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USING THE PRICE EQUATION TO PARTITION THE EFFECTS OF BIODIVERSITY LOSS ON ECOSYSTEM FUNCTION

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Abstract. Species loss can impact ecosystem functioning, but no general framework for analyzing these impacts exists. Here I derive a general partitioning of the effects of species loss on any ecosystem function comprising the summed contributions of individual species (e.g., primary productivity). The approach partitions the difference in ecosystem function between two sites (a “pre-loss” site, and a “post-loss” site comprising a strict subset of the species at the pre-loss site) into additive components attributable to different effects. The approach does not assume a particular experimental design or require monoculture data, making it more general than previous approaches. Using the Price Equation from evolutionary biology, I show that three distinct effects cause ecosystem function to vary between sites: the “species richness effect” (SRE; random loss of species richness), the “species composition effect” (SCE; nonrandom loss of high- or low-functioning species), and the “context dependence effect” (CDE; post-loss changes in the functioning of the remaining species). The SRE reduces ecosystem function without altering mean function per species. The SCE is analogous to natural selection in evolution. Nonrandom loss of, for example, high-functioning species will reduce mean function per species, and thus total function, just as selection against large individuals in an evolving population reduces mean body size in the next generation. The CDE is analogous to imperfect transmission in evolution. For instance, any factor (e.g., an environmental change) causing offspring to attain smaller body sizes than their parents (imperfect transmission) will reduce the mean body size in the next generation. Analogously, any factor causing the species remaining at the post-loss site to make smaller functional contributions than at the pre-loss site will reduce mean function per species, and thus total function. I use published data to illustrate how this new partition generalizes previous approaches, facilitates comparative analyses, and generates new empirical insights. In particular, the SCE often is less important than other effects.

Key words: biodiversity; context dependence effect; ecosystem function; Price Equation; species composition effect; species richness effect.

INTRODUCTION

Many ecosystem functions on which life depends comprise the summed functional contributions of individual species. For instance, primary productivity is the sum of the productivities of all plant species. How will biodiversity (species) loss affect such ecosystem functions (Loreau et al. 2001, Hooper et al. 2005)?

Theories based on a null model address this question by comparing species' observed functional contributions at each site of interest to those expected under a null model (Loreau and Hector 2001, Fox 2005). Compar-

ison with a null model factors out certain effects often regarded as uninteresting or artifactual (e.g., the “sampling effect”; Huston 1997), so that any remaining variation in function among sites can be attributed to variation in the strength of interesting ecological effects (e.g., “selection effect,” “niche complementarity,” “dominance effect”; Loreau and Hector 2001, Fox 2005). Theories based on a null model have provided numerous insights; for instance, niche complementarity often is stronger at more species-rich sites (Loreau and Hector 2001). However, current theories based on a null model apply only in the context of a substitutive experimental design in which all species occupy a single trophic level and every species is grown in monoculture (Loreau and Hector 2001, Fox 2005). It is unclear if the insights provided by theories based on a null model can be

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extended to other contexts. While other theories of biodiversity and ecosystem function are not based on null models, these theories are, to varying degrees, system and function specific, rather than general (e.g., Tilman et al. 1997, Loreau 1998, Thébaud and Loreau 2003, Fox 2003, 2004, Ives and Cardinale 2004, Petchey et al. 2004, Solan et al. 2004, Gross and Cardinale 2005, Larsen et al. 2005). System- and function-specific assumptions are essential in order to predict variation in ecosystem function. However, generalizing across functions and systems requires a more general theoretical framework that incorporates different system- and function-specific models as special cases. For instance, in evolutionary biology system-specific models predict how particular traits will evolve under particular evolutionary scenarios, while Darwin's theory of evolution by natural selection provides a general framework that incorporates system-specific models as special cases and thereby allows evolutionary dynamics to be meaningfully compared across systems (Endler 1986).

Lack of a general framework relating biodiversity and ecosystem function has led to disagreement about appropriate study design and analysis, since it is unclear what general effects empirical studies should aim to measure (Allison 1999, Loreau et al. 2001, Huston and McBride 2002, Schmid et al. 2002, Petchey 2003, Benedetti-Cecchi 2004, Bell et al. 2005). For instance, can the effects of biodiversity on ecosystem function be cleanly partitioned, in principle, into effects of species richness vs. species composition, and if so, how can we separate these effects in practice (Allison 1999, Loreau et al. 2001, Huston and McBride 2002, Schmid et al. 2002, Petchey 2003, Benedetti-Cecchi 2004, Bell et al. 2005)? Lack of a general framework also has inhibited empirical generalization across studies and systems (e.g., Raffaelli et al. 2002, Giller et al. 2004, Hooper et al. 2005). For instance, approaches based on a null model reveal how plant diversity affects ecosystem function via selection effects and niche complementarity (Loreau and Hector 2001, Fox 2005). But since these approaches cannot be applied to experiments in which species are lost from multiple trophic levels, it is unclear if the same effects (or closely analogous effects) occur in multitrophic experiments (Raffaelli et al. 2002, Giller et al. 2004).

Here I derive a novel theoretical framework for biodiversity and ecosystem function. The framework partitions the difference between two sites in the level or rate of an ecosystem function into additive components attributable to different effects. This new approach applies to any ecosystem function comprising the summed functional contributions of individual species, is not based on a null model, and is not tied to a particular experimental design, therefore making it quite general.

This new approach is based on the Price Equation, which in evolutionary biology partitions the evolutionary change in mean phenotype between parents and their offspring into additive components attributable to two effects: natural selection and imperfect transmission

(Price 1970, 1972, 1995, Frank 1997). Loreau and Hector (2001) incorporated part of the Price Equation into a theory based on a null model of ecosystem function, and Fox (2005) refined their approach. Here, I use an extension of the full Price Equation to partition the observed difference in ecosystem function between two sites, rather than the difference between observed function and a null expectation. Next I derive this new "Price Equation partition" and discuss its interpretation, showing how it clarifies current conceptual issues in studies of biodiversity and ecosystem function. I then apply the Price Equation partition to several published data sets, showing that the partition gives new empirical insights, and allows quantitative comparative analyses that would otherwise be impossible. I also illustrate how the Price Equation partition generalizes system- and function-specific models (e.g., Ives and Cardinale 2004).

THE PRICE EQUATION PARTITION

To begin the derivation (described in more detail in Appendix A, along with a worked example), consider a more diverse site with s species, and a less diverse site comprising, for whatever reason, a strict subset s' of those species. For instance, after an extinction event, the "post-loss" (less diverse) site will comprise a strict subset of the species in the "pre-loss" (more diverse) site, and the effects of species loss can be quantified by comparing the former to the latter. However, it is important to recognize that I make no assumptions about why one site comprises a strict subset of the species in the other. The sites therefore may be separated in space, time, or both. Because the approach compares observed sites to one another, rather than to a null expectation, the approach does not require data on species' functional contributions in monoculture, unlike approaches based on a null model (Loreau and Hector 2001, Fox 2005). For concreteness, I will refer to the more diverse site as the pre-loss site, and the less diverse site as the post-loss site. Two sites with exactly the same species comprise a limiting case to which the approach also applies; in this limiting case either site may be arbitrarily designated the pre-loss site.

Let z_i be the functional contribution of species i ($i = 1, 2, \dots, s$) in the more diverse site, and z'_i be its contribution in the less diverse site. Throughout, primes denote attributes of the less diverse site and the species in it. For instance, if the function of interest was the rate of CO₂ uptake by trees, z_i would be the CO₂ uptake rate of tree species i at the more diverse site. The z_i and z'_i values can be positive or negative, depending on the ecosystem function and the scale of measurement. I assume that the s species include all and only those species performing the function of interest. Species absent from the post-loss site do not contribute to post-loss function (z'_i , undefined), a fact accounted for in the notation developed below (see Eq. 3).

I make no assumptions about the determinants of z and z' , as these determinants are presumably system and function specific. Understanding the determinants of

species' functional contributions is not essential here, since the goal of the approach is to analyze differences in ecosystem function between sites. Analogously, in evolutionary biology, ignorance of the species- and trait-specific genetics underlying species' phenotypic traits does not prevent the Price Equation from quantifying the causes of evolutionary change in phenotype (Frank 1997).

Define the difference between total pre- and post-loss function T and T' as

$$\Delta T = T' - T = \sum_i z'_i - \sum_i z_i = s' \bar{z}' - s \bar{z} \quad (1)$$

where overbars denotes means, explicit expressions for which are developed below (see Eqs. 2 and 3). Expressing total function as the product of species richness and mean function per species allows the functional effect of loss of species richness per se (i.e., declining number of species, independent of which species are lost) to be quantified.

We can write \bar{z} as

$$\bar{z} = \sum_i \frac{1}{s} z_i. \quad (2)$$

Next, we require an expression for \bar{z}' that incorporates only the s' remaining species, but retains the information about which species were lost (Price 1995). We cannot renumber the remaining species $j = 1, 2, \dots, s'$ and then take an unweighted mean across these s' species because this would discard the information about which species were lost. Instead, we use a notational trick to write \bar{z}' as a weighted mean of the functional contributions of all s species. We assign z'_i weight w_i , where $w_i = 0$ if species i is lost and 1 otherwise, and write

$$\bar{z}' = \sum_i \frac{1}{s'} w_i z'_i. \quad (3)$$

Eq. 3 equals the unweighted mean functional contribution of only the s' remaining species, but the w values retain the information about which species were lost.

In assigning weights w it will sometimes be desirable to distinguish between species absent from the post-loss ecosystem ($w_i = 0$), and species present in the post-loss ecosystem, but making zero functional contribution ($w_i = 1$ and $z'_i = 0$). In particular, in experiments designed to simulate species loss (e.g., Spehn et al. 2005), initial species composition is under experimental control. It is useful in these cases to distinguish species absent due to the experimental design ($w_i = 0$) from species absent due to failure to persist ($w_i = 1$ and $z'_i = 0$, due, for example, to intense competition from other species). Assigning $w_i = 0$ to all absent species is equally valid mathematically, and will be a practical necessity whenever the causes of species presence/absence are unknown, but would of course result in a different partitioning of ΔT (see Eq. 4). The Price Equation is extremely general and flexible, which gives it great power. The interpretation of any

particular application of the Price Equation necessarily depends on the way in which its parameters are defined (Price 1995, Frank 1997).

Substituting Eqs. 2 and 3 into Eq. 1, rearranging, and applying the standard definitions of population covariance (Cov) and expectation (E) gives

$$\Delta T = \bar{z} \Delta s + s' \Delta \bar{z} = \bar{z} \Delta s + s' \left[\frac{\text{Cov}(w, z)}{\bar{w}} + \frac{E(w \Delta z)}{\bar{w}} \right] \quad (4)$$

where $\Delta \bar{z} = \bar{z}' - \bar{z}$, $\Delta s = s' - s$, $\Delta z_i = z'_i - z_i$, and $\bar{w} = \sum_i (1/s) w_i = s'/s$ (see Appendix A for details). The bracketed term in Eq. 4 is the Price Equation from evolutionary biology (Price 1970, 1972, 1995, Frank 1997). Its presence in Eq. 4 indicates a fundamental analogy between species loss and phenotypic evolution, which I discuss below.

To complete the derivation, we multiply through the brackets in Eq. 4 by s' , thereby removing all dependence of the bracketed terms on s or s' , and obtaining what I will call the Price Equation partition of the difference in ecosystem function ΔT :

$$\Delta T = \bar{z} \Delta s + \text{Sp}(w, z) + \sum_i w_i \Delta z_i \quad (5)$$

where Sp denotes the sum of products [i.e., $\text{Sp}(w, z) = \sum_i (w_i - \bar{w})(z_i - \bar{z})$].

INTERPRETING THE PRICE EQUATION PARTITION

The Price Equation partition (Eq. 5) has three additive components. The first, $\bar{z} \Delta s$, is the "species richness effect" (SRE). The SRE is that part of the difference in total function attributable to loss of species richness per se, independent of which species are lost and the response of the remaining species to species loss. It is the value of ΔT expected to occur if species are lost at random with respect to their pre-loss functional contributions and nothing else changes.

The SRE refines a common verbal argument about the conditions under which species richness per se will affect ecosystem function. Several authors (e.g., Lawton et al. 1998) suggest that ecosystem function will not vary with species richness if all species are identical, since species loss would be perfectly compensated for by the remaining species. The Price Equation partition refines this argument by separating the direct effect of loss of species richness (the SRE) from any compensatory responses by the remaining species (which would contribute to the "context dependence effect," discussed later in this section). Separating the direct effects of species loss from post-loss responses by the remaining species will be useful in those cases where different mechanisms determine species' pre-loss functional contributions (z_i values) and their responses to species loss (e.g., Fox 2003). In such cases, species with identical z_i values will not necessarily compensate perfectly for one another following species loss.

The SRE is proportional to \bar{z} , so mechanisms that cause species to function at a high level, on average, will

increase the amount by which total function would be expected to decline due to random loss of any given number of species. For instance, all else being equal, \bar{z} might be higher if species facilitate one another or exhibit substantial niche differentiation.

The SRE differs from the species richness effect estimated by the statistical models typically applied to experiments on biodiversity and ecosystem function (e.g., Hector et al. 2002, Schmid et al. 2002). A typical experimental design comprises multiple species richness levels, each represented by several species compositions chosen at random from a larger species pool (e.g., Hector et al. 2002). Conventional statistical models estimate the functional form of the relationship between ecosystem function and species richness (e.g., linear, log-linear) while statistically controlling for other sources of variation (Hector et al. 2002). In contrast, the absolute magnitude of the SRE in the Price Equation partition necessarily is linearly related to the difference in species richness, Δs , with a slope given by mean function per species at the pre-loss site, \bar{z} (Eq. 5). A conventional statistical analysis does not estimate the SRE, and a linear SRE does not foretell the shape of the statistical relationship between total function and species richness (Appendix B). This does not indicate that either conventional statistical analyses or the Price Equation partition are incorrect, but merely emphasizes the need for careful interpretation of each. They measure different things. Depending on the precise goals of a study, either the SRE or the statistically defined relationship between total function and species richness might be of greater interest.

The second component of the Price Equation partition, $Sp(w, z)$, is the “species composition effect” (SCE), attributable to species loss that is nonrandom with respect to species’ pre-loss functional contributions. The SCE is that portion of the difference in total function attributable to differences in species composition per se, as opposed to the difference in species richness. The SCE is necessarily accompanied by, but is completely distinct from, the SRE. When species are lost, part of the difference in ecosystem function (ΔT) will always be attributable to the SRE (random species loss). The SCE captures any additional difference in ecosystem function (either positive or negative) due to nonrandom species loss.

The SCE is analogous to natural selection in evolution; more precisely, it is an example of what Price (1995) terms “subset selection.” For instance, death of (selection against) large-bodied individuals reduces the mean body size of an evolving population, other things being equal. Analogously, loss of (selection against) high-functioning species reduces mean function per species (and thus total function), other things being equal.

The SCE differs from the sampling effect (under random species loss the post-loss site is less likely to contain any given species; Huston 1997, Loreau and

Hector 2001), since the expected value of the SCE equals zero under random species loss. The SCE also differs from the selection effect (Loreau and Hector 2001), and the dominance effect (Fox 2005), which consider how the functional contributions of species within a single site differ from a null expectation, rather than the between-site effects of species loss.

The distinction between effects of species richness and composition on ecosystem function has been the subject of extensive conceptual discussion (e.g., Huston 1997, Loreau et al. 2001). By defining the SRE and SCE, the Price Equation partition helps to clarify certain points. First, some authors argue that differences in species composition and richness are necessarily confounded, since species loss necessarily changes both species richness and composition (e.g., Schmid et al. 2002). According to this view, it is impossible to completely separate the effects of species richness and composition on ecosystem function. However, that the SCE is necessarily accompanied by the SRE does not imply that the two effects are confounded in the sense of being inseparable. Indeed, the SRE and SCE can be calculated even when a study includes only two sites, so that species richness and composition are completely confounded from a conventional statistical perspective (see *Applying the Price Equation partition*). This shows that whether or not the effects of species richness and composition on ecosystem function are separable depends on how these effects are defined. Second, it could be argued that loss of species richness per se cannot be said to affect ecosystem function. According to this view, if species are lost and nothing else changes, then any change in ecosystem function is attributable entirely to loss of those particular species. Attributing part of the change in ecosystem function to loss of species richness is merely a statistical fiction. The Price Equation partition suggests that this point of view misses the ecologically interesting distinction between random species loss and nonrandom species loss. However, the Price Equation partition also can be modified to accommodate this point of view. The sum of the SRE and SCE gives the “total direct effect” of species loss on ecosystem function—the total change in function that would occur if species were lost and nothing else changed (i.e., $z_i = z'_i$ for all remaining species). If the SRE is regarded as a statistical fiction, then instead of considering the SRE and the SCE to be two distinct components of ΔT , we can consider their sum as a single component of ΔT that gives the total direct effect of species loss on ecosystem function.

The third component of the Price Equation partition, $\sum_i w_i \Delta z_i$, is the context dependence effect (CDE), attributable to between-site variation in the functional contributions of the species present in both ecosystems. The CDE quantifies the combined effects of all factors causing species’ functional contributions to vary between sites, including between-site variation in environmental conditions. The CDE also includes responses to

species loss by the remaining species (compensatory or otherwise).

The CDE is analogous to imperfect transmission in evolution (Frank 1997). Various factors (e.g., epistasis) can cause offspring to exhibit phenotypes that differ from those of their parents (imperfect transmission). Analogously, various factors (e.g., environmental differences, loss of competitors) can cause the species remaining post loss to make different functional contributions than they did pre loss. Like the SCE, the CDE is not confounded with the SRE, since it does not depend on Δs . Nor is the CDE confounded with the SCE, since only the CDE depends on species' post-loss functional contributions.

That the SRE, SCE, and CDE are not confounded does not imply they will be uncorrelated, since they might covary due to shared underlying causes. For instance, a shared underlying cause (e.g., an environmental change) might cause low-functioning species to go extinct (generating a SCE and a SRE), and cause the remaining species to function at a lower level (a CDE). The data of Solan et al. (2004) provide an example (see *Applying the Price Equation Partition*). The power of the Price Equation partition is that it quantifies and separates different, possibly correlated effects, independent of the underlying system- and function-specific causes.

The CDE in particular often will reflect the net outcome of many underlying mechanisms, possibly making it difficult to interpret. It would be useful to partition the CDE into more easily interpretable subcomponents. We can further partition the CDE into subcomponents by defining $z_i = n_i p_i$, where n_i and p_i , respectively, are the pre-loss abundance and pre-loss per capita functional contribution of species i . Similarly, we can define $z'_i = n'_i p'_i$. Substituting these definitions into the CDE and rearranging yields

$$\text{CDE} = \sum_i w_i \Delta z_i = \sum_i (w_i p_i \Delta n_i + w_i n_i \Delta p_i + w_i \Delta n_i \Delta p_i) \quad (6)$$

where $\Delta n_i = n'_i - n_i$ and $\Delta p_i = p'_i - p_i$. Eq. 6 partitions the CDE into three additive subcomponents. The first, $\text{CDE}_n (= \sum_i w_i p_i \Delta n_i)$, quantifies context dependence of species' abundances. The second, $\text{CDE}_p (= \sum_i w_i n_i \Delta p_i)$, quantifies context dependence of species' per capita functional contributions. The third, $\text{CDE}_i (= \sum_i w_i \Delta n_i \Delta p_i)$, quantifies the interaction of context dependence in abundance and per capita contribution. Partitioning the CDE into subcomponents aids interpretation when different underlying mechanisms determine species' abundances and per capita functional contributions. In particular, in substitutive experiments species in less diverse sites are more abundant than species in more diverse sites. Approaches based on a null model factor out the effect of variation in species' abundances among sites in the context of a substitutive experimental design (Loreau and Hector 2001, Fox 2005). The Price Equation partition achieves essentially

the same goal without assuming a substitutive design by partitioning the CDE into subcomponents. CDE_n identifies that part of context dependence that in substitutive experiments simply reflects the experimental design. However, outside the context of substitutive experiments, CDE_n reflects the ecological processes that determine species' abundances.

The CDE is the sum of context dependence in the functional contributions of all species remaining post loss. A near zero CDE can arise either because no species' functional contribution is context dependent, or because species' functional contributions are context dependent in opposite ways. When $\text{CDE} \approx 0$, inspecting the individual $w_i \Delta z_i$ values reveals which of these two possibilities obtains, and thereby aids interpretation of the CDE.

Whenever its assumptions are met, the Price Equation partition comprises a complete, exact partitioning of the difference in total function between any two sites, thereby providing a basis for comparison across studies and systems (Price 1970, 1972, 1995, Frank 1997). The Price Equation partition does not predict the magnitudes of different effects of species loss, just as Darwin's theory of evolution by natural selection does not predict, for example, how strong natural selection will be (Price 1970, 1972, 1995, Frank 1997). Predicting and explaining the magnitudes of the SRE, SCE, and CDE requires knowledge of the system-specific determinants of species' functional contributions, and the system-specific causes of species loss. The value of the Price Equation partition is that it shows how to express the outcomes of these system-specific phenomena so as to allow comparisons across studies and systems.

APPLYING THE PRICE EQUATION PARTITION

Next I apply the Price Equation partition to selected studies, with further studies analyzed in Appendix B. I discuss both study-specific insights and cross-study comparisons.

Petchey et al. (1999) assembled five replicates (sites) of a diverse pre-loss set of eukaryotic microbes and bacterial decomposers in aquatic laboratory microcosms, and mimicked species loss by assembling 10 replicates of a post-loss set comprising a strict subset of the eukaryotes in the pre-loss set. Species not initially present in the post-loss set were assigned $w_i = 0$, while other species were assigned $w_i = 1$. Both the pre- and post-loss sets included eukaryotes filling various trophic roles (primary producers, bacteriovores, herbivores, omnivores, predators). Pre-loss replicates were maintained at constant temperature, while half of the post-loss replicates experienced constant temperature and the other half experienced gradually increasing temperature. Temperature differences between pre- and post-loss replicates might be expected to generate context dependence in species' functional contributions. Petchey et al. (1999) conducted this experiment twice using different species in the pre-loss set. I examined the effects

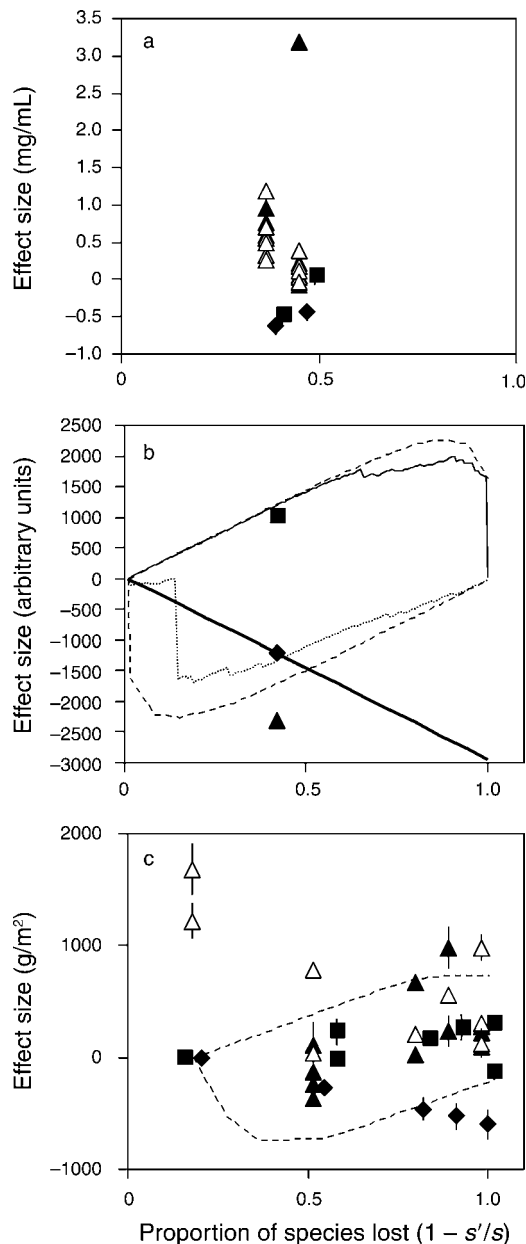


FIG. 1. Effects of species loss on ecosystem function in different studies. Symbols represent mean SRE (random loss of species richness; diamonds), SCE (nonrandom loss of high- or low-functioning species; squares), and CDE (post-loss changes in the functioning of the remaining species; triangles) for each post-loss site. Error bars (which may be zero or too small to display) represent \pm SE and reflect variation among the pre-loss site to which the post-loss site is compared. Some points coincide; some are jittered horizontally for clarity. (a) Effects on total biomass of eukaryotes in experimental microcosms (sites; Petchey et al. 1999). Data from different proportions of species lost indicate results from two different experiments. Solid and open triangles, respectively, indicate CDEs from post-loss sites having the same environments as the pre-loss sites, or different, experimentally altered environments. (b) Effects on community bioturbation potential (BP_c) of macroinvertebrates at marine benthic sites (Solan et al. 2004). The bold solid straight line indicates the SRE that would be observed for a given

of species loss and environmental change on total eukaryotic biomass after six weeks (dozens of generations) of ecosystem development. I calculated estimates of the SRE, SCE, and CDE for each post-loss replicate by comparing each post-loss replicate to each of the pre-loss replicates. In each experiment this procedure provides five estimates of the SRE, SCE, and CDE for each post-loss replicate, corresponding to the five pre-loss replicates to which the post-loss replicates were compared. In both experiments $CDE = CDE_n$ while CDE_p and $CDE_i = 0$ because species' per capita functional contributions (body sizes) did not vary. Petchey et al. (1999) also subjected replicates of the pre-loss ecosystems to increasing temperatures; for simplicity I do not consider these data.

Application of Price Equation partition to the study of Petchey et al. (1999) shows that the Price Equation partition separates the effects of species richness and composition even when species richness and composition are completely confounded in a statistical sense (Fig. 1a). This illustrates that the Price Equation partition and conventional statistical analyses define the effects of species richness and composition in different ways. The CDE is large and positive in most replicates of both temperature treatments (Fig. 1a). Since increasing temperature probably did not directly enhance the performance of any species (Petchey et al. 1999), positive CDEs indicate strong density compensation in response to species loss that overwhelmed any direct negative effects of increasing temperature on the performance of the remaining species. Interestingly, strong compensatory responses occurred even though species occupied several trophic levels and did not interact solely as competitors.

Solan et al. (2004) collected data on macroinvertebrate species richness, composition, species' body sizes (mean individual biomasses), and species' abundances at two sites in Inner Galway Bay, Ireland. I use the term "species" for the sake of simplicity, even though 21% of the species were actually coarser taxonomic aggregations (e.g., genera). The more diverse (pre-loss) site is pristine and comprises 139 species. The less diverse (post-loss) site is disturbed and comprises 82 species also found in the more diverse site. The less diverse site also has eight taxa not found at the more diverse site. I follow Solan et al. (2004) in excluding these species from the analysis. An index of the bioturbation potential of species i , BP_i , can be calculated from knowledge of abundance, mean body size, mobility, and sediment reworking mode (Solan et al. 2004). The community bioturbation

← proportion of species lost. The thin solid curved line indicates SCEs that would be observed if rare species were lost first. The dotted line indicates SCEs that would be observed if large-bodied species were lost first. Dashed lines indicate maximum and minimum possible SCEs. (c) Effects on total aboveground plant biomass in experimental plots (sites; Mulder et al. 1999). Solid and open triangles are as in (a); dashed lines are as in (b).

potential, BP_c , is the sum of the BP_i values of all the species at a site, and is the ecosystem function analyzed here. Bioturbation is a primary determinant of sediment oxygen concentrations, which affect rates of decomposition and nutrient regeneration (Solan et al. 2004). Solan et al. (2004) converted BP_c into an estimate of biogenic mixing depth, BMD, using an empirically derived nonlinear transformation. I analyze the BP_c because it is impossible to separate the contributions of the SRE, SCE, and CDE to intersite variation in BMD, due to the nonlinear relationship between BP_c and BMD. Solan et al. (2004) simulated the changes in BMD that would result at the pristine (pre-loss) site from a variety of hypothetical extinction scenarios. Using BP_c instead of BMD as the ecosystem function, I examined the values of the SRE and SCE under four hypothetical extinction scenarios from the more diverse, pristine site.

The value of the SRE for any given level of species loss is the same for all extinction scenarios, since it is independent of which species are lost (Fig. 1b). The minimum and maximum possible values of the SCE are those values that would occur if species were lost in order, or in reverse order, of bioturbation potential BP_i . These two scenarios bound the SCE values that would be observed under other scenarios. Loss of species in order of rarity leads to positive SCE values equal or near to the maximum possible (Fig. 1b), since rare species generally are those with small BP_i values (Solan et al. 2004). These positive SCE values largely cancel the negative SRE values, so that total function does not greatly decline in this scenario until most species are lost (see also Solan et al. 2004). Loss of species in order of body size leads to negative SCE values equal or near to the minimum possible (Fig. 1b), since large-bodied species generally are those with large BP_i values (Solan et al. 2004). When species are lost in order of body size, additional function is lost, above and beyond that expected under random species loss, so that even low levels of species loss lead to large declines in function (see also Solan et al. 2004).

All extinction scenarios in Fig. 1b assume no post-loss changes in the BP_i values of the remaining species (i.e., $CDE=0$, not plotted in Fig. 1b). Solan et al. (2004) refer to these as “worst case” scenarios because of the absence of density compensation. However, these scenarios are the worst case only if abundances of the remaining species cannot decline post loss. The data from the disturbed site reveal a situation worse than the worst case. Assuming that species’ body sizes do not vary between the pristine and disturbed sites, we can partition the difference in BP_c between these two sites (Fig. 1b). The disturbed site lacks many species with small pre-loss BP_i values (=positive SCE), but most of the remaining species are less abundant at the disturbed site than at the pristine site, leading to lower post-loss BP_i values and a strongly negative CDE (Fig. 1b).

Mulder et al. (1999) randomly varied plant species richness and composition in an experimental Swedish

grassland in a substitutive design. Insecticide spraying removed insect herbivores from some plots (sites). Insects are a crucial component of the plants’ environment, so their removal might be expected to generate context dependence in plant function. I compared total aboveground plant biomass in each of the less than maximally diverse (post-loss) plots to each of the four maximally diverse unsprayed (pre-loss) plots to estimate effect sizes. Two species (*Phalaris arundinacea* and *Phleum pratense*) that could not be reliably distinguished were considered a single species. Attributing half their combined biomass to each species in plots where both were planted produced only minor quantitative changes in the results. Species planted in the maximally diverse plots but not the less diverse plot were assigned $w_i = 0$, while other species were assigned $w_i = 1$. This procedure provides four estimates of the SRE, SCE, and CDE for each less diverse plot. Less diverse plots can also be compared to one another, as well as to the most diverse plots, as long as the plots to be compared meet the assumptions of the Price Equation partition. However, these additional comparisons provide little additional ecological insight and are omitted. I also calculated the subcomponents of the CDE (CDE_n , CDE_p , CDE_i) for each less diverse plot.

Application of the Price Equation partition indicates that the decline in total plant biomass with declining plant species richness in unsprayed plots is attributable solely to loss of plant species richness per se (the SRE), since the SCE and CDE either do not vary or increase with decreasing post-loss richness (Fig. 1c). The absolute magnitude of the CDE (which reflects compensatory responses of the species remaining post loss, as well as the substitutive design) frequently exceeds that of the SCE, even when pre- and post-loss sites share the same insect treatment (Fig. 1c). Indeed, the CDE often is greater in absolute magnitude than any possible SCE (Fig. 1c).

Interestingly, the SCE and SRE are uncorrelated with the CDE (all $|r| < 0.30$, all $P > 0.05$), indicating that which, or how many, species are lost does not affect the compensatory response by the remaining species. This is a common result in substitutive plant diversity experiments, although in some cases the SCE and CDE are negatively correlated, indicating that loss of high-functioning species leads to an increased compensatory response by the remaining species (Appendix B).

Herbivore presence/absence drives much of the variation in the CDE in Mulder et al. (1999). In particular, context dependence is very large in herbivore removal plots with no plant species lost (Fig. 1c). That removal of insect herbivores increases context dependence at high but not low plant species richness is consistent with theoretical predictions that sensitivity of total yield to herbivory increases with plant species richness (King and Pimm 1983). This result probably occurs because in less diverse plots intense intraspecific

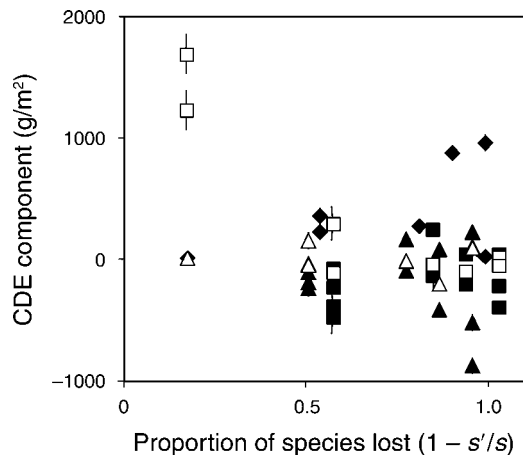


FIG. 2. Subcomponents of the context dependence effect (CDE) in Mulder et al. (1999) vs. proportion of species lost (see *Interpreting the Price Equation partition*). Data are the mean CDE_n , which quantifies context dependence of species' abundances (diamonds), CDE_p , which quantifies context dependence of species' per capita functional contributions (squares), and CDE_i , which quantifies the interaction of context dependence in abundance and per capita contribution (triangles), for each less diverse post-loss experimental plot. For the CDE_p and CDE_i , solid symbols indicate data from plots with insect herbivores present, while open symbols indicate data from plots sprayed with insecticide to remove insects. The value of the CDE_n does not depend on insecticide treatment because it depends only on how planted abundances of species vary between the most diverse and less diverse plots. Error bars represent $\pm SE$. Some points are jittered horizontally for clarity.

competition limits the response of species to herbivore removal.

When no species are lost, any difference in function between sites equals CDE_p , since the SRE and SCE equal zero by definition, and CDE_n and CDE_i equal zero due to the substitutive experimental design (Fig. 2). When species are lost, CDE_n is necessarily equal or greater than zero in substitutive experiments, since the species remaining in a less diverse plot are always more abundant than they are in the most diverse pre-loss plots (Fig. 2). CDE_p summarizes context dependence of species' per capita biomasses that is independent of context dependence of species' abundances (Fig. 2). CDE_p does not vary with species loss, as expected since environmental conditions did not vary with species loss, and is higher on average in insect removal plots (Fig. 2). CDE_i summarizes context dependence of the interaction between abundance and per capita functional contribution (Fig. 2). CDE_i is generally (but not necessarily) less than zero, and tends to decrease as more species are lost (Fig. 2). These trends in CDE_i reflect the fact that species tend to perform better on a per capita basis when they occur at low abundance (i.e., in high-diversity plots), since species in high-diversity plots interact mostly with other species that presumably occupy different niches.

Several intriguing generalizations emerge from comparing across studies (see also Appendix B). First, the

absolute magnitude of the SRE generally becomes large relative to other effects only when $\sim 50\%$ or more of species are lost. Loss of species richness per se is of minor importance when only a small fraction of species is lost. Second, the CDE often is larger in absolute magnitude than the SCE, and often larger than any possible SCE, indicating that which species are lost often is not a major determinant of post-loss ecosystem function. Third, net compensatory responses to species loss (positive CDEs) are common, even when species do not interact solely as competitors, suggesting that we still have much to learn about the ecological mechanisms driving functional compensation. Fourth, studies in which pre- and post-loss sites differ strongly in environmental conditions do not necessarily find larger CDEs, relative to other effects, than studies lacking strong environmental variation among sites. This is because the species remaining post loss may respond to environmental change in opposite ways, and because species loss and associated alteration of species' interactions is itself a major source of context dependence in species' functional contributions. Finally, in substitutive experiments on plant diversity, the commonly observed decline in total plant biomass with declining species richness is solely due to the SRE, although the precise statistical form of the decline also depends on the SCE and CDE. None of these quantitative generalizations would have been possible without the Price Equation partition, since the studies compared include studies of different ecosystem functions, performed by different species, using different study designs.

The Price Equation partition also facilitates comparative analysis by identifying which studies are comparable. In particular, the Price Equation partition does not apply to studies in which the species being considered do not perform the function of interest, and so affect function only indirectly, for instance by feeding on the species performing the function of interest (e.g., decomposition rate in McGrady-Steed et al. [1997]). Nor does the Price Equation partition apply to ecosystem functions that are "emergent" features of the whole system (e.g., resilience sensu Pimm [1984]), rather than simple sums of the separate contributions of individual species. Finally, the Price Equation partition does not apply when sites of differing richness do not comprise strictly nested subsets of species. When the Price Equation partition does not apply, species loss affects ecosystem function via unknown effects qualitatively different from those identified here. Other approaches to analyzing ecosystem function, such as approaches based on a null model, will be especially useful in cases where the Price Equation partition does not apply.

Appendix B applies the Price Equation partition to other empirical studies by Wardle et al. (1997), Spohn et al. (2004; the BIODEPTH experiment), and Belnap et al. (2005). Appendix B further shows that the Price Equation partition can also generalize system- and

function-specific models. An example is the work of Ives and Cardinale (2004), who modeled the effect of species loss on ecosystem tolerance to environmental stress. Many other system- and function-specific models also can be analyzed within the framework of the Price Equation partition (e.g., Tilman et al. 1997, Loreau 1998, Fox 2003, 2004, Gross and Cardinale 2005, Larsen et al. 2005).

CONCLUSIONS

Understanding how biodiversity affects ecosystem function in different systems requires both system-specific models and a more general theoretical framework that subsumes system-specific models as special cases. System-specific models are essential for prediction. A unifying framework synthesizes system-specific studies, allowing novel comparative insights to emerge and aiding interpretation of system-specific studies (Frank 1997). Conceptual debates about how biodiversity affects ecosystem function, and the limited scope and heuristic nature of proposed empirical generalizations, indicate lack of a general theoretical framework. The Price Equation partition provides an important step towards such a framework. Future studies should aim to describe and understand how the relative magnitudes of the species richness effect (SRE), species composition effect (SCE), and context dependence effect (CDE) vary in different situations, and extend the Price Equation partition to cover other cases.

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APPENDIX A

Detailed derivation of the Price Equation partition, and a worked example (*Ecological Archives* E087-162-A1).

APPENDIX B

Applications of the Price Equation partition to the empirical studies of Wardle et al., Belnap et al., and Spehn et al., and to the theoretical model of Ives and Cardinale (*Ecological Archives* E087-162-A2).