

# The relative importance of pollinator abundance and species richness for the temporal variance of pollination services

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**Abstract.** The relationship between biodiversity and the stability of ecosystem function is a fundamental question in community ecology, and hundreds of experiments have shown a positive relationship between species richness and the stability of ecosystem function. However, these experiments have rarely accounted for common ecological patterns, most notably skewed species abundance distributions and non-random extinction risks, making it difficult to know whether experimental results can be scaled up to larger, less manipulated systems. In contrast with the prolific body of experimental research, few studies have examined how species richness affects the stability of ecosystem services at more realistic, landscape scales. The paucity of these studies is due in part to a lack of analytical methods that are suitable for the correlative structure of ecological data. A recently developed method, based on the Price equation from evolutionary biology, helps resolve this knowledge gap by partitioning the effect of biodiversity into three components: richness, composition, and abundance. Here, we build on previous work and present the first derivation of the Price equation suitable for analyzing temporal variance of ecosystem services. We applied our new derivation to understand the temporal variance of crop pollination services in two study systems (watermelon and blueberry) in the mid-Atlantic United States. In both systems, but especially in the watermelon system, the stronger driver of temporal variance of ecosystem services was fluctuations in the abundance of common bee species, which were present at nearly all sites regardless of species richness. In contrast, temporal variance of ecosystem services was less affected by differences in species richness, because lost and gained species were rare. Thus, the findings from our more realistic landscapes differ qualitatively from the findings of biodiversity–stability experiments.

**Key words:** abundance; biodiversity; composition; ecosystem services; Price equation; richness; variance.

## INTRODUCTION

The relationship between diversity and the stability of communities and ecosystems is a fundamental question in theoretical and experimental ecology (MacArthur 1955, Mellinger and McNaughton 1975, Tilman et al. 1996, 1998, Doak et al. 1998, Ives and Hughes 2002, Valone and Hoffman 2003, Loreau and de Mazancourt 2008, Grman and Suding 2010, Hector et al. 2010, Thibaut and Connolly 2013). Beginning in the 1990s, and sparked by clear experimental results showing that species richness decreased the temporal variance of ecosystem function (Tilman et al. 1996), biodiversity research contributed to a broader discussion about how worldwide declines in biodiversity would affect ecosystem services (ES) on which humans rely (Daily 1997). A major

goal of biodiversity research has involved separating the relative importance of richness (number of species), composition (identities of species), and abundance as drivers of temporal variance in ES. However, both the study designs and the analytical approaches used vary between experimental and observational studies. At smaller scales, the field of biodiversity–ecosystem–function research has used controlled experiments and a well-developed body of mathematical theory to explore how species richness and composition affect temporal variance. In contrast, at larger scales, the field of biodiversity–ecosystem–services research has been built mostly on correlative studies conducted in real-world systems (but see e.g., Duffy et al. 2016, Grace et al. 2016), where “real-world” means communities that are not directly manipulated, in which it is difficult to rigorously separate the causal roles of richness, composition and abundance (Millennium Ecosystem Assessment 2005, Cardinale et al. 2012). Because species loss continues to occur at high rates worldwide (Pimm et al. 2014, Gonzalez et al. 2016), it is critical to gain a better

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understanding of how species richness affects temporal variance of ES. This requires the development of novel analytical approaches that can separate the effects of richness, composition, and abundance without experimental manipulations, which are difficult if not impossible to conduct at landscape scales.

An examination of ES in real-world systems is needed because controlled experiments that typify most biodiversity–ecosystem-function research do not fully represent ecological reality (Kremen 2005, Larsen et al. 2005, Balvanera et al. 2014); specifically, these experiments do not mimic realistic species abundance distributions or species loss scenarios. First, a skewed or “hollow curve” species abundance distribution, meaning that communities are composed of few common but many rare species, is ubiquitous in nature (Fisher et al. 1943, Whittaker 1965, Gaston et al. 2000) yet biodiversity–ecosystem-function experiments have not mirrored this pattern and have instead used substitutive designs that equalize initial abundances among species (Dangles and Malmqvist 2004, Kirwan et al. 2007, Byrnes and Stachowicz 2009, Winfree 2013, but see Wilsey and Potvin 2000). Although substitutive designs are arguably preferable for isolating the effects of species richness, they do make experimental communities less realistic and decrease the potential for one dominant species to provide the bulk of ecosystem function. Second, species are lost from communities non-randomly, with environmentally sensitive and rare species being at greater risk of extirpation (Robinson and Quinn 1988, Duncan and Young 2000). In contrast, most biodiversity–ecosystem-function experiments have assigned species to plots at random to avoid confounding species richness and species composition. It is well known that, because of this design, comparing high- and low-richness experimental plots reveals the effects of random species loss, which will under- or overestimate the effects of non-random species loss, depending on whether species with high or low contributions to function are lost first (Schmid and Hector 2004). However, biodiversity–ecosystem-function researchers have countered that understanding the effects of random species loss is an important starting point, given that future patterns of species loss may be unpredictable (Schmid and Hector 2004). Throughout this paper, we use species loss to indicate local (rather than global) extinctions, because ES are delivered by local populations (Kremen 2005). Despite an awareness of these systematic differences between biodiversity–ecosystem-function experiments and real-world ES, there is no consensus on whether species richness will contribute more (Duffy 2008, Cardinale et al. 2012) or less (Jiang et al. 2009) to function when experimental results are scaled up to larger, more complex systems.

Scaling up biodiversity–ecosystem-function research is further complicated because analyzing observational data creates challenges not present in experiments. First, few if any real-world ecosystems allow researchers to independently assess services provided by each species in

the community. This precludes the use of analytical approaches commonly used in biodiversity–ecosystem-function research, especially analyses requiring single-species monocultures (Loreau and Hector 2001, Fox 2006, Thibaut and Connolly 2013, Gross et al. 2014). Second, communities assemble and disassemble non-randomly with respect to species’ contributions to ES, making it difficult to separate the effect of richness from the effects of species identity. Third, the ubiquity of skewed species abundance distributions in nature (McGill et al. 2007) makes it hard to separate the effect of abundance from species identity, if the same species are dominant across sites. Because of these issues, no general analytical method exists for biodiversity–ecosystem-services studies and, perhaps for this reason, no consensus exists on the importance of different components of biodiversity (richness, composition, abundance) for ES (Cardinale et al. 2012).

Here, we present a novel version of the Price equation that can analyze temporal variance of any ES, so long as the ES can be expressed as a sum of species-level contributions. Our work builds on the original Price equation (Price 1970, 1972) from evolutionary biology, and its recent adaptations for biodiversity research (Fox 2006, 2010, Kerr and Godfrey-Smith 2009, Fox and Kerr 2012). Fox (2010) provided the original framework for analyzing temporal variance with the Price equation, and here we extend it so that it can be used with observational data even if species composition is not nested between sites (see *Methods* for a more thorough description of this point). Our version of the Price equation partitions between-site differences in temporal variance into three additive terms: variance in ES attributable to richness (random species loss and gain), composition (non-random species loss and gain), and context dependence (between-site variation in the variance and covariance of ES provided by species present at both sites). Here, we use “abundance” in place of “context dependence” because, in our data, this term is determined by patterns of abundance fluctuation over time (see *Methods* for a more thorough justification of this terminology). The richness term establishes an expectation for how species loss and gain would affect ES if species were identical in the ES each provides. The composition term captures the effects of deviations from this expectation. The abundance term quantifies the extent to which species present at both sites contribute more (or less) to temporal variance of ES at each site.

We explore the temporal variance of pollination services using two large, multi-year data sets on pollination provided by bees. Using the new derivation of the Price equation described above, we ask: What is the relative importance of changes in species richness, composition, and abundance to the temporal variance of ecosystem services? Specifically, we compare the relative importance of richness and composition (which together represent the effects of species loss and gain) vs. abundance.

## METHODS

*Field surveys*

Our study systems consist of the wild bee pollinators of watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai; Cucurbitaceae, native to southern Africa) and northern highbush blueberry (*Vaccinium corymbosum* L.; Ericaceae, native to Eastern North America) plants, both of which rely on insect pollination for successful fruit production. Over five years (2005, 2008, 2010–2012), we sampled wild bee communities at 10 commercial watermelon fields in central New Jersey and eastern Pennsylvania, USA. We also, over three years (2010–2012), sampled wild bee communities at 16 commercial blueberry fields in southern New Jersey. In a post-hoc analysis, we confirmed that differences in our results between study systems were not due to length of sampling (i.e., 3 vs. 5 yr; Appendix S1). Hereafter, we refer to these fields as sites. We ensured that all sites were at least 1 km apart, beyond the typical foraging radius of most bee species in our study (Greenleaf et al. 2007). We did not include the honey bee (*Apis mellifera*) in our data collection, primarily because in our system the honey bee is a managed species that is kept in hives and moved in and out of crop fields by bee-keepers and farmers. Thus, the temporal and spatial variation in honey bee abundance is driven by hive placement rather than ecological factors. In addition, honeybees are the property of bee-keepers and farmers, so we cannot collect them. Finally, honeybees are present at nearly all sites, so including them would likely increase the relative importance of “abundance,” making it conservative with respect to our findings to leave the honey bee out of the analysis. Because watermelon is an annual species, farmers do not necessarily plant it in the same locations each year. To exclude potential effects of spatial variation (e.g., crops grown in higher- or lower-quality environments in different years) on wild bee communities, we included watermelon sites in our analyses only if the maximum among-year distance between transects was  $\leq 435$  m; this is within the typical foraging radius of all but the smallest bee species in our study (Greenleaf et al. 2007).

*Pollination services*

To measure bee richness and the pollination services delivered at each site on each date, we collected two forms of data: the number of individual wild bees visiting flowers, and the number of pollen grains deposited per flower visit. We then multiplied each species' abundance by the mean pollen deposition of its morphological group to obtain that species' contribution to pollen deposition. To measure bee abundance, we established a 50-m transect at each watermelon or blueberry site. We collected bees visiting flowers by net throughout the transect and then processed voucher specimens for species-level identification by taxonomists (completed

by J. Ascher and J. Gibbs). At each site, data were collected on three days during each plant species' peak bloom period, with three temporally stratified 20-min collections during the day; all data collection days were sunny, partly cloudy, or bright overcast with limited wind. Total collection effort was 135 d for watermelon and 144 d for blueberry.

We measured the pollination efficiency per flower visit for different pollinator groups (defined below) in field experiments. We offered a virgin flower to an individual bee foraging in the field, allowed the bee to visit the flower one time, and recorded the pollinator group of the bee (Kremen et al. 2002). These pollen deposition experiments were conducted in three years (2005, 2006, 2012) for watermelon, and in two years (2011, 2012) for blueberry. Back in the laboratory, we use a compound microscope to count the number of conspecific pollen grains deposited during the single flower visit. To prepare slides, watermelon stigmas were softened in 10% KOH, and stained with 1% fuchsin. Blueberry stigmas were softened in 1 mol/L NaOH, and then stained for 48 h in 0.01% analine blue buffered in 1 mol/L  $K_3PO_4$ . In the pollen deposition experiment, individuals were placed into morphologically similar groups that could be differentiated in the field (11 groups for watermelon, 7 for blueberry; Appendix S2). Due to the difficulty of collecting single-visit pollen deposition data, we did not collect these at all sites and in all years. However, we do know that that different morphological groups differed significantly in pollen deposition rates, while species within groups did not (Rader et al. 2013). Further details of all data collection methods, and site details, are available for both watermelon (Winfree et al. 2015) and blueberry (Benjamin et al. 2014).

Because there is substantial variability within each morphological group's distribution of pollen deposition rates, we conducted a sensitivity analysis to test whether choosing a single pollen deposition value (i.e., the mean) and discarding the remaining variability affected our results. Instead of multiplying each bee species' abundance by its morphological group's mean pollination efficiency, for each individual bee, we randomly drew one pollination efficiency value from the correct morphological group's distribution. We repeated this sensitivity analysis 1000 times, and found that the same results were obtained using either the “mean” or “sensitivity” versions of the analysis (Table 1).

*Temporal variance of pollination services*

Our data exists along three axes: sites, species, and years. We organized this data in a series of matrices, with one matrix for each site. Specifically, let  $S_i$  be an  $m \times n$  matrix describing the contribution of bee species  $n$  to pollen deposition in year  $m$  at site  $i$ . The contribution of bee species  $n$  equals its abundance times its group's mean pollination efficiency (see previous paragraph). Then, let  $V_i$  be the variance of  $S_i$ , which is an  $n \times n$

TABLE 1. Comparison of results for total temporal variance, variance, summed covariances.

	COMP-L/RICH-L	COMP-G/RICH-G	Amount due to species loss/gain (%)	
			Main analysis	Sensitivity
Watermelon				
Total temporal variance	−0.854	−0.777	8.6	8.4–14.9
Variance	−0.960	−0.864	2.8	3.7–10.7
Summed covariance	−0.684	−0.629	17.1	16.2–24.6
Blueberry				
Total temporal variance	−0.234	−0.757	41.8	36.0–51.8
Variance	−0.242	−0.610	45.9	41.7–55.8
Summed covariance	−0.227	−2.476	38.7	36.0–48.1

*Notes:* Negative values in the first two columns indicates that composition (COMP) terms cancel corresponding richness (RICH) terms. The −L and −G suffixes indicate loss and gain, respectively. The third column lists the percentage of between-site differences in total temporal variance, variance, or summed covariance explained by species loss and gain; the remaining amount must be due to abundance. The fourth column gives the 95% confidence intervals of a sensitivity analysis designed to evaluate error associated with our estimates of per-individual function. We do not expect the confidence intervals to be symmetric about the mean (or even to necessarily contain the mean) because, after the sensitivity analysis alters each species' contributions to ecosystem services, temporal variance is calculated and the resulting data is run through the Price equation.

variance-covariance matrix, with the diagonal elements describing the variances of each species, and the off-diagonal elements representing the covariances between any pair of species. The sum of  $\mathbf{V}_i$  is then the total temporal variance of ES at site  $i$ . The Price equation decomposes the differences in total temporal variance of ES between any two sites, e.g., between  $\mathbf{V}_1$  and  $\mathbf{V}_2$ .

Total temporal variance must be non-negative, but an individual species can have negative contributions to total temporal variance if its summed covariance is negative and greater in magnitude than its variance. Thus, there is no restriction on the shape of the relationship between species richness and total temporal variance, except that total temporal variance must be non-negative. Although most biodiversity–stability studies have measured stability using the inverse of the coefficient of variation ( $1/\text{CV}$ ; Jiang and Pu 2009, Hector et al. 2010, Campbell et al. 2011), the CV is not always a good indicator of stability because it conflates how mean ES and temporal variance of ES respond to the same environmental changes (Carnus et al. 2015). In addition, the CV of ES cannot be expressed as a sum of independent species-level contributions and thus a broadly applicable Price equation partition is not possible, although versions can be developed for particular cases (see Fox 2010; Supplementary Material for details).

#### Price equation partition

Our partition combines the advances of two previous versions of the Price equation. First, Fox (2010) showed the general framework for using the Price equation to analyze temporal variance. Second, Fox and Kerr (2012), presenting a Price equation partition of mean ES (not temporal variance), showed how to relax a previously existing “nestedness” requirement. In ecology, the

nestedness requirement means that, when comparing two sites, only one site could contain a species not found at the other site (i.e., if both sites contain a unique species, the “nestedness” requirement is not met). That step is crucial for real-world applications because species composition is rarely nested. Here, we apply the logic of Fox and Kerr (2012), specifically, how to remove the nestedness requirement, to extend Fox's (2010) method for analyzing temporal variance with the Price equation. The result is the first version of the Price equation suitable for analyzing temporal variance of ES in real-world systems.

Total temporal variance (sum of matrix  $\mathbf{V}$  for any site) can be subdivided into variance ( $\mathbf{V}_{\text{var}}$ ) and summed covariance ( $\mathbf{V}_{\text{cov}}$ ) components. In  $\mathbf{V}$ , each species has its own row, and thus its own “summed covariance” value, which is equal to its row sum excluding the matrix diagonal. Between-site differences in  $\mathbf{V}_{\text{var}}$  and  $\mathbf{V}_{\text{cov}}$  are partitioned by Eqs. 2 and 3. Then, let  $\mathbf{V}$  and  $\mathbf{V}'$  represent the total temporal variance in ES at any two sites, referred to as a baseline and a comparison site, respectively, such that the difference between any two sites is

$$\Delta \mathbf{V} = \Delta \mathbf{V}_{\text{var}} + \Delta \mathbf{V}_{\text{cov}} = (\mathbf{V}'_{\text{var}} - \mathbf{V}_{\text{var}}) + (\mathbf{V}'_{\text{cov}} - \mathbf{V}_{\text{cov}}). \quad (1)$$

Let  $s$  or  $s'$  represent the number of species at the baseline and comparison sites, and  $s_c$  denote the number of species common to both sites;  $s_c$  must be  $\geq 1$ . Let the  $s$  baseline species be indexed  $i = 1, 2, \dots, s$  and the  $s'$  comparison site species be indexed  $j = 1, 2, \dots, s'$ . For convenience, we index species shared by both sites first and in the same order for both sites. Let  $E$  and  $E'$  represent species-level measures of ecosystem services (i.e., pollen deposition) at the baseline and comparison sites, respectively. Then, we complete separate partitions for the variances and summed covariances



$$\begin{aligned}
\Delta V_{\text{var}} &= (V'_{\text{var}} - V_{\text{var}}) = \sum_{j=1}^{s'} \text{var}(E'_j) - \sum_{i=1}^s \text{var}(E_i) \\
&= \overbrace{\text{var}(E)(s_c - s)}^{\text{RICH}_L} + \overbrace{\text{var}(E')(s' - s_c)}^{\text{RICH}_G} \\
&\quad + \overbrace{\text{Sp}(w, \text{var}(E))}^{\text{COMP}_L} + \overbrace{[-\text{Sp}(w', \text{var}(E'))]}^{\text{COMP}_G} \\
&\quad + \overbrace{\sum_{i=1}^{s_c} \text{var}(E'_i) - \text{var}(E_i)}^{\text{ABUN}}
\end{aligned} \tag{2}$$

$$\begin{aligned}
\Delta V_{\text{cov}} &= (V'_{\text{cov}} - V_{\text{cov}}) \\
&= \sum_{j=1}^{s'} \sum_{m \neq j} \text{cov}(E'_j, E'_m) - \sum_{i=1}^s \sum_{k \neq i} \text{cov}(E_i, E_k) \\
&= \overbrace{\sum_{k \neq i} \text{cov}(E_i, E_k)(s_c - s)}^{\text{RICH}_L} + \overbrace{\sum_{m \neq j} \text{cov}(E'_j, E'_m)(s' - s_c)}^{\text{RICH}_G} \\
&\quad + \overbrace{\text{Sp}(w_i, \sum_{k \neq i} \text{cov}(E_i, E_k))}^{\text{COMP}_L} + \overbrace{[-\text{Sp}(w'_j, \sum_{m \neq j} \text{cov}(E'_j, E'_m))]}^{\text{COMP}_G} \\
&\quad + \overbrace{\sum_{i=1}^{s_c} \sum_{j \neq i} (\text{cov}(E'_i, E'_j) - \text{cov}(E_i, E_j))}^{\text{ABUN}}
\end{aligned} \tag{3}$$

where  $\text{Sp}$  denotes the sum of products operator (e.g.,  $\text{Sp}(w, \text{var}(E)) = \sum_{i=1}^s (w_i - \bar{w})(\text{var}(E_i) - \overline{\text{var}(E)})$  and  $\text{Sp}(w', \text{var}(E')) = \sum_{j=1}^{s'} (w'_j - \bar{w}')(\text{var}(E'_j) - \overline{\text{var}(E')})$ ),  $w_i$  and  $w'_j$  are binomials, which are one if a species is present at both sites and zero otherwise, and overbars denote unweighted averages across all  $s$  or  $s'$  species (e.g.,  $\overline{\text{var}(E)} = \frac{1}{s} \sum_{i=1}^s \text{var}(E_i)$ ,  $\overline{\sum_{k \neq i} \text{cov}(E_i, E_k)} = \frac{1}{s} \sum_{i=1}^s (\sum_{k \neq i} \text{cov}(E_i, E_k))$ ,  $\bar{w} = \frac{1}{s} \sum_{i=1}^s w_i$ , and  $\bar{w}' = \frac{1}{s'} \sum_{j=1}^{s'} w'_j$ ).

The first two terms in Eqs. 2 and 3 are richness loss (abbreviated as  $\text{RICH}_L$ ) and gain ( $\text{RICH}_G$ ) terms, respectively. These terms quantify the extent to which the strict effects of random species loss and gain, independent of composition or compensatory responses of persisting species, explain between-site differences in total temporal variance of ES. In Eq. 2,  $\text{RICH}_L$  must be negative and  $\text{RICH}_G$  must be positive, because variances must be positive,  $s_c - s \leq 0$  and  $s' - s_c \geq 0$ . In Eq. 3, covariances, and thus  $\text{RICH}_L$  and  $\text{RICH}_G$ , can be positive or negative. Thus, the total effect of richness (that is, the sum of all  $\text{RICH}$  terms across Eqs. 2 and 3) can be negative or positive. It is important to note that, unlike many analyses of biodiversity–ecosystem–function experiments, which aim to estimate the shape of the relationship between richness and function while statistically controlling for other variables, the  $\text{RICH}$  terms are linear by definition (Fox 2006). The third and fourth terms in Eqs. 2 and 3 are “composition” terms

( $\text{COMP}_L$  and  $\text{COMP}_G$ ) that account for any non-randomness, with respect to the variance or covariance they contribute, in the identity of the species that are lost or gained between sites. When species with high (or low) contributions to variance or covariance are systematically lost across sites, the composition effect will be large and negative (or positive). Thus, as for  $\text{RICH}$ , the sign of  $\text{COMP}$  terms matters. The fifth term is generally named the “context dependent effect” (Fox 2006, 2010, Fox and Kerr 2012) and captures, for all species present at both sites, any factor that causes these species’ contribution to total temporal variance of ES to vary across the two sites. Here, we refer to the context-dependent effect as the “abundance effect” ( $\text{ABUN}$ ) because in our data it arises only from between-site variation in the temporal variances and covariances of species’ abundances (we assume species’ per-capita pollen deposition rates do not vary across sites or over time, as described earlier).

There are three points to consider when interpreting the  $\text{ABUN}$  effect. First, even though our sites are commercial farms in a single geographic region, conditions vary somewhat among sites. These include abiotic conditions such as temperature and precipitation and biotic conditions such as the availability of floral resources. However, this variation is not an issue for the Price equation because none of these factors directly affect pollen deposition; rather, they act indirectly by influencing bee abundance. Second, mean ES and temporal variance of ES are linked by mean–variance scaling. Species will likely exhibit higher temporal variances at sites where they are more abundant on average. Thus, abiotic and biotic environmental factors can affect temporal variance of ES either by changing mean pollinator abundance, or the variance of pollinator abundance over time. Third, changes in the temporal variances and covariances of persisting species following species loss and gain would also be captured by the  $\text{ABUN}$  effect. All Price equation terms are described in more detail elsewhere (Fox 2010, Fox and Kerr 2012).

We present results for (1) variances (Eq. 2), (2) summed covariances (Eq. 3), and (3) variances plus summed covariances (i.e., total temporal variance). We found that results were qualitatively similar regardless of whether we analyzed variances, summed covariances, or total temporal variance (Table 1, Appendix S3); thus we focus our interpretation on total temporal variance. A post-hoc analysis revealed that this similarity is due to a tight, positive correlation between species-level summed covariances and variances (where summed covariances and variances were determined for each species at each site, and then summed across sites to give one variance and summed covariance value for each species; watermelon, Spearman’s  $\rho = 0.537$ ,  $P < 0.001$ ; blueberry, Spearman’s  $\rho = 0.472$ ,  $P = 0.004$ ). All references to Price terms (e.g., richness-loss, abundance) in the main text hereafter refer to effects on total temporal variance

(e.g., richness-loss hereafter refers to the sum of the richness-loss terms in Eqs. 2 and 3).

Because we designate the baseline site as the one with higher total temporal variance, the sum of all five Price equation terms must be negative (but no restrictions are placed on the sign or relative importance of any individual term). All analyses use code written for this paper using R version 3.2.2 (R Core Team 2015) (see Data S1 for R code and Metadata S1 for instructions).

*What is the relative importance of changes in species richness, composition, and abundance to the variance of ecosystem services?*

To determine the relative importance of abundance compared with species loss and gain, we created a composite term representing the total effects of species loss and gain:  $RICH_L + COMP_L + RICH_G + COMP_G$ , hereafter  $RICH + COMP$ . Using the composite term allows for a simple analytical framework: Between-site differences in total temporal variance of ES are due either to species loss and gain ( $RICH + COMP$ ) or because species present at both sites have greater abundance fluctuations at one site than the other ( $ABUN$ ). We quantified the relative importance of  $RICH + COMP$  as  $|\overline{RC}|/(|\overline{RC}| + |\overline{A}|)$  and  $ABUN$  as  $|\overline{A}|/(|\overline{RC}| + |\overline{A}|)$ , where  $|\overline{RC}|$  and  $|\overline{A}|$  are the mean absolute values of  $RICH + COMP$  and  $ABUN$ , respectively, across all pairwise comparisons of sites. We use absolute values because  $|\overline{RC}|$  and/or  $|\overline{A}|$  may have a large negative value at some sites and a large positive value at others, and simply taking the mean of these values would obscure the overall importance of  $|\overline{RC}|$  and/or  $|\overline{A}|$ . Relatedly,  $|\overline{RC}|$  and  $|\overline{A}|$  should not be interpreted as an indication that richness has a positive or negative effect on stability, but rather should be interpreted as non-directional effect sizes. As such, the relative importance of  $|\overline{RC}|$  and  $|\overline{A}|$  does not reveal whether species loss and gain, or abundance, increases total temporal variance; rather, it means that differences between a low- and high-variance site are explained mostly by either species loss and gain or by  $ABUN$  (between-site differences in the temporal variances and summed covariances of species present at both sites).

To gain a better understanding of what drives  $|\overline{RC}|$ , we calculated  $\overline{COMP_L}/\overline{RICH_L}$  and  $\overline{COMP_G}/\overline{RICH_G}$ , where overbars indicate we took the mean value of each component across all pairwise comparisons of sites. A negative value indicates that actual species loss or gain had less impact on total temporal variance of ES than expected compared to random loss or gain, and a positive value indicates the opposite.

## RESULTS

In the watermelon system, we collected 3044 individual wild bees belonging to 59 species (all but three pollen collectors and all but two native), 14 genera, and 5 families. Sites ranged in total temporal variance from 2.3 million

to 51.1 million grains of pollen ( $21.3 \text{ million} \pm 19.7 \text{ million}$  [mean  $\pm$  SD]), in richness from 20 to 32 species ( $26.0 \pm 4.0$ ), and in abundance from 140 to 435 individuals ( $304.4 \pm 96.0$ ); richness and abundance values are summed across years. In the blueberry system, we collected 1,067 individual wild bees belonging to 36 species (all native pollen collectors, including known blueberry specialists such as *Andrena bradleyi*, *Andrena carolina*, *Colletes validus*, and *Habropoda laboriosa*), 9 genera, and 4 families. Sites ranged in total temporal variance from 2.6 to 875,154 grains of pollen ( $207,477 \pm 257,418$ ), in richness from 3 to 19 species ( $10.6 \pm 4.6$ ) and in abundance from 4 to 143 individuals ( $66.7 \pm 45.2$ ). The range (maximum richness minus minimum richness) of richness values is similar to the range found in experiments that study various ecosystem services (Balvanera et al. 2006), although only two of our sites had species richness values similar to the lower end of richness manipulations (<5 species). The rank-abundance distributions for each system are shown in Fig. 1.

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The five Price equation terms are measures of directional effect size, where positive or negative values tell how strongly each term decreases or increases between-site differences in the total temporal variance of ES. For both systems, all richness-loss terms were negative and all richness-gain terms positive, with richness-loss greater in magnitude (Fig. 2). This reflects the fact that total temporal variance of ES is generally higher at higher richness sites.

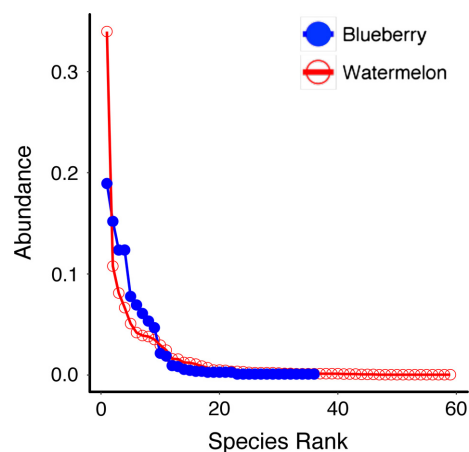


FIG. 1. The rank-abundance distributions for the watermelon (red, open circles) and blueberry (blue, filled circles) systems, where each point represents one species and abundance (proportion of total) is summed across all sites and years. Both systems show skewed distributions with many singletons, but the pattern is especially pronounced for the watermelon system.

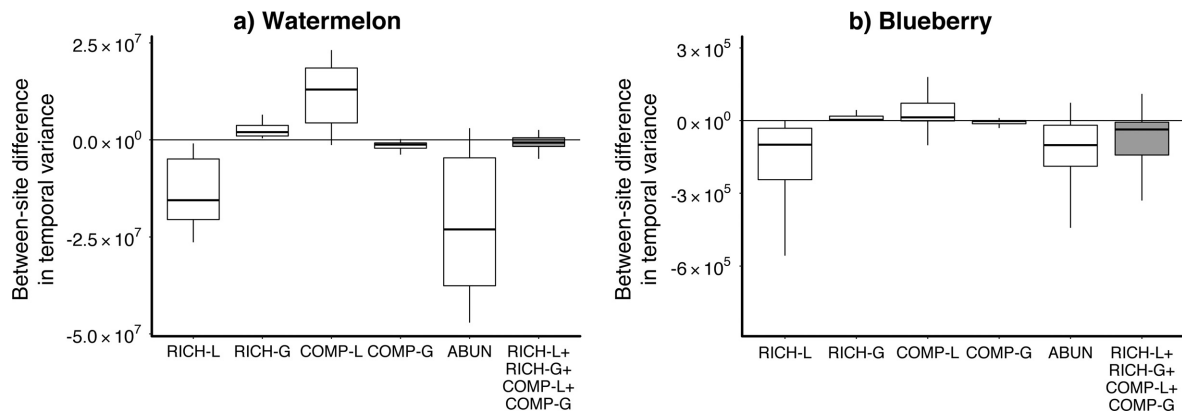


FIG. 2. The effect size of all five Price terms and an additive term, richness (RICH) plus composition (COMP) (shaded gray), on the total temporal variance (variance plus covariance) in the pollination services delivered to (a) watermelon and (b) blueberry. The y-axis is a measure of directional effect size, where positive (or negative) values show how strongly each term decreases (or increases) total temporal variance of pollen deposition. Together, positive composition loss and negative composition gain indicate that species loss and gain affected temporal variance less than expected if species losses had been random with respect to their contributions to total temporal variance. The mid line of boxplots is the mean, and boxes encompass the 25th to 75th percentiles and whiskers extend to the last data point within another 1.5 times the interquartile range. Variability in the box plots is from the distribution of all pairwise site comparisons. The -L and -G suffixes indicate loss and gain, respectively.

All composition-loss terms were positive and all composition-gain terms negative, such that in all cases, composition terms partially cancelled their corresponding richness terms. This means that both the lost and gained species tended to have below-average contributions to total temporal variance of ES. Specifically, the positive composition-loss indicates that observed reductions in species richness resulted in less reduction in total temporal variance than would be the case if species losses had been random with respect to total temporal variance. Similarly, the negative composition-gain indicates that observed increases in species richness resulted in less increase in total temporal variance than would be the case if species gains had been random. In the watermelon system, composition-loss cancelled 86% of richness-loss and composition-gain cancelled 78% of richness-gain; in the blueberry system, these same value were 23% and 76%. Results were similar when total temporal variance was partitioned into variances and summed covariances (Table 1).

In both systems, between-site differences in abundance fluctuations of species present at both sites were more important than species loss and gain to between-site differences in total temporal variance of ES, although only slightly so in the blueberry system. Specifically, in watermelon only 9% of between-site differences in total temporal variance of ES was attributable to species loss and gain, while the remainder was attributable to between-site differences in the abundance fluctuations of the species present at both sites. For blueberry, 42% of the total temporal variance was attributable to species loss and gain, with abundance fluctuations of species present at both sites accounting for the remainder. Results were similar when total temporal variance was partitioned into variances and summed covariances, and in the sensitivity analysis in which (Table 1).

## DISCUSSION

We found that abundance fluctuations of common species, rather than species richness per se, was the stronger driver of total temporal variance of an ES. This result was especially strong in the watermelon system, and less pronounced in the blueberry system. Thus, our results contribute to a growing collection of studies that emphasize the importance of abundant, broadly distributed species to ecosystem services (Jiang et al. 2009, Gaston 2012, Kleijn et al. 2015, Winfree et al. 2015). Abundance fluctuations accounted for 91% and 58% of the between-site differences in total temporal variance in pollination for watermelon and blueberry, respectively, with the remaining 9% and 42% accounted for by losses and gains of species. There are two reasons for this result.

First, the skewed species abundance distribution results in few highly abundant species (Fig. 1) capable of large abundance fluctuations and many rare pollinator species, whose abundance fluctuations are constrained by their rarity. For example, singletons and doubletons combined account for 28% and 45% of the species in the watermelon and blueberry data sets, respectively. Second, rare species were more likely to be lost and gained between sites, accounting for most changes in richness between sites. As a corollary, the highly abundant species with the greatest impacts on the variance in pollination were present at all (watermelon) or most (blueberry) sites, and the variance they contributed to ES was generally not attributable to species loss or gain between sites. Although it is possible that richness could determine ES if dominant species were more likely to be found at higher-richness sites, we found the dominant species were present regardless of species richness. This contrasts with randomly assembled biodiversity-ecosystem-function experiments

in which richness increases the chances of including a high-ES species that may then become dominant in mixtures (the “selection” or “sampling” effect). Thus, for the ES we studied, richness and temporal variation of ES are decoupled from each other, because the rare species accounting for the richness changes contribute little to the variance.

While observational studies in un-manipulated systems could examine the shape of the richness-variance relationship without considering composition, the result would be misleading because not only composition, but also evenness and abundance covary with richness but are not captured by the  $x$ -axis (i.e., “richness”). The Price equation approach resolves this issue by defining effects of richness changes as those that are random with respect to species’ contributions to total temporal variance, such that the Price equation richness terms are not confounded with composition (Fox 2006). The composition terms capture only those effects of species loss and gain that are non-random with respect to species’ contributions to total temporal variance, and so depend on the identity of lost and gained species. Accordingly, the Price equation does not attempt to replicate the approach used in biodiversity–ecosystem-function studies (Fox 2006). Rather, it provides a different perspective on the question that originally motivated much biodiversity–ecosystem-function research: how will ongoing species losses affect ES? In our study, the Price equation allowed us to separate richness and composition effects, showing that because of the non-random identity of lost species, namely, they tended to be rare species with little impact on temporal variance, reductions in richness did not greatly affect temporal variance of ES.

Synchrony or asynchrony of species responses to environmental changes potentially has a major impact on the stability of ES, with asynchronous fluctuations stabilizing ES over time and synchronous fluctuations increasing the temporal variance of ES. We found that native bee species’ abundances exhibit positively correlated fluctuations (at the species level, summed covariances were tightly and positively correlated with variances). While we might expect competing species to show compensatory dynamics (Vasseur and Fox 2007, Loreau and de Mazancourt 2008, Gonzalez and Loreau 2009, but see Vasseur et al. 2014), competition does not appear to be a major determinant of population dynamics in bees (Steffan-Dewenter and Tscharntke 2000, Roubik and Wolda 2001), and therefore the lack of negative covariances is unsurprising. Because of positive correlations between species’ variances and summed covariances, our analyses produced very similar results regardless of whether we analyzed variances or summed covariances by themselves, or total temporal variance (Table 1). In other words, changes in richness and composition across sites had little effect on aggregate covariance, because the species accounting for these changes were rare and had low summed covariances. In contrast, within each system, species with high, positive

covariances were present at nearly all sites, regardless of species richness, and explained most between-site differences in aggregate covariance.

Some mechanisms through which richness or composition could reduce the variance of ES are excluded by our methods, and would need to be investigated with more detailed field studies. For example, because our estimates of per-visit pollen deposition are based on one individual bee visiting a virgin flower, our methods may not capture how multiple bee species sequentially visiting a plant may lead to complementarity in pollen deposition, either in space or in time (Blüthgen and Klein 2011). Likewise, for each pollinator taxon we apply a pooled value of per-visit pollen deposition rather than allowing this to change among sites. Potential functional compensation among species is thus merged into the ABUN term in our approach. Similarly, we exclude any factors that disrupt the relationship between pollen deposition and fruit yield; however, a recent analysis of hundreds of crop fields found that pollen deposition is generally a good proxy for fruit set (Garibaldi et al. 2013).

The Price equation method presented here is general and can accommodate data from different ES. The method requires multiple years of information on both species abundance and species efficiency (i.e., ES provided per individual) across spatial replicates. In some cases, it may not be logistically feasible to obtain efficiency estimates for every individual in the study. Here, we estimated efficiency using single-visit experiments and others wishing to apply this method will need to develop their own system-specific method of estimating efficiency. In some cases (e.g., plant productivity), this could involve destructive sampling or allometric equations that estimate biomass from height and other characteristics.

In conclusion, we developed and used a new analytical method to show that abundant species, not species richness, is the stronger driver of total temporal variance of ES in two pollination systems. This new method is the first to partition between-site differences in the total temporal variance of ES into terms attributed to richness, composition, and abundance. Here, abundance had a strong effect because—as is true for nearly all ecological communities—our study systems contained few abundant and many rare species, and because between-site differences in richness were due to rare species that did not greatly affect total temporal variance of ES. The Price approach as developed here is a broadly applicable framework, which can be used to analyze the temporal variance of any ES that is expressible as a sum of species contributions (Fox 2006); for example, aboveground carbon storage in forests or fisheries yields. Given its generality, we believe this method can help better resolve pressing questions about the relative importance of richness and abundance for the stability of ecosystem services.

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