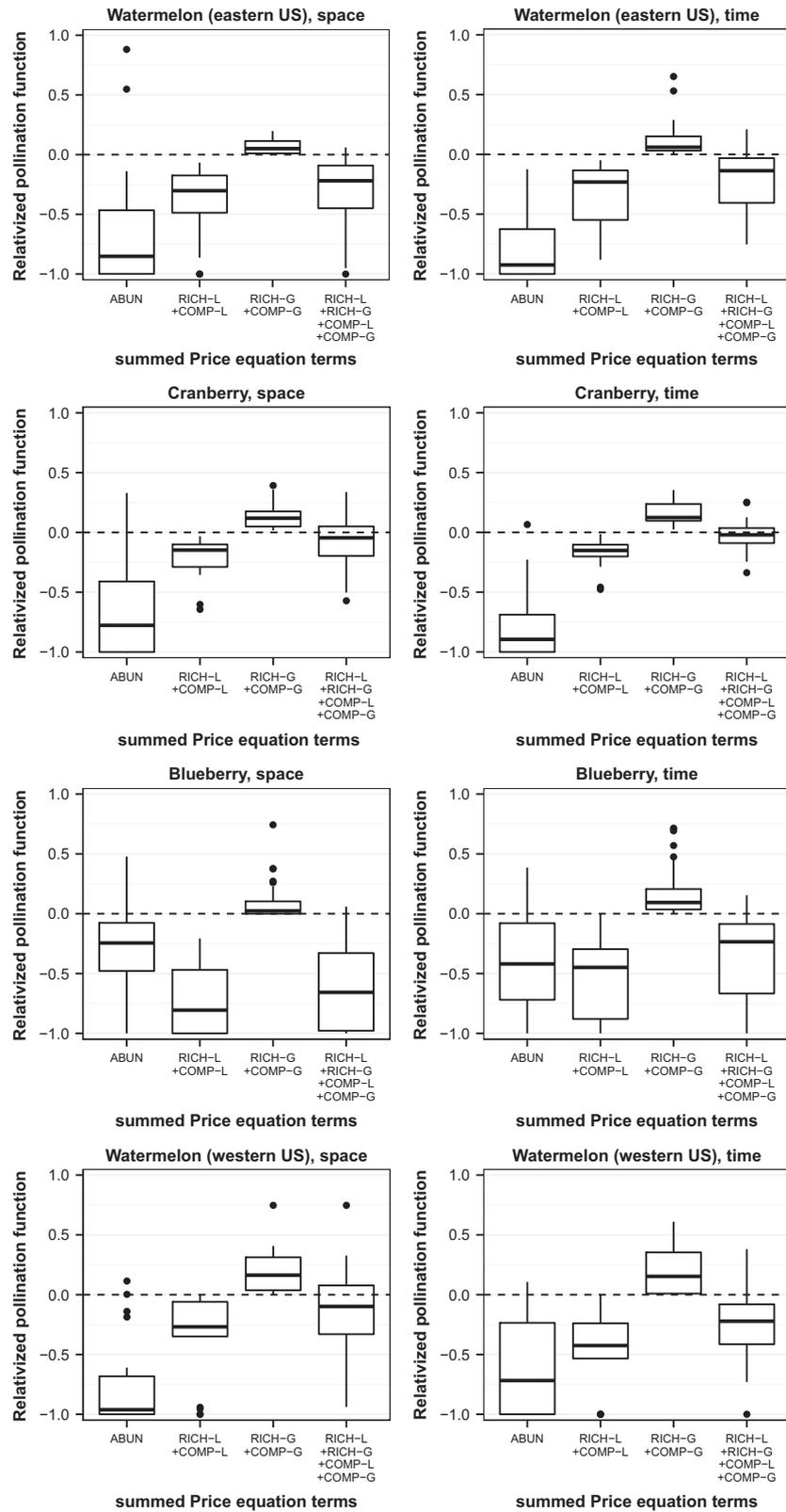
In all four systems, abundance variation was driven by the dominant pollinator species, which varied greatly in abundance (up to two orders of magnitude) across sites and years where they were always present. In contrast, functionally unimportant species, because they were rare, contributed little to abundance fluctuations.

#### DISCUSSION

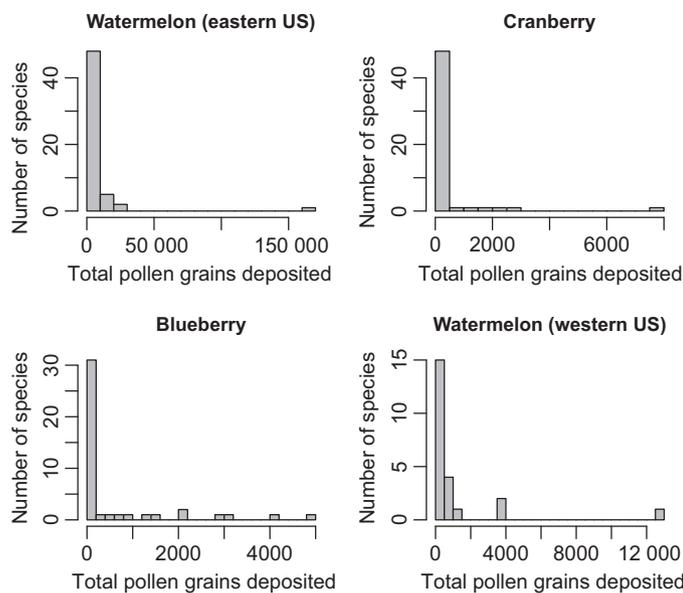
We conducted one of the first large-scale studies to separate the effects of species richness, composition, and abundance on real-world ecosystem services. We found some similarities with the findings of smaller scale biodiversity-ecosystem functioning experiments, but also some important differences. Consistent with BEF experiments, we found that random loss of species has (or would have) large functional effects, and that the identity of the species that are lost is also important. Unlike most BEF experiments, our data sets arose from real-world species-abundance distributions and species loss orders, and these factors largely ameliorated the effects of random species loss. Specifically, species loss was highly non-random with respect to function, with the less functionally important



**Figure 2** Relative importance of the five terms in explaining differences in pollination function across sites within a year (spatial analysis; left column) and across years at a given site (temporal analysis; right column). Y axis is originally in units of pollen grains but has been normalized within a site-year such that it represents the relative strength of the five effects. Boxes encompass the 25th–75% quartiles and whiskers extend to the last data point within another 1.5 times the interquartile range.



**Figure 3** Parallel to Fig. 2, but now comparing the original abundance effect (ABUN) with three combinations of terms representing effects of the following: total changes in function due to species loss (RICH-L+COMP-L); total changes in function due to species gain (RICH-G+COMP-G); and total changes in richness and composition (RICH-L+COMP-L+RICH-G+COMP-G).



**Figure 4** The species-function histograms for each of the four study systems. Function is measured as total number of conspecific pollen grains deposited and is summed within bee species over sites and years.

species accounting for most richness losses (Fig. 2). Thus, the total observed effect of species loss on function, including both its random and non-random components, was relatively weak (Fig. 3). Our second major finding is that, in three of our four systems, abundance fluctuations had larger effects on ES than did all species-related effects combined (Fig. 3). In BEF experiments, abundance is generally standardized both across and within the experimental communities, such that all communities have the same aggregate abundance and high evenness (Dangles & Malmqvist 2004; Kirwan *et al.* 2007; Cardinale *et al.* 2012). This makes it more likely that species-related effects will be detected, both because variation due to abundance is controlled, and because evenness maximizes complementarity among species, which is a main mechanism for increasing function with increasing richness (Jiang *et al.* 2009; Crowder *et al.* 2010). In contrast, in real-world systems abundance variation is commonplace.

The mechanism behind our findings is the skewed species-function distribution, which decoupled the relationship between species richness and function. A few common and functionally dominant species drive the changes in function, whereas many rare but functionally unimportant species drive richness. Given that real-world ecological communities universally have strongly skewed species-abundance distributions, our result could be a general one (McGill *et al.* 2007). When species contribute to function in proportion to their abundance, as proposed by the mass ratio hypothesis (Grime 1998), and supported empirically for pollination systems (Vázquez *et al.* 2005), then in general a small number of dominant species would make disproportionate contributions to function (as we found here). We would expect rare species to be lost and gained most frequently for both biological and statistical (sampling) reasons (Smith & Knapp 2003; Suding *et al.* 2005; Winfree *et al.* 2014). In contrast, the dominant

species, which have strong functional effects, rarely contribute to changes in species richness or composition because they are present at most sites in most years. However, the abundance fluctuations of common species contribute strongly to abundance effects. In our study, one of our four systems had more functionally dominant species, and these turned over more often between sites and years. This system also showed stronger richness effects and weaker abundance effects (Fig. 3, Fig. 4), suggesting that the exact shape of the species-function distribution could be a strong determinant of the BES relationship. Other real-world studies conducted in grassland and stream communities, while being done at smaller spatial scales than ours, have likewise found that dominant species are more important to function than are the rare species that compose most of the species richness (Smith & Knapp 2003; Dangles & Malmqvist 2004).

Most studies investigating the functional effects of species loss order on real-world ecosystem services have focused on traits of species that predict both response to disturbance, or extinction sensitivity ('response traits'), and those that predict a large contribution to function ('effect traits') (Larsen *et al.* 2005; Selmants *et al.* 2012). When the same natural history trait serves as both a response and an effect trait – for example large body size – then the most functionally important species are lost first, leading to a rapid decay in function (Larsen *et al.* 2005). Rarity has less often been considered as a trait in this context, but might in fact have wider generality as a response trait than do morphological and other natural history traits, given the extinction-proneness of rare species (Davies *et al.* 2004). The generality of rarity as an effect trait will depend on the functional importance of rare species, which is a controversial topic about which there is conflicting evidence (Zavaleta & Hulvey 2004; Lyons *et al.* 2005; Vázquez *et al.* 2005; Gaston 2010; Mouillot *et al.* 2013; Wielgoss *et al.* 2014).

Here, we use a new analytical tool, Price equation analysis, for the first time with landscape-scale BES data. The Price equation is ideally suited for such data because it partitions the functional effects of species richness, composition, and abundance into additive components. It also separates the random and non-random components of species loss, which is likewise difficult to do without combinatorial experiments. In our analyses, the Price equation clearly showed that species richness changes involved a non-random subset of low-functioning species, because the terms representing the non-random component of species richness changes (COMP-L and COMP-G) are always opposite in sign to the random terms (RICH-L and RICH-G; Fig. 2). Furthermore, random and non-random components of species loss tend to cancel each other: larger negative values of RICH-L are associated with larger positive values of COMP-L (mean Spearman's coefficient =  $-0.50$ ). Thus, regardless of how many species were lost, the net effect of species loss on function tends towards zero.

However, our approach also has limitations as a method for assessing the real-world biodiversity-ecosystem services relationship. One issue is that the Price equation evaluates the drivers of changes in ecosystem service delivery over space or time, but does not provide information about how many species are necessary in order to achieve some target level of ser-

vice delivery (and indeed we did not measure total pollination, relative to some target, in our study). Thus, although we know that pollinator species richness declines by a mean of 30% as one moves from sites with the most pollination services to sites with less, our analysis methods do not determine what level of pollinator biodiversity is necessary to achieve sufficient pollination. A related point is that although we know the magnitude of species loss, we do not know the causes, which may or may not be the same as the causes of larger scale (regional and global) pollinator species declines. A second limitation is that our data collection methods, while being based on real-world crop flower visitation rates, do not allow us to capture the full real-world complexity of ecosystem service delivery. For example, because our measures of pollination function are based on single-visit experiments with virgin flowers, we do not capture species interactions such as spatial or temporal complementarity, which have been found to increase crop production in some systems (Klein *et al.* 2009). Likewise, because we measured pollen deposition, not crop yield, our study excludes any potential nonlinearity or other factors that modify this relationship. However, a synthetic analysis of hundreds of crop fields shows that pollinator visitation rate, pollen deposition, and crop fruit set are positively and significantly correlated, suggesting that pollen deposition should be a good proxy for crop yield, in general (Garibaldi *et al.* 2013). Lastly, because our time series were only 2–3 years, our results likely underestimated the insurance effects of species richness, wherein a pollinator species that is not important to ecosystem services now might be important in the future (but see Kremen *et al.* 2002, where significant insurance effects were detected in a 2-year time series).

In conclusion, we use a promising new analytical method to show that the effects of species richness and composition on a valuable ecosystem service are generally weaker than the effects of abundance variation in a few dominant species. Our study contributes to the growing evidence for the importance of common species in ecosystem functioning, and to the importance of including realistic species-abundance distributions in explorations of ecosystem function. Our findings bear on the current debates about the extent to which the conservation of ecosystem services, which is rapidly becoming a justification for biodiversity conservation in policy circles, in fact requires the conservation of rare and threatened species (Adams 2014), and whether declines in abundance have large functional consequences that are currently under-recognized (Dirzo *et al.* 2014).

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#### AUTHORSHIP

RW collected data, performed analysis and wrote the manuscript; NMW and DPC collected data; JW and JR performed analysis; and all authors contributed substantially to revisions.

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69 been the case had the same number of species been lost from the baseline site at random with  
 70 respect to their  $z_i$  values.

71 The fourth term,  $-\sum_i (z'_i - z_i)$ , is the COMP-G, the mirror image of the COMP-L. It  
 72 captures the effects of changes in species composition arising from non-random gain of species  
 73 at the comparison site. For example, if species that deposit little pollen at the comparison site are  
 74 absent from the baseline site, while species that deposit much pollen at the comparison site are  
 75 present at the baseline site, then this increases total pollen deposition above what would have  
 76 been the case.

77 The fifth term,  $\sum_i (z'_i - z_i)$ , is the ABUN effect (termed context dependence  
 78 by Fox and Kerr [2012]). This is the sum, over the species common to both sites, of the between-  
 79 site differences in their pollen deposition ( $z'_i - z_i$ ). Species present only at one of the two sites  
 80 do not contribute to this sum because for these species  $z'_i = z_i = 0$ . We refer to this effect as the  
 81 ABUNdance effect because between-site variation in pollen deposition by species  $i$  can only  
 82 arise from between-site variation in abundance of species  $i$  in our dataset, due to the way we  
 83 estimated pollen deposition. For example, if for some reason pollinator species  $i$  deposits less  
 84 pollen at the comparison site than it does at the baseline site (despite being present at both sites),  
 85 this will reduce total pollen deposition at the comparison site compared to the baseline site.

86 The interpretation of the final three terms on the right hand side of equation (3) is  
 87 clarified by writing them in a different, mathematically-equivalent way:

$$88 \quad s_c(\bar{z}' - \bar{z}) + s_c(\bar{z}_c - \bar{z}) - [s_c(\bar{z}'_c - \bar{z}')] + s_c(\bar{z}'_c - \bar{z}_c), \quad (4)$$

89 where  $\bar{z}_c = \frac{1}{|I|} \sum_{i \in I} z_i$  and  $\bar{z}'_c = \frac{1}{|I|} \sum_{i \in I} z'_i$  respectively give the mean pollen deposition per  
 90 species at the baseline and comparison sites by the  $s_c$  species common to both sites. The term  
 91  $s_c(\bar{z}_c - \bar{z})$  equals the COMP-L. It captures whether the species common to both sites differ in

92 their average pollen deposition at the baseline site from all species at that site. If they do, this  
93 implies that the lost species comprise a non-random subset of all baseline site species. Similarly,  
94 the term  $[-s_c(\overline{z'_c} - \overline{z'})]$  equals the COMP-G. This term captures whether the species common  
95 to both sites differ in their average pollen deposition at the comparison site from all species at  
96 that site. If they do, this implies that the gained species comprise a non-random subset of all  
97 comparison site species. Finally, the term  $s_c(\overline{z'_c} - \overline{z_c})$  equals the ABUN effect. This term  
98 captures between-site variation in the average pollen deposition of the species common to both  
99 sites.

100           It might seem surprising that the Price equation can completely separate effects of species  
101 richness, species composition, and abundance in observational datasets. Such a complete  
102 separation is not ordinarily possible with conventional statistical approaches such as general  
103 linear models (GLMs), even when species richness and composition are experimentally  
104 manipulated (Schmid et al. 2002). Two key factors explain how the Price equation can  
105 completely separate the five effects it identifies.

106           First, just because changes in species composition necessarily accompany changes in  
107 species richness does not make their effects confounded in the sense of being partially or  
108 completely inseparable. Whether or not the effects of species richness and composition are  
109 separable depends on how those effects are defined. The Price equation defines effects of species  
110 richness and composition differently than do GLMs or other conventional statistical approaches  
111 (Fox 2006).

112           Second, the Price equation retains all the information about which species are present at  
113 which sites or times, as well as all of the information about the functioning of each species, and  
114 then compares sites or times in a pairwise fashion so as to make full use of that information. In

115 contrast, conventional statistical approaches omit or average away some or all information about  
116 the identities of the species present at each site or time and their individual functional  
117 contributions, in order to combine many sites or times into a single analysis (Fox 2006).

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