

## *Ecological Archives E087-162-A1*

**Jeremy W. Fox. 2006. Using the Price equation to partition the effects of biodiversity loss on ecosystem function. *Ecology* 87:2687-2696.**

Appendix A. Detailed derivation of the Price Equation partition, and a worked example. A [pdf file](#) is also available.

### *Derivation of the Price Equation partition*

Here I present a more detailed derivation of the Price Equation partition. All terms are defined as in the main text. I first use the Price Equation (Price 1970, 1972, 1995, Frank 1997) to partition  $\Delta\bar{z}$ , the difference between sites in mean function per species, and then extend the Price Equation to develop to a partition of  $\Delta T$ , the difference between sites in total function.

In general, the Price Equation partitions the difference between two “corresponding” populations in the weighted mean of some property of the “objects” comprising the populations (Price 1970, 1972, 1995, Frank 1997). In order to calculate these weighted means, objects are categorized into “types” according to their property values, with all objects of a given type having the same property value (the average value of objects of that type). The weight assigned to each type of object is some measure of the frequency or amount of objects of that type in the population. Populations “correspond” when the objects comprising one population have some kind of 1:1 relationship with the objects in the other population (Price 1995).

The generality and the power of the Price Equation arise from the broad applicability of its terms (“population”, “object”, “type”), and the flexibility with which “correspondence” may be defined (Price 1972, 1995, Frank 1997). The difficulty of the Price Equation arises from the fact that way in which “correspondence” is defined partially dictates how objects are categorized into “types” (Frank 1997). For instance, in evolutionary biology, the two populations comprise parents and their offspring, with offspring “corresponding” to their parent(s) (Price 1970, 1972, 1995, Frank 1997). If the property of interest is some aspect of the phenotype of individual organisms (the “objects”), then the frequency of parents of phenotype (“type”)  $i$  is simply the relative abundance of parents of phenotype  $i$ . However, the nature of the 1:1 correspondence between parents and offspring dictates that the frequency of offspring of type  $i$  be defined as the relative abundance of offspring of parents of phenotype  $i$ , not the relative abundance of offspring of phenotype  $i$  (Price 1972, 1995, Frank 1997). That is, offspring are indexed by the phenotype of their parents, not their own phenotype. For example, if parents of type 1 have 10 offspring, and the total number of offspring produced by all parents is 100, then the frequency of offspring of type 1 is  $10/100 = 0.1$ . Defined in this way, the ratio of offspring frequency to parental frequency measures parental relative fitness—the fittest parental phenotypes are those whose offspring occur at high frequency in the offspring population, relative to the parent’s own frequency. Indexing offspring by their own phenotype is inappropriate because doing so ignores which parents gave rise to which offspring, thereby treating the parent and offspring populations as if they were unrelated (no 1:1 correspondence). Indexing offspring by parental phenotype allows phenotypic evolution (difference in weighted mean phenotype between parental and offspring populations) to be partitioned into components attributable to natural selection (any non-random association between parental phenotype and parental fitness) and imperfect transmission (any differences between phenotypes of offspring and their parents) (Price 1972, 1995, Frank 1997).

To examine the effects of species loss on ecosystem function, it is natural to define “objects” as species, each of which is a unique “type” of object. I define species’ properties as their pre- and post-loss functional contributions  $z_i$  and  $z'_i$ , respectively, assumed to be measured in the same units for every species  $i$ . We will typically consider all the species performing the function of interest. For instance, if the function of interest were primary productivity in a grassland,  $z_i$  would be the pre-loss productivity of plant species  $i$ , where  $i = 1 \dots s$  and  $s$  is the number of plant species in the more-diverse grassland. If the function of interest was the primary productivity of trees (rather than of all plants),  $s$  would be the species richness of trees in the most tree-rich ecosystem. Species not performing the function of interest (e.g., species that feed on those performing the function of interest) are considered to be part of the environment.

Having defined species' properties (functional contributions), we next need to make explicit the 1:1 correspondence between the species in each site. I assume that the species in the more-diverse (species rich) site correspond in 1:1 fashion with the species present in, or absent from, the less-diverse site. In other words, I assume that the less-diverse site comprises a strict subset of (or, in the limit of no species loss, the same species as) the species in the more-diverse site. Because of this assumption, my approach does not apply to pairs of sites comprising partially-overlapping or disjunct species compositions.

We now need to define the frequency of each species in each site. By definition, total function in either site is just the sum of the functional contributions of all species present. Therefore, the frequency  $q_i$  of species  $i$  in the more diverse

(“pre-loss”) site is simply  $\frac{1}{s}$ . The frequency of a species is not determined by its relative or absolute abundance, since two species with identical  $z_i$  values make identical contributions to ecosystem function, even if, e.g., one is rare and the other common. Therefore, mean function per species  $\bar{z}$  in the pre-loss site is

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

Equation (A.1) is equation (2) in the main text. In the less-diverse (“post-loss”) site total function is just the sum of the functional contributions of the persisting species, while lost species make no functional contribution by definition.

$$q'_i = q_i \frac{w_i}{w} = \frac{1}{s} \frac{w_i}{s'} = \frac{w_i}{s'}$$

Therefore, the post-loss frequency of species  $i$  is  $\frac{w_i}{s'}$ , where  $w_i = 1$  for “persisting” (present) species and 0 for “lost” (absent) species. The weights  $w$  capture the 1:1 correspondence between the species present in the pre-loss ecosystem, and present or absent from the post-loss ecosystem. The weights  $w$  allow  $\bar{z}'$  to be written in an ecologically-meaningful form that retains the information about which species were lost:

$$\bar{z}' = \sum_i q'_i z'_i = \sum_i \frac{1}{s'} w_i z'_i. \quad (\text{A.2})$$

Equation (A.2) is equation (3) in the main text.

Next I define the difference in mean function per species between the two sites as

$$\Delta\bar{z} = \bar{z}' - \bar{z}. \quad (\text{A.3})$$

Equation (A.3) defines the more-diverse site as the “standard of reference” to which the less-diverse site is compared. This is a mathematically-arbitrary choice, since defining  $\Delta\bar{z} = \bar{z} - \bar{z}'$  is equally valid from a mathematical perspective. However, (A3) is the more natural definition of  $\Delta\bar{z}$  from an ecological perspective if we are primarily concerned with analyzing the functional effects of species loss. In the limiting case when the two sites comprise exactly the same species, the choice of the “standard of reference” is of course ecologically as well as mathematically arbitrary.

To build from (A.3) to an analysis of difference in total function  $\Delta T$ , define

$$\Delta T = T' - T = s'z' - s\bar{z}. \quad (\text{A.4})$$

Equation (A.4) is equation (1) in the main text. By defining  $\Delta T = T' - T$  rather than  $\Delta T = T - T'$ , (A.4) maintains the convention that the more-diverse site is the standard of reference. Equation (A.4) can be expanded as follows:

$$\Delta T = s'z' - s\bar{z} = (s + \Delta s)(\bar{z} + \Delta \bar{z}) - s\bar{z}. \quad (\text{A.5})$$

Noting that  $\Delta s \Delta \bar{z} = (s' - s)(\bar{z}' - \bar{z})$ , we can expand (A.5) and cancel, obtaining

$$\Delta T = s\Delta \bar{z} + \bar{z}\Delta s + s'\bar{z}' - s'\bar{z} - s\bar{z}' + s\bar{z}. \quad (\text{A.6})$$

Recollecting terms in (A.6) and cancelling partitions  $\Delta T$  into two additive components:

$$\Delta T = \bar{z}\Delta s + s'\Delta \bar{z}. \quad (\text{A.7})$$

The first component of (A.7),  $\bar{z}\Delta s$ , is the SRE, and the second,  $s'\Delta \bar{z}$ , is the sum of the SCE and the CDE.

An alternative partitioning to (A.7), which arises from a different recollection of terms in (A.6), is

$$\Delta T = \bar{z}'\Delta s + s\Delta \bar{z}. \quad (\text{A.8})$$

Although the alternative partitioning (A.8) is mathematically valid, the partitioning given by (A.7) is more logical and useful for three reasons. First, scaling the difference in species richness  $\Delta s$  by mean post-loss functional contribution  $\bar{z}'$ , as in (A.8), confounds the effect of loss of species richness *per se* with the effects of the processes that determine species' post-loss functional contributions. In (A.7) the SRE isolates the effect of loss of species richness, while the CDE isolates the effect of post-loss processes. Second, scaling the difference in species richness  $\Delta s$  by mean post-loss functional contribution  $\bar{z}'$ , as in (A.8), amounts to using the post-loss ecosystem as the “standard of reference” against which to judge the effect of loss of species richness (the SRE). This is out of keeping with the earlier decision to use the pre-loss ecosystem as the standard of reference (see [A.3]). Third, equation (A.7) scales  $\Delta \bar{z}$  by  $s'$ . As demonstrated below, this scaling removes  $s$  and  $s'$  from the definitions of the SCE and the CDE, ensuring that these effects are not confounded with the SRE. Equation (A.8) scales  $\Delta \bar{z}$  by  $s$ , leaving the definitions of the SCE and the CDE dependent on  $s$  and  $s'$  and thus confounding the SCE and CDE with the SRE.

Substituting (A.1-2) into (A.3), and (A.3) into (A.7), we obtain

$$\Delta T = \bar{z}\Delta s + s' \left[ \sum_i \frac{1}{s'} w_i z'_i - \sum_i \frac{1}{s} z_i \right]. \quad (\text{A.9})$$

Substituting  $z_i + z'_i - z_i = z_i + \Delta z_i$  for  $z'_i$ ,  $\frac{1}{s} \frac{w_i}{\bar{w}}$  for  $\frac{1}{s'} w_i$ , and rearranging yields

$$\Delta T = \bar{z}\Delta s + s' \left[ \sum_i \frac{1}{s} \frac{w_i}{\bar{w}} z_i - \sum_i \frac{1}{s} z_i + \sum_i \frac{1}{s} \frac{w_i}{\bar{w}} \Delta z_i \right]. \quad (\text{A.10})$$

The third term inside the brackets in (A.10) equals  $\frac{E(w\Delta z)}{\bar{w}}$ , the expectation term of the Price Equation (Price 1972, Frank 1997). The first two terms inside the brackets in (A.10) together form the covariance term of the Price Equation,  $\frac{\text{Cov}(w, z)}{\bar{w}}$ . To see this, note that the first term inside brackets in (A.10) is equal to  $\frac{E(wz)}{\bar{w}}$ , and the second is equal to  $\bar{z} = E(z)$ . Using the fact that the expected value of the product of two random variables equals the product of their expectations plus their covariance, we can rewrite (A.10) as

$$\Delta T = \bar{z}\Delta s + s' \left[ \frac{E(w)E(z)}{\bar{w}} + \frac{\text{Cov}(w, z)}{\bar{w}} - E(z) + \frac{E(w\Delta z)}{\bar{w}} \right]. \quad (\text{A.11})$$

Since  $E(w) = \bar{w}$ ,  $\frac{E(w)E(z)}{\bar{w}} = E(z)$  and (A.11) simplifies to

$$\Delta T = \bar{z}\Delta s + s' \left[ \frac{\text{Cov}(w, z)}{\bar{w}} + \frac{E(w\Delta z)}{\bar{w}} \right]. \quad (\text{A.12})$$

The term in brackets in (A.12) is the Price Equation (Price 1970, 1972, 1995, Frank 1997), which partitions  $\Delta \bar{z}$  into two additive components. Since  $\text{Cov}(w, z) = \frac{1}{s} \text{Sp}(w, z)$  where Sp denotes the sum of products (i.e.,  $\text{Sp}(w, z) = \sum_i (w_i - \bar{w})(z_i - \bar{z})$ ),  $E(w\Delta z) = \frac{1}{s} \sum_i w_i \Delta z_i$ , and  $\bar{w} = \frac{s'}{s}$ , multiplying through the brackets in (A.12) by  $s'$  and simplifying yields the Price Equation partition of the effect of species loss on ecosystem function (equation (5) in the main text):

$$\Delta T = \bar{z}\Delta s + \text{Sp}(w, z) + \sum_i w_i \Delta z_i. \quad (\text{A.13})$$

In the main text I describe how to extend equation (A.13) by partitioning the CDE into subcomponents attributable to context dependence of abundance, context dependence of per-capita functional contribution, and their interaction.

A recent paper on the Price Equation in an evolutionary context raises technical concerns about whether the covariances and expectations in the Price Equation represent properties of populations or random samples from populations (van Veelen 2005). These technical concerns are not relevant in the present context, since in the present context the covariance (Cov) and expectation (E) operators also can be interpreted simply as notational shorthand (e.g.,

see (A.10), where  $\frac{E(w\Delta z)}{\bar{w}}$  can be taken as shorthand for  $\sum_i \frac{1}{s} \frac{w_i}{\bar{w}} \Delta z_i$  and  $\frac{\text{Cov}(w, z)}{\bar{w}}$  can be taken as shorthand for  $\sum_i \frac{1}{s} \frac{w_i}{\bar{w}} z_i - \sum_i \frac{1}{s} z_i$ ). Interpreting the terms of the Price Equation as notational shorthand is consistent with the usage of Price and subsequent authors (e.g., Price 1970, 1972, 1995, Frank 1997), does not alter any of the fundamental insights gained from the Price Equation, and is not criticized by van Veelen (2005).

Finally, note that I make no assumptions about when species' pre- and post-loss functional contributions are measured, save that all elements of  $z$  are measured at the same time as one another, and similarly for the elements of  $z'$ . In particular, I do not assume that either the pre- or post-loss site is at equilibrium. In general, the magnitude and sign of the CDE will depend on when species' pre- and post-loss functional contributions are measured. For instance, measurement of  $z'$  immediately after an extinction event likely would lead to a small CDE, since the post-loss functional contributions of the remaining species would have little time to change from their pre-loss values. The Price Equation partition provides a framework in which to analyze time series of changes in ecosystem function (e.g., due to a sequence of extinction events) by comparing every subsequent ecosystem to the initial most-diverse ecosystem (e.g., Fig. B5 in [Appendix B](#)).

#### *Applying the Price Equation partition: a worked example*

Here I present a worked example of the application of the Price Equation partition to hypothetical data, strictly for the purpose of clarifying the required calculations. Consider a pre-loss site with  $s = 4$  species, where the functional contribution of species  $i$  ( $i = 1, 2, 3, 4$ ) is  $z_i = i$  (e.g.,  $z_4 = 4$ ). Assume that species 1 and 2 are lost (i.e.,  $w_1 = w_2 = 0$ ), so that post-loss richness  $s' = 2$ . Assume that the post-loss functional contributions of the remaining species are  $z'_3 = 2$  and  $z'_4 = 6$ . The remaining species have  $w_3 = w_4 = 1$ , and  $\bar{w} = 0.5$ . Mean pre-loss functional contribution per species

$\bar{z}$  is  $\frac{1}{s} \sum_i z_i = \frac{1+2+3+4}{4} = 2.5$ , and mean post-loss functional contribution per species  $\bar{z}'$  is

$\frac{1}{s'} \sum_i w_i z'_i = \frac{0+0+2+6}{2} = 4$ . The SRE is given by  $\bar{z}\Delta s = (2.5)(2-4) = -5$ . The SCE is given by

$\text{Sp}(w, z) = \sum_i (w_i - \bar{w})(z_i - \bar{z}) = (0 - 0.5)(1 - 2.5) + (0 - 0.5)(2 - 2.5) + (1 - 0.5)(3 - 2.5) + (1 - 0.5)(4 - 2.5) = 2$ . The CDE

is given by  $\sum_i w_i \Delta z_i = 0 + 0 + (1)(2-3) + (1)(6-4) = 1$ . The difference in total function  $\Delta T$  calculated from summing the SRE, SCE, and CDE is  $-5 + 2 + 1 = -2$ , which equals the difference calculated directly from species' pre- and post-loss functional contributions:  $(2 + 6) - (1 + 2 + 3 + 4) = -2$ .

#### LITERATURE CITED

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