

# Price Equations for Understanding the Response of Ecosystem Function to Community Change

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**ABSTRACT:** The relationship between biodiversity and ecosystem function (BEF) remains unclear in many natural ecosystems, partially for lack of theoretical and analytical tools that match common characteristics of observational community data. The ecological Price equation promises to meet this need by organizing many different species-level changes into a few ecologically meaningful categories that sum to total ecosystem function change. Current versions of the ecological Price equation focus on species richness and presence-absence. However, abundance and relative abundance are better estimated in samples and are likely showing a stronger response to global change. Here, we present a novel, abundance-based version of the ecological Price equation in both discrete and continuous forms and explain the similarities and differences between this method and a related, previously developed richness-based method. We also present new empirical techniques for applying the Price equation to ecological data. Our two demonstration analyses reveal how additive effects of increasing abundance on total function are modified by concurrent selection effects due to shifts in species' composition as well as intraspecific change in species' per capita function. The ecological Price equations derived here complement existing approaches and together offer BEF researchers analytical tools and a unifying framework for studying BEF in observational community data.

**Keywords:** abundance, additive, biodiversity, composition, ecosystem function, Price equation.

## Introduction

Understanding the effects of biodiversity and ecosystem function (BEF) has been central to ecological research for more than two decades (Tilman et al. 1996; Cardinale et al. 2012; Hooper et al. 2012; Jochum et al. 2020). While species richness clearly improves ecosystem function in experiments, understanding how much richness matters for eco-

system function in nature has always been challenging (Cardinale et al. 2012). Composition and abundance change nonrandomly alongside species richness, and environmental gradients have combined direct and indirect effects on species' function (Brose and Hillebrand 2016; Spaak et al. 2017). Adaptations of the Price equation from evolutionary biology (Price 1970; Gardner 2008) have been promising for disentangling the effects of richness from these other ecological drivers of ecosystem function (Fox 2006; Fox and Kerr 2012). In large part, the BEF work described above has been motivated by a sense that declines in species richness would threaten ecosystem function in natural communities. However, recent meta-analyses suggest that the focus on richness may be misplaced. While species richness is clearly in decline at global scales, composition and abundance are more commonly changing at local scales (Vellend et al. 2013; Dornelas et al. 2014; McGill 2015; but see Cardinale et al. 2018). An expanded theoretical framework is needed to understand how declines in abundance, independent of any change in richness, affect ecosystem function in natural communities. Here, we present such a framework, using a novel Price equation partition to explain change in ecosystem function based on changes in species' absolute and relative abundances.

All ecological adaptations of the Price equation, including the one we present below, can be used to analyze variation in any ecosystem functions that can be expressed as a sum across species—for example, biomass, pollination, or carbon storage (Fox 2006). Under controlled experimental conditions, the ecological Price equation isolates function due to complementarity among species in diverse mixtures (Loreau et al. 2001; Fox 2005). In observational data, it has been used to separate the effects of declining richness from changes in species composition, both of which are common dynamics in natural communities experiencing global change (Larsen et al. 2005; Winfree

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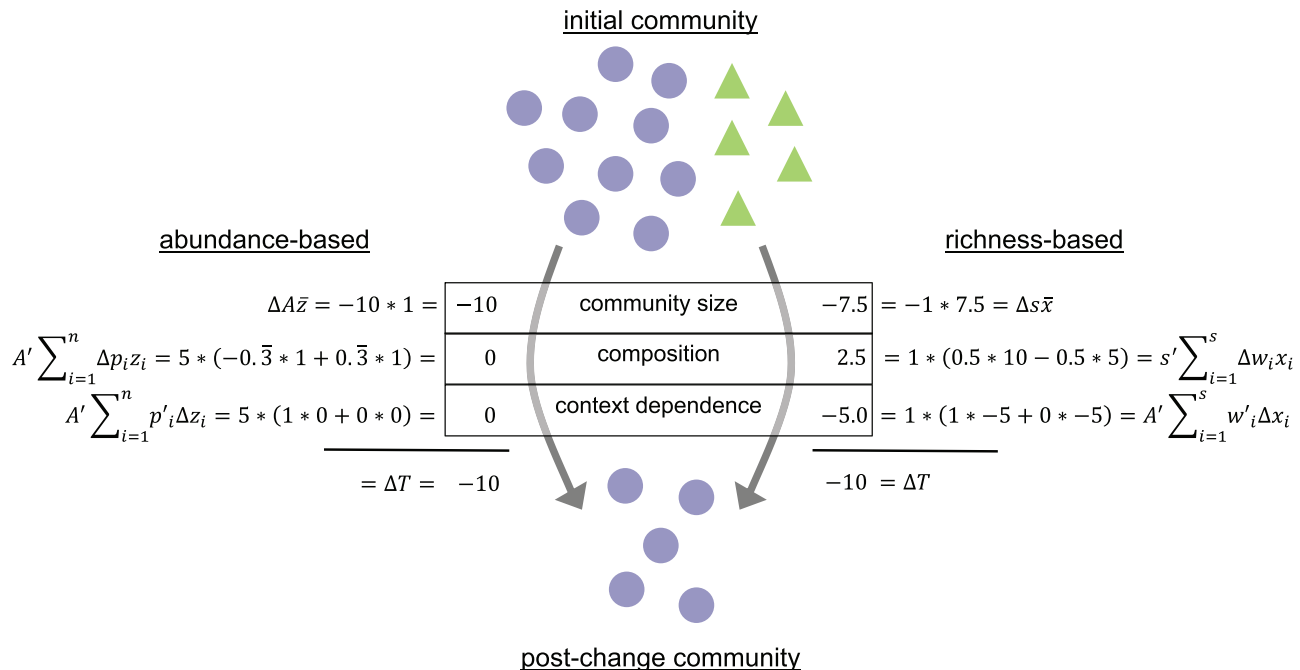
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et al. 2015; Mateo-Tomás et al. 2017; Bloom et al. 2019). The Price equation itself makes no distinction between specific ecological drivers of change; for example, community change due to species invasion versus human disturbance would not be treated differently.

Current applications of the ecological Price equation focus on the relationship between ecosystem function and species richness (Fox and Kerr 2012), in accordance with a historical emphasis on richness as the key component of biodiversity (Cardinale et al. 2012). This focus on richness is challenged by a current consensus, however, that emphasizes the arbitrary nature of richness as a metric (e.g., its dependence on sampling effort; Larsen et al. 2018; Roswell et al. 2021), the potential for abundance changes to outpace the effects of changing richness (Winfree et al. 2015), and the greater sensitivity of other components of biodiversity, such as abundance, to global change (McGill et al. 2015). For example, at local scales declines in sensitive species are often compensated by increases in tolerant species, buffering species richness loss while producing large changes in species' total and relative abundance (Mayfield and Daily 2005; Vellend et al. 2013; Supp and Ernest 2014; Dornelas et al. 2014; Elahi et al. 2015; Hillebrand et al. 2018; Komatsu

et al. 2019). When global change pressures are particularly strong, local richness loss is accompanied by sharp abundance declines and strong changes in species composition (Karp et al. 2012; Newbold et al. 2015). Biodiversity experiments are not generally designed to test the combined effects of changes in richness and abundance, but the Price equation is well suited for this task. Adapting the ecological Price equation to study the functional consequences of abundance change is important for increasing the relatively few theoretical and empirical studies focusing on abundance-function relationships (Vellend et al. 2013; Winfree et al. 2015; Wardle 2016; Spaak et al. 2017) and understanding the impacts of biodiversity loss as it occurs in natural communities.

Here, we work toward one central goal and then make two supporting points. Our central goal is the derivation of a novel, abundance-based version of the ecological Price equation. Supporting this central goal, in box 1 and figure 1 we discuss how our abundance-based version differs from the existing richness-based version (Fox 2006; Fox and Kerr 2012). Second, we discuss practical considerations for applying the ecological Price equation to specific research questions, both in a general sense and through demonstration



**Figure 1:** A simple scenario for comparing the abundance- and richness-based Price ecological equations. Each shape is one individual, with triangles and circles indicating different species. All shapes are the same size to represent per capita equivalence in function (i.e.,  $z_i = z'_i = \bar{z} = 1$  for all  $i$ ). From the abundance-based perspective, total function change is fully explained by abundance loss, since per capita function contribution is constant. From the richness-based perspective, total function change is due to both richness loss and change in mean per-species function (driven by change in abundance). In general, we recommend choosing either the richness- or abundance-based version, depending on the relevant data and hypothesis, rather than using both versions and trying to compare the results. We give more detail on the abundance- and richness-based Price equations in the supplemental PDF, both analytically (supplement B) and using the first demonstration analysis (watermelon pollination; supplement C).

analyses. Taken together, the new derivation and supporting points provide a flexible framework for analyzing BEF relationships in observational data.

### Previous Use of Ecological Price Equations to Understand Changes in Species Properties

We first present the ecological Price equation in an abstract form, borrowing notation from Frank (2012). This version lacks the covariance term that readers may expect in the Price equation, but it is mathematically equivalent to the canonical Price equation (see supplement A) and still captures the same selection and transmission bias effects, albeit transferred to an ecological context. We then show that the ecological version can likewise be written to describe discrete (Price 1970) or continuous (Price 1972) change. The general form of the ecological Price equation partitions a change in any community mean property. The remainder of the text includes many variables, which are defined in table 1. Imagine we have observed species' relative frequencies  $\sum_{i=1}^n p_i = 1$  and some species property  $z_i$  for a community of  $i = 1, 2, \dots, n$  species. Species relative frequency may be based on any type of data (e.g., presence-absence, counts, percent area, biomass), and the species property may be any trait, ecosystem function, or other quantity that can be measured on a per-individual basis. The mean property value across individuals (community-weighted mean) is then  $\bar{z} = \sum_{i=1}^n p_i z_i$ . We are interested in how change in this community-level mean,  $\Delta\bar{z} = \bar{z}' - \bar{z}$ , is related to species-level changes in the constituent factors, relative frequencies  $\Delta p_i = p'_i - p_i$ , and property values  $\Delta z_i = z'_i - z_i$ . The Price equation achieves this decomposition with a simple algebraic rearrangement of the difference between two means (derivation in supplement A):

$$\Delta\bar{z} = \sum_{i=1}^n (\Delta p_i z_i) + \sum_{i=1}^n (p'_i \Delta z_i). \quad (1)$$

This expression states that all mechanisms that affect a mean property in ecological communities can be organized

into two processes: interspecific changes in species relative frequencies  $\Delta p_i$ , weighted by the original property distribution  $z_i$ , plus intraspecific changes in species properties  $\Delta z_i$ , weighted by species' final relative frequencies  $p'_i$ . Generality means that  $p$  and  $z$  are abstract placeholders for the relative frequencies and properties (examples given above), which can be replaced by any metric judged reasonable for an application (Frank 2018). All ecological Price equations are extensions or modifications of this general form. The general form of the Price equation unfortunately precludes analysis of functions that cannot be summed across individuals, as is common in ecosystem ecology (decomposition, nutrient cycling, etc.).

In the derivation above, change is described as a difference between discrete baseline and comparison states. This is an intuitive way to present the Price equation (Gardner 2008; Frank 2012), and it corresponds naturally to some real-world problems, such as communities before and after a disturbance event (Fox 2006). However, it is just as valid to describe change as a continuous process (Robertson 1966; Price 1972), which corresponds to other scenarios, such as change through time or along environmental gradients (Ellner et al. 2011; Norberg et al. 2012). The continuous ecological Price equation describes continuous change in a mean property  $\bar{z}$  along some gradient  $t$ , assuming each species' relative frequency  $p$  and property  $z$  is also a continuous and differentiable function of  $t$  (derivation in supplement A):

$$\frac{d\bar{z}}{dt} = \sum_{i=1}^n \frac{dp_i}{dt} \cdot z_i + \sum_{i=1}^n p_i \cdot \frac{dz_i}{dt}. \quad (2)$$

This expression, conceptually equivalent to equation (1), states that all mechanisms that drive change in a community mean property over gradient  $t$  can be organized into two processes: the rates of change in species relative frequencies over the gradient  $dp_i/dt$  relative to the species' property distribution  $z_i$ , plus rates of intraspecific changes in species' properties over the gradient  $dz_i/dt$ , weighted by species' relative frequencies  $p_i$ . Equation (2) has previously been used to understand how community mean traits

**Table 1:** Definitions of variables and notation

Variable	Definition
$A$	Total abundance, summed across species within a community
$E$	Statistical expectation, used in the context of the expected site
$i$	Indicates a specific species for summations
$n$	Richness (i.e., the total number of species in a community)
$p$	Relative abundance (i.e., proportion of total abundance)
Prime symbol	Refers to comparison sites (corresponding variables without prime notation refer to baseline sites)
$t$	Time, used in the context of trait values or ecosystem function changing over time
$T$	Total ecosystem function, summed across species within a community
$z$	A species property, such as pollen deposition or biomass

change over gradients (Collins and Gardner 2009; Norberg et al. 2012; Govaert et al. 2016). For example, earlier work focused on understanding community-level phenotypic change in response to climate change developed an eco-evolutionary model in which the first term of equation (2) captured ecological effects and the second term captured evolutionary effects (Norberg et al. 2012). The continuous Price equation has seen use in ecology as well. One prominent example comes from Ellner et al. (2011), who combined the continuous Price equation with the approach of Hairston et al. (2005) to understand how genotype, phenotype, and the environment interact to affect a chosen response variable.

### Novel Ecological Price Equations for Changes in Ecosystem Function

Adapting the above approaches to incorporate changes in abundance, as shown below, is the key advance presented here. To use the ecological Price equation to analyze changes in total ecosystem function, mean function must be scaled by total community size, introducing a third partition term (Fox 2006). The derivation proposed here is an abundance-based partition of total ecosystem function. Thus, abundance is our measure of community size, and total ecosystem function ( $T$ ) is total abundance ( $A$ ) times the community weighted mean ( $\bar{z}$ ). We treat  $p_i$  as species' relative abundance in a community and  $z_i$  as each species' per capita contribution to ecosystem function. Discrete change in total function,  $\Delta T = T' - T$ , can then be decomposed into changes in total abundance  $\Delta A = A' - A$  and community mean per capita function  $\Delta \bar{z} = \bar{z}' - \bar{z}$ , which can be further decomposed using equation (1) into changes in species relative abundance and per capita function (derivation in supplement A):

$$\Delta T = \Delta A \cdot \bar{z} + A' \sum_{i=1}^n (\Delta p_i z_i) + A' \sum_{i=1}^n (p'_i \Delta z_i). \quad (3)$$

This equation is a novel three-term partition for analyzing ecosystem function change due to changes in species' absolute and relative abundances. The first term,  $\Delta A \cdot \bar{z}$ , equals the total amount of function change due to total abundance change, holding mean per capita function fixed at its original value. The second and third terms partition the change in total function due to the change in mean per capita function (eq. [1]), holding abundance fixed at its final value  $A'$ . In the second term,  $\Delta p_i = p'_i - p_i$ . As in equation (1), there is no explicit covariance term in equation (3), but  $\Delta p_i z_i$  is equivalent to a covariance (supplement A). To understand why, it may be helpful to consider that for  $\Delta p_i z_i$  to be large and positive, large positive  $\Delta p_i$  values must coincide with large  $z_i$  values. A par-

allel extension to the continuous Price equation (eq. [2]) can be used to partition continuous change in total function along a gradient (derivation in supplement A).

### Ecological Price Equations and Models of Community Change

When two communities are compared, each may have species that are absent in the other. One should decide, for a given data set, whether such species gains are more likely statistical (e.g., due to incomplete sampling) or ecological (e.g., the species can persist at only some sites). If one considers statistical effects more likely, as we did in the demonstration analyses below, no modifications of the above equations are needed. Given that most species are rare (McGill et al. 2007), it is difficult to fully sample communities, and we consider that an increase in abundance from 0 to 1 often holds similar information to an increase in abundance from 1 to 2. However, if one considers an ecological effect more likely, as may be the case when species absences are clearly controlled by different processes than the relative abundance of present species, an alternative is available because equation (3) may be extended to separate the functional effect of adding new species from the effects of frequency changes among original residents. This extension was first developed in evolutionary biology by Kerr and Godfrey-Smith (2009) and then adapted for richness-based ecological Price equations by Fox and Kerr (2012); it is equally valid for abundance-based analysis (supplement B).

Allowing  $p_i$  to equal zero is a departure from evolutionary versions of the Price equation, where such a decision would be incoherent. It would suggest that parental group  $i$  had zero relative frequency and that offspring had descended from zero parents. While offspring may belong to a different subgroup than their parents, they still represent their parents' productivity. Therefore, the new relative frequencies  $p'_i$  must be calculated as the fraction of offspring descended from parents in the  $i$ th subgroup (Frank 2012). However, in transferring the Price equation to ecology, "descent" metaphorically refers to the shared identity between members of the same species in two different communities. There is no useful sense in which members of one species may be descended from a different species, so we can calculate species' new relative frequencies  $p'_i$  directly from species' frequencies in the new community.

In the existing richness-based partition (equation in box 1), the magnitude of the selection effect (composition effect) is closely constrained by the observed change in richness (Fox 2006), especially when treating species loss and gain separately (Fox and Kerr 2012; see also eq. [S9] in supplement B). Therefore, the selection effect cannot be directly compared with the richness effect but can be

### Box 1: Comparing abundance- and richness-based ecological Price equations

Equation (3) factors total function into total abundance and the per capita function of the average individual in the community,  $T = A\bar{z}$ . It is equally valid to factor total function into species richness  $s$  and the total functional contribution of the average species in the community  $T = s\bar{x}$ , where  $\bar{x}$  is the total function provided the average species in the community. Applying the Price equation to analyze the contributions of change in each of these factors to change in total function results in Fox's previously published (2006) partition:

$$\Delta T = \Delta s \cdot \bar{x} + s' \sum_{i=1}^n \Delta w_i \cdot x_i + s' \sum_{i=1}^n w_i' \cdot \Delta x_i. \quad (4)$$

In the equation above,  $w_i$  is the vector of species' presence-absence in the community relativized (i.e., divided) by total richness,  $x_i$  is each species' total functional contribution, and  $n$  is the number of unique species across both sites. The partitions in equations (3) and (4) must sum to the same  $\Delta T$ , so changes assigned to a term under the abundance-based partition may be assigned to a different term, or combination of terms, under the richness-based partition. To demonstrate, we present parallel calculations for abundance- and richness-based approaches in figure 1.

compared with the range of possible selection effects given the observed change in richness (Fox 2006). In our partition, the magnitude of the selection effect is less constrained because there are many more ways to lose a proportion of individuals than to lose a proportion of species from a community, especially when many species are abundant. On the other hand, when the site-species matrix is sparse (as may occur in degraded environments or with undersampling), adding or losing individuals will force changes in composition even if the ecological processes driving abundance loss and gain is random with respect to species identity (Karp et al. 2012). This will induce dependence between the abundance and composition terms, which may be explored with further analysis (Blüthgen et al. 2006) or null models (Karp et al. 2012)

#### Applying the Ecological Price Equation to Data

Previous applications of the ecological Price equation partitioned pairwise differences in function among replicate samples and then summarized a subset of the pairwise comparisons—for example, comparisons for which  $\Delta T$  is negative (Fox 2006; Winfree et al. 2015; Mateo-Tomás et al. 2017; Genung et al. 2020) or comparisons with one site selected to represent the extreme end of an ecological gradient (Bloom et al. 2019). This approach is simple to implement because equation variables are represented by raw data. However, the resulting summaries (means or medians) of subsets of pairwise partitions are difficult to interpret. A post hoc standardization is needed to compare partition values from many different baseline sites, and the meaning of variability in partition values calculated from many nonindependent site pairs is unclear.

Instead of summarizing a subset of pairwise comparisons, an alternative approach begins by imagining that ob-

served communities are random samples from a regional species abundance distribution. Then, we propose an “expected community” in which each species' abundance, relative abundance, and per capita function is equal to its mean across all observed communities. We use the adjective “expected” because this is the community we expect if  $n$  individuals are drawn from the regional species abundance distribution at random, where  $n$  is the average abundance across all observed communities. We then use the Price equation to partition deviations from or changes in the expected community, which takes on the role of the baseline (Ellner et al. 2011; Okasha and Otsuka 2020). In this analytical framework, partition values can be calculated for single communities, representing comparison sites that deviate from the baseline. Adding this expected community's expected ecosystem function to any community's partition value produces the absolute function that would be observed at that community if only one attribute of the community differed between that community and the baseline. We think that this interpretation, together with a clearly defined role for community-level replication, is intuitive and powerful enough to justify the larger up-front analytical effort, relative to pairwise comparisons of raw data. For this approach, we show a demonstration analysis that uses the discrete Price equation to study variability in crop pollination across replicated farms, unconditioned by spatial or environmental gradients.

The expected community approach is less reasonable if communities occur along a clearly identified gradient in time or space (e.g., seasonal variation, elevation, and latitude). If communities are changing deterministically along an identifiable gradient in either space or time, the continuous Price equation may be more appropriate. To demonstrate the continuous Price equation approach, we present a second demonstration analysis to study total invertebrate

biomass across samples collected along a strong pollution gradient. All analyses were run in R version 4.0.5 (R Core Team 2021).

### How Does Bee Abundance and Composition Drive Variability in Watermelon Crop Pollination across Farms?

To obtain pollinator visitation rates to crop flowers, we net-collected wild pollinator specimens from standard areas of flowering watermelon crop at 16 replicated farms in 2012. We also collected single-visit pollen deposition data to get a point estimate for the number of watermelon pollen grains deposited on a watermelon stigma by an average visit by a member of each bee genus. Crop pollination rates were estimated by multiplying pollinator visitation rates with their per-visit pollen deposition. Our data summarize per-visit effectiveness as a genus-level property; we do not consider variability in per-visit effectiveness within species across farms. This is common in landscape pollination studies, since collecting single-visit pollen deposition data is labor intensive and pollinator effectiveness is strongly correlated with species traits such as hairiness (Stavert et al. 2016). Additional study design and data collection details are published in Winfree et al. (2015).

Our question is whether variability in crop pollination is driven by variability in bee abundance or composition (selective change in relative abundance across genera with different per-visit function). Variability is generally measured as a summary of the deviation between individual sample values and their collective mean. We use the Price equation to partition the difference in function between each observed community and the expected community. Crop pollination at each farm is the product of total bee abundance  $A$  and the mean per-visit pollination efficiency at that farm  $\bar{z}$ . The covariance of two random variables is  $\text{cov}(x, y) = \mathbf{E}(xy) - \mathbf{E}(x) - \mathbf{E}(y)$ . Therefore, the expected community's total function is the product of the average total abundance and the expected community weighted mean function calculated across all farms, plus any covariance between farm abundance and mean per-visit function:  $\mathbf{E}(T) = \mathbf{E}(A\bar{z}) = \mathbf{E}(A) \cdot \mathbf{E}(\bar{z}) + \text{cov}(A, \bar{z})$ . The term  $\mathbf{E}(T)$  corresponds with  $T'$  in the sense that it is compared with the observed site's function, but while  $T'$  represents a second site where sampling occurred,  $\mathbf{E}(T)$  represents an expected community. Bars indicate abundance-weighted means across species within sites (community-weighted means), and expected value  $\mathbf{E}$  indicates the unweighted means of community properties across sites. Since our main goal here is conceptual rather than empirical, we use only point values, but a more rigorous analysis would acknowledge uncertainty in estimating the expected community by treating  $\mathbf{E}(A)$  and  $\mathbf{E}(\bar{z})$  as distributions.

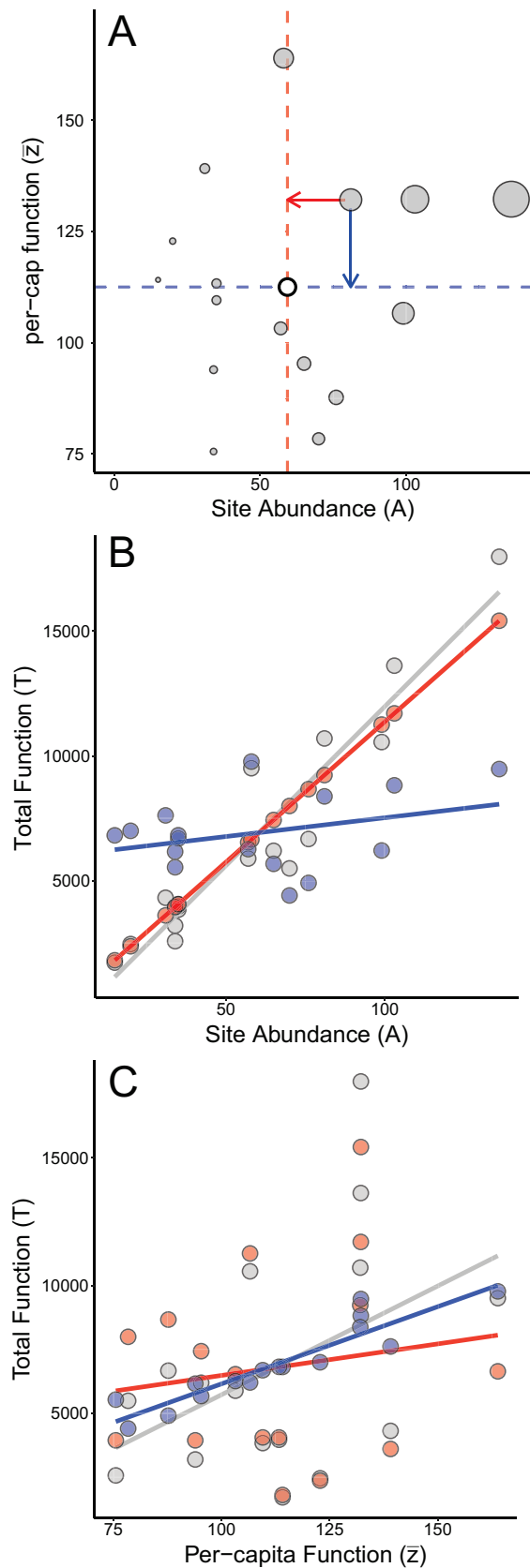
We can use equation (3) to partition the difference in function between each farm and the uncorrelated component of average function across farms,  $\mathbf{E}(A)\mathbf{E}(\bar{z})$  (detailed derivation in supplement C):

$$T - \mathbf{E}(T) = [A - \mathbf{E}(A)]\mathbf{E}(\bar{z}) + A[\bar{z} - \mathbf{E}(\bar{z})] - \text{cov}(A, \bar{z}). \quad (5)$$

The first right-hand term gives the deviation in pollen deposition at a farm if its per capita function is equal to the mean per capita function across all farms. The second right-hand term gives the deviation in pollen deposition due to the farm having a different per capita function. In these data, species' per capita function is fixed across farms, so the values of the second partition will be driven by how much a farm's species relative abundance distribution differs from composition of the regional species pool. If comparing equation (5) to equation (3), note that the second term of equation (5) combines the second and third terms of equation (3), because species per capita function does not vary across sites. If species per capita function did vary across sites, we could further partition  $\bar{z} - \mathbf{E}(\bar{z})$  using the derivation for equation (1).

The final term in equation (5), the covariance between abundance and mean per capita function across farms, captures an important truth: the extent to which two factors covary is exactly the extent to which we cannot learn about their independent effects on a third outcome (total function). In experimental studies, this covariance is deliberately minimized by good study design. In observational studies, this covariance can be partitioned out (as in eq. [S14], supplement C), allowing us to learn from the residual orthogonal variation. In the watermelon crop pollination data set, covariance between abundance and mean per capita function across farms was very low (1.7% of mean total function  $\mathbf{E}(T)$ ), indicating that our Price equation partition terms carry a lot of information about the relative importance of the two factors (fig. 2A). Data underlying figure 2 have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.8kpr4xqf>; Genung et al. 2022).

We added the mean total function  $\mathbf{E}(T)$  to each partition value to calculate the absolute pollen deposition expected at each farm if only abundance or only per capita function deviated from the mean community. We present these alternative scenario pollination levels plotted against bee abundance at each farm (fig. 2B). We found that across the watermelon farms, the addition of an individual bee increased pollination service to a farm by a total of 128 ( $\pm 25$ ) pollen grains (slope of gray line in fig. 2B, with 95% confidence interval). Of this increase, 113 pollen grains were contributed via abundance effects (the slope of the red line is equal to mean per capita function in the expected community; thus, the fit is perfect, and a confidence interval is



not appropriate) and  $15 (\pm 25)$  pollen grains via selection effects (slope of blue line). It is no coincidence that the slopes of the blue and red lines must sum to the slope of the gray line; this will always be the case. The expected community method, proposed in the “Applying the Ecological Price Equation to Data” section, provided key benefits for this analysis. By calculating the expected function ( $E(T)$ ), we were able to plot the three alternative scenarios described above (fig. 2) and calculate slope estimates showing how much function was provided by abundance versus selection effects, neither of which would have been possible with methods used by previous applications of the ecological Price equation.

We have focused on changes in abundance instead of changes in per capita function because changes in abundance are more predictive of changes in function. However, one could instead ask how a one-unit increase in per capita function affects total function (fig. 2C). We include this panel to fully illustrate the proposed method. For the watermelon analysis, however, this relationship is not significant, and the panel thus contains little useful information.

For comparison, we used the previously published richness-based Price equation (Fox and Kerr 2012) to conduct a parallel analysis of the same watermelon pollination data. We found that higher richness was associated with higher total function and that this increase was closely matched by a scenario in which only per species function varied (holding richness and composition function fixed). However, in the scenario where only composition varied, higher richness was associated with function loss, since additional species were likely to have low baseline function due to rarity (a negative selection effect; supplement C).

**Figure 2:** A, Crop pollination at farms can be factored into total bee abundance ( $x$ -axis) and mean per capita function at each farm ( $y$ -axis). The total pollen deposition at each farm is therefore the product of the two axes and corresponds to the size of each gray point ( $N = 16$ ). Since the correlation between total abundance and per capita function is low ( $r = 0.16$ ), total function in the expected community can be approximated as the product of average abundance and average per capita function (open circle) into components due to deviation in abundance (red arrow) and per capita function (blue arrow). B, C, These panels, which have different  $x$ -axes, plot the total function for each site under scenarios of abundance variation only (red points) or per capita function variation only (blue points). Each of these scenarios can be compared with the observed total pollen deposition for the 16 watermelon farms (solid gray points). There are only two lines because species’ per capita function did not vary across sites, reducing the number of terms in equation (5) to two. In data where the per capita function also varies across sites, a complete analysis would produce a corresponding third line. Of the two, B is more informative because its  $x$ -axis (abundance) is the better predictor of total function.

### How Do Abundance, Composition, and Body Size Drive Change in Total Stream Invertebrate Biomass across a Pollution Gradient?

We adapted the continuous Price equation to study changes in total community biomass in a previously published publicly available data set of stream invertebrates collected from 25 sites along a strong, continuous pollution gradient (Pomeranz et al. 2019a). Specimens were individually measured and assigned to one of six functional groups. Finer taxonomic resolution is available in the original study, but we use functional groups here to get enough data to effectively model. Additional study details are found in Pomeranz et al. (2019a). Acidic mining pollution strongly reduced stream invertebrate abundance and richness, so communities in the most polluted sites were dominated by a single group of larval midges (Diptera: Orthocladiinae). Since we are using biomass as a proxy for ecosystem function, a functional group's per capita contribution to function is its average body size across specimens collected at a site. We excluded functional groups with no observed specimens at a site from the calculation for that site's average body size; an alternative would be to use zero as the body size for missing functional groups, which we do not recommend because it would conflate changes in composition with change in body size. We want to know the extent to which the loss in total biomass across the pollution gradient is explained by loss of total abundance, selective shifts in functional group composition, and within-group changes in body size. We first modeled each of these factors (abundance, each functional group's relative abundance and body size) as continuous linear functions of the pollution gradient  $g$ . For example, the relative abundance of the  $i$ th functional group is modeled as  $\hat{p}_i(t) = \alpha_{p_i} + \beta_{p_i} \cdot g$ . The slope of this linear function captures the rate of change in the group's relative abundance over the pollution gradient, that is, a derivative in the continuous Price equation (eq. [2]). Using all model slopes  $\beta_A$ ,  $\beta_{p_i}$ ,  $\beta_{z_i}$  and intercepts  $\alpha_A$ ,  $\alpha_{p_i}$ ,  $\alpha_{z_i}$ , together with a simplifying linear approximation, we parameterized a continuous Price equation that partitions the rate of change in total biomass along the gradient into three additive components, each capturing the rate of change in only one factor (abundance, composition, or body size) while holding the remaining factors fixed at intercept values (supplement D):

$$\frac{dT}{de} \approx \beta_A \sum_{i=1}^n (\alpha_{p_i} \alpha_{z_i}) + \alpha_A \sum_{i=1}^n (\beta_{p_i} \alpha_{z_i}) + \alpha_A \sum_{i=1}^n (\alpha_{p_i} \beta_{z_i}). \quad (6)$$

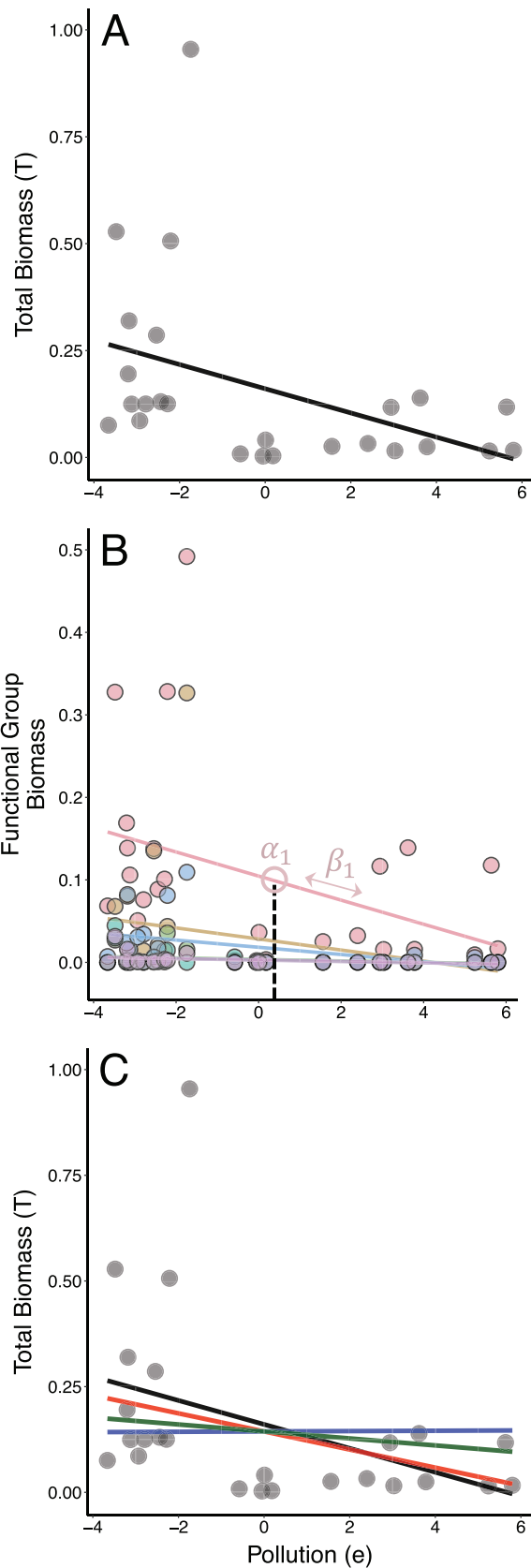
(Note that  $n$  represents functional groups, which have taken the place of species in this analysis.) To interpret

the analysis in terms of absolute function rather than change in function, we can substitute each partition value for the slope in the equation for total biomass  $T$  over the pollution gradient  $g$ ,  $\hat{T} = \alpha_T + \beta \cdot e$ . After some simplifying algebra (details in supplement D), we can express total biomass given a change in one factor—for example, relative abundance—as  $\hat{T}|\beta_{p_i} = \alpha_A \sum \hat{p} \alpha_{z_i}$ . This is the total biomass that would have been observed along the pollution gradient if species' relative abundances changed at their modeled rates while total abundances and per capita biomass remained fixed at the values observed at midpoint sites (i.e., intercept values). The corresponding counterfactuals for change in total abundance and per capita function are  $\hat{T}|\beta_A = \hat{A} \sum \alpha_p \alpha_{z_i}$  and  $\hat{T}|\beta_{z_i} = \alpha_A \sum \alpha_p \hat{z}_i$ , respectively. Plotting all three counterfactuals together (fig. 3) shows that loss of total abundance is the primary driver of loss in total biomass (red line, slope = 0.023). Data underlying figure 3 have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.v6g985s>; Pomeranz et al. 2019b). Change in composition, however, has barely any effect (blue line, slope < 0.001). Finally, loss of body size within functional groups explains a modest amount of biomass loss (green line, slope = 0.008).

### Discussion

The abundance-based ecological Price equation describes a linear relationship between abundance and function, a simple model that is nevertheless essential for understanding how function responds to global change in real-world ecosystems. Additive abundance effects are a common, well-validated assumption in the wider BEF literature (Vázquez et al. 2005; Kleijn et al. 2015; Spaak et al. 2017; Sonkoly et al. 2019), but their potential to explain ecosystem function loss is limited in common BEF study designs that restrict the range of abundance to isolate nonadditive biodiversity effects (Cardinale et al. 2011; Wardle 2016). Positive linear relationships between abundance and function might be expected wherever abundance is highly variable and interactions are weak. These conditions describe competitive plant communities under strong environmental stress (Spaak et al. 2017) as well as many mobile animal communities (Kremen et al. 2007). Accordingly, our demonstration analyses of two invertebrate communities both found that total ecosystem function loss was closely matched by a linear effect of abundance loss. By identifying strong abundance-function relationships in observational data, the abundance-based ecological Price equation can help resolve a long-standing debate about the importance of additive biodiversity effects in natural systems (Cardinale et al. 2011; Hooper et al. 2012; Vellend et al. 2013; Winfree





et al. 2015; Eisenhauer et al. 2016; Wardle 2016; Duffy et al. 2017; Hillebrand et al. 2018).

The ecological Price equation is an exact partition of total ecosystem function change and therefore must include the net effect of all drivers, including the species complementarity mechanisms that are central to both BEF theory and many empirical BEF relationships (Hooper et al. 2012; Duffy et al. 2017). Species complementarity may affect ecosystem function via per capita function (Loreau and Hector 2001) or abundance (Cardinale et al. 2011). In our demonstration analysis, direct effects of pollution on stream invertebrate body size may have been augmented (or mitigated) by shifting biotic interactions—for example, loss of predators (Pomeranz et al. 2019a)—and the strong additive abundance effects observed in the watermelon pollination data are partially supported by complementarity in species responses to daytime temperatures (Rader et al. 2013). However, there is no direct mapping between Price equation partitions of observational data and partitions of experimental data, such as Loreau and Hector's (2001) complementarity term.

The abundance-based ecological Price equation and the previously developed richness-based ecological Price equation (Fox 2006) are conceptually analogous partitions of the same total function change, but they are not easily compared. Lost richness represents lost individuals, but these same individuals may be alternatively interpreted as lost abundance. Therefore, we can find that total variation in watermelon pollination is explained by the richness and per species function terms under the richness-based partition or by the abundance term under the abundance-based partition. When an entire community is lost at once, as in a cleared forest, ascribing function loss to richness or abundance is a distinction without a difference. In less extreme scenarios, it may be helpful to distinguish systems where richness loss is primary and abundance loss secondary (highly selective drivers and biogeographic spatiotemporal scales) from the reverse (drivers shared by many species and smaller scales). To our knowledge, the

**Figure 3:** A, This panel shows the pattern we are trying to explain, namely, the total biomass of stream invertebrates declining over a pollution gradient. We use the Price equation to partition the change in function (biomass) along the pollution gradient into components due to deviation in abundance, composition (relative abundance), and per capita function. B, Total biomass can be subdivided into six functional groups (each color indicates one functional group). We modeled the intercept ( $\alpha$ ) and linear slope ( $\beta$ ) of biomass for each functional group ( $\alpha_1$  and  $\beta_1$ , shown as examples) as functions of the pollution gradient. C, Using equation (6), the intercepts and slopes are used to calculate biomass under three counterfactual scenarios of community response to the pollution gradient: abundance loss only (red line), change in composition (i.e., relative abundance) only (blue line), and change in per capita function only (green line).

conceptual overlap between additive richness and abundance effects has not been resolved in the BEF literature, and this may not be possible since it arises from the close mathematical interdependence between richness and abundance (Gotelli and Colwell 2001).

The general ecological Price equation conceptually unites ecological selection effects that have been defined throughout the BEF literature. Just as evolutionary selection effects capture covariance between changes in traits and fitness, ecological selection effects capture covariance between changes in species' frequencies and species' baseline function. Thus, ecological selection effects include the effects of higher function species being selected by chance into a local community (Huston 1997), displacing low-performing species during community growth (Loreau and Hector 2001), disproportionately benefiting from complementarity (Fox 2005), or being particularly robust or sensitive to environmental stress (Larsen et al. 2005; Mateo-Tomás et al. 2017; Spaak et al. 2017). In these examples, composition change occurs in response to different drivers (random assembly, growth, environmental change) and may be correlated with species' baseline function for various, largely unknown reasons (Carroll et al. 2011; Funk et al. 2017). But these various ecological processes have one shared consequence for ecosystem function: altered relative proportions of species with different baseline function. The Price equation shows that a selection effect can be a component of every change in a community mean (in some cases the selection effect will be zero), although isolating it in a Price partition may or may not be important for a particular research question. We found weak selection effects in both of our demonstration analyses because composition changes were not strongly correlated with species' per capita function. In other words, farms that received high pollination simply had high bee abundance, rather than individual bees belonging to especially efficient species. Similarly, biomass decreased along the pollution gradient because fewer individuals were present, not because the individuals at high-pollution sites were small bodied. However, if communities have limited size, even random composition changes must eventually result in selective loss of interspecific variability in function (ecological drift; Vellend 2010). In the following concluding paragraphs, we explore other ways the ecological Price equation invites analogy between community ecology and evolution in populations.

Field norms in BEF research and wider community ecology place high value on describing, explaining, and predicting empirical patterns. Therefore, having adapted the Price equation for BEF questions, it is tempting to immediately apply the equation to data analysis (Fox 2006), as we have done in this article. In contrast, the evolutionary Price equation's most important contributions have been theoretical, such as the proof that kin selection

and group selection are equivalent (Gardner 2008). The power of evolutionary theory derives from the tautological nature of the Price equation and natural selection itself (Frank 2012). The trade-off loss of ability to predict real-world systems is an ongoing challenge for evolutionary biology (Hunt 2014; Okasha and Otsuka 2020). Adapting the Price equation to empirical questions is therefore a work in progress that benefits both evolutionary biology and BEF research. For example, our analysis of biomass loss is inspired by an analysis of trait change over environmental gradients (Ellner et al. 2011) and the partitioning of trait change into ecological and evolutionary components (Norberg et al. 2012). On the other hand, the Price equation is already a proven theoretical tool, so its best use in BEF research may be for developing the theoretical structure needed to organize the field's overlapping hypotheses and contingent empirical patterns.

One way this may be achieved is by using the Price equation to formalize some of the verbal parallels between evolution and ecology (Vellend 2010). Trait distributions are subject to any number of interacting biotic and abiotic drivers, which evolutionary theory reorganizes into a small, logically complete set of universally relevant processes: mutation, selection, drift, and dispersal. This conceptual compression is powerful because a pattern ("finch beaks are bigger") has both a specific contingent explanation ("more hard-shelled seeds") and an abstract generalizable explanation ("natural selection"). Similarly, the BEF pattern "species richness increases total biomass" has specific explanations that can be demonstrated only in experimental settings ("reduced competition," "increase in limiting resources") and general explanations that can be applied in any context ("selection for species with higher per capita function"). By reframing the BEF hypothesis in just three terms, the ecological Price equation offers a highly generalizable framework for describing how changes in species' distributions and function result in changes in total community function.

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#### Statement of Authorship

T.H. and M.A.G. conceptualized the study. M.A.G. and R.W. acquired funding. T.H. developed the new abundance-based partitions with assistance from M.A.G. All authors wrote the original draft and contributed to revisions.

### Data and Code Availability

Data are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.8kpr4xqf>; Genung et al. 2022). Code is available on Zenodo (<https://doi.org/10.5281/zenodo.6093273>).

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