

GENERALIZATION OF THE PRICE EQUATION FOR EVOLUTIONARY CHANGE

Benjamin Kerr^{1,2} and Peter Godfrey-Smith^{3,4}

¹Department of Biology, University of Washington, Seattle, Washington 98195

²E-mail: kerrb@u.washington.edu

³Department of Philosophy, Harvard University, Cambridge, Massachusetts 02138

⁴E-mail: pgs@fas.harvard.edu

Received June 22, 2008

Accepted October 7, 2008

The Price equation is recognized as a general statistical description of evolutionary change with the potential to represent diverse processes. Here we present a new structurally symmetric equation for change that allows for arbitrary causal connectivity between ancestors and descendants, accounts for previously unaddressed processes (such as migration), and yields the Price equation as a special case.

KEY WORDS: Connectivity equation, covariance, migration.

The “Price equation” provides an abstract statistical decomposition of evolutionary change (Price 1970, 1972) and has been applied to a diverse array of phenomena (Wade 1985; Queller 1992; Frank 1995; Page and Nowak 2002; Henrich 2004; Rice 2004; Fox 2006; Okasha 2006). Despite its range of application, the Price equation does make certain limiting assumptions about the causal connectivity between the entities described. Here we explore a new equation for change based on less restrictive assumptions. The resulting equation is structurally symmetric and has the capacity to represent phenomena that cannot be accounted for by a standard Price equation.

Consider a population whose state can be described at two different points in time, t^a and t_d , the ancestral and descendant time points, respectively (we use superscripts to indicate ancestors and subscripts to indicate descendants in all that follows). Let there be n^a entities at t^a and n_d entities at t_d . Let C_j^i be an indicator variable for *connection* between ancestral entity i and descendant entity j . So

$$C_j^i = \begin{cases} 1 & \text{if ancestral entity } i \text{ connects to descendant entity } j \\ 0 & \text{if ancestral entity } i \text{ does not connect to descendant entity } j \end{cases}$$

Thus, ancestral entity i connects to a total of $C_*^i = \sum_{j=1}^{n_d} C_j^i$ descendant entities, and descendant entity j connects to $C_j^* =$

$\sum_{i=1}^{n^a} C_j^i$ ancestral entities. Let C_*^a and C_d^* be variables representing the total number of connections for an ancestor and the total number of connections for a descendant, respectively. The total number of connections in the population is $C_*^* = \sum_{i=1}^{n^a} C_*^i = \sum_{j=1}^{n_d} C_j^* = \sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i$. The only assumption regarding connectivity required by our analysis is that there should be *at least one* connection between the ancestral and descendant ensembles. The Price equation, in contrast, only permits unconnected members in the ancestral population.

We are interested in tracking change in some property of the entities within our population over time. Let the value of some measurable character of ancestral entity i be X^i and that of descendant entity j be X_j . Again, let X^a and X_d be variables representing ancestral and descendant character, respectively. We quantify evolution by the change in average character value between t^a and t_d , namely $\Delta \bar{X} = \bar{X}_d - \bar{X}^a = \sum_{j=1}^{n_d} (X_j/n_d) - \sum_{i=1}^{n^a} (X^i/n^a)$.

Following Price's (1972) lead, we identify “ave” and “cov” as the average and covariance functions at the level of the *entire population* (as opposed to random samples from the population). Using the variables and parameters defined above, we can then derive the following equation for character change (see Appendix 1):

$$\Delta \bar{X} = \frac{\text{cov}(C_*^a, X^a) + \text{ave}[C_*^a(\Delta X)^a] - (n_d/n^a)\text{cov}(C_d^*, X_d)}{C_*^*/n^a}, \quad (1)$$

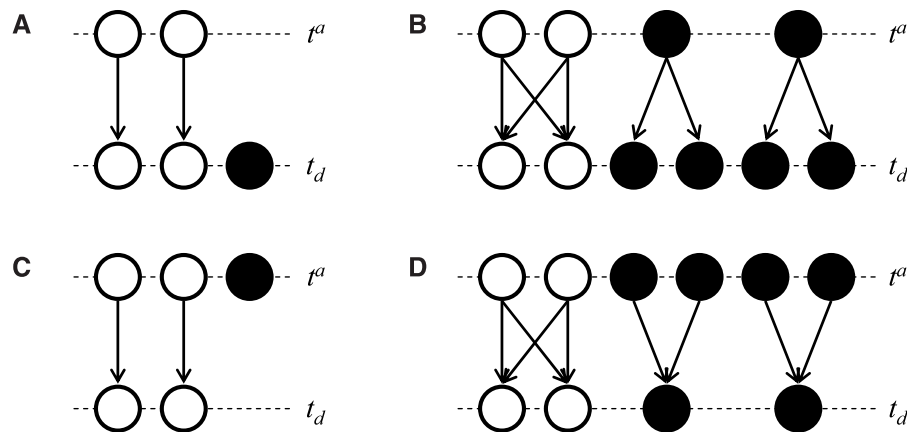


Figure 1. Evolutionary change through covariance. (A) Individuals with $X = 0$ (open circles) present at t^a survive until t_d (or, alternatively, asexually produce a single identical offspring). However, an individual with $X = 1$ (filled circle) migrates into the population at t_d . Evolutionary change is wholly accounted for by the third term of equation (1) ($\Delta \bar{X} = 1/3 = -(n_d/C_d^*)\text{cov}(C_d^*, X_d)$). (B) Reproduction in individuals with $X = 0$ (open circles) is sexual, whereas individuals with $X = 1$ (filled circles) reproduce asexually. Because each parent has two offspring and each offspring is identical to its parent, the first two terms of (1) are zero ($\text{cov}(C_d^*, X^a) = \text{ave}[C_d^*(\Delta X)^a] = 0$). The third term, measuring the covariance between offspring phenotype and number of parents, accounts for change ($\Delta \bar{X} = 1/6 = -(n_d/C_d^*)\text{cov}(C_d^*, X_d)$). (C) This population is identical to that shown in part (A), with the time points t^a and t_d reversed. Viability selection (the filled circle perishes) is the mirror image of migration ($(n^a/C_d^*)\text{cov}(C_d^*, X^a)$ from this population is equal to $(n_d/C_d^*)\text{cov}(C_d^*, X_d)$ from the population in [A]). (D) This population is identical to that shown in part (B), again with t^a and t_d reversed. Fecundity selection is the mirror image of a mix of reproductive modes ($(n^a/C_d^*)\text{cov}(C_d^*, X^a)$ from this population is equal to $(n_d/C_d^*)\text{cov}(C_d^*, X_d)$ from the population in [B]).

The quantity $(\Delta X)^i = \frac{\sum_{j=1}^{n_d} C_j^i (X_j - X^i)}{C_i^a}$ is the average deviation in character between ancestral entity i and its connected descendant entities. Again, $(\Delta X)^a$ is the variable of which $(\Delta X)^i$ is an instance. Note that $(\Delta X)^a$ is undefined when the ancestral entity is unconnected (i.e., $C_i^a = 0$), but in such cases we let $C_i^a(\Delta X)^a$ be zero. Finally, C_i^*/n^a is the average number of connections per ancestor.

The first two terms in the numerator of the right-hand side of equation (1) map to the terms found in a standard Price equation. Connections between ancestral and descendant entities are usually then interpreted as representing relations of reproduction. The first term is a covariance between the character value of an ancestor and the number of descendants to which it is connected. If C_i^a is taken to be a measure of reproductive output, then $\text{cov}(C_i^a, X^a)$ is the covariance between ancestral character and (realized) fitness. The second term measures the overall tendency of an ancestor's descendants to diverge from it in character. The third term in the numerator, which is not part of a standard Price equation, is like a mirror image of the first term. It measures the covariance between descendant character and the number of ancestors to which the descendant is connected.

The first two terms are often seen as giving a complete decomposition of evolutionary change. However, change is consistent with zero values for Price's two terms. Two simple phenomena can be used to illustrate the role of the third term. One is migration into the population from outside (Fig. 1A). A migrant

is, in the context of our analysis, a descendant without an ancestor. When some individuals in the descendant ensemble are migrants and some are not, and the migrants differ in average character from the locals, $\text{cov}(C_d^*, X_d)$ will be nonzero. The other phenomenon is a mixture of biparental and uniparental reproduction (Fig. 1B). Then, again, individuals will differ in their number of parents, and if those with more or fewer parents also differ in character from the others, $\text{cov}(C_d^*, X_d)$ will be nonzero. Within a standard Price equation framework, mixes of biparental and uniparental reproduction can be accommodated by giving parents only "half credit" for sexually produced offspring. Migration might be represented by simply adding a new term to express the contribution to the descendant population made by any immigrants. In our analysis, in contrast, these phenomena are treated in a unified way, as examples of processes by which descendants can differ in ancestor number.

We have presented the analysis so far in terms of a one-way flow of influence that matches the direction of the arrows in Figure 1, but the analysis can also be reversed. As there are no constraints on the pattern of connectivity (other than the presence of one connection in the system), and unconnected individuals can appear in both the ancestral and descendant ensembles, an analysis using equation (1) could describe change *from* the descendant ensemble *to* the ancestral ensemble. In fact, the treatment can be made still more symmetrical. Equation (1), like standard forms of the Price equation, does its accounting from the "ancestral point

of view.” If we instead consider relative measures of ancestral and descendant connectedness, given by $\tilde{C}_*^a = C_*^a/(C_*^a/n^a)$ and $\tilde{C}_d^* = C_d^*/(C_*^*/n_d)$ respectively, it is possible to derive a “connection-based” equation (see Appendix 2)

$$\Delta\bar{X} = \text{cov}(\tilde{C}_*^a, X^a) + \text{ave}((\Delta X)_d^a) - \text{cov}(\tilde{C}_d^*, X_d). \quad (2)$$

Here $(\Delta X)_j^i = C_j^i (X_j - X^i)$ and the second term in (2) is the average change in character from an ancestor to a descendant across a connection. Equation (2) replaces an ancestral perspective of analysis with a purely connection-based perspective.

The symmetry in equations (1) and (2) gives rise to some novel analogies. Migration of an individual into the descendant ensemble is analogous to a failure to exert influence (a failure to survive or reproduce) on the part of an ancestor when the temporal perspective is flipped (compare Figs. 1A and 1C). Mixtures of biparental reproduction with uniparental reproduction map onto differences in fecundity (compare Figs. 1B and 1D). Variation in parent number corresponds, when the analysis is reversed, to variation in offspring number. More generally, when the temporal perspective is inverted, the two covariance terms exchange roles; the “differential fitness” term becomes the “differential convergence” term, and vice versa. This symmetry illustrates that phenomena that were previously unaccounted for, such as migration, are actually the mirror images of phenomena, such as selection, that are familiar to the standard Price equation.

Our framework decomposes evolutionary change into three factors that represent different forms of causal connectivity between ancestral and descendant ensembles. First, there is the relationship between ancestral character and connectedness to descendants. This is captured by the first covariance term in equation (2), which measures the contribution of “differential divergence” to evolution. Second, we have the change in character from ancestor to descendant across a connection. This is captured by the second term in equation (2), which measures the contribution of “transformation” to evolution. Third, there is the relationship between descendant character and connectedness to ancestors. This is captured by the third term in equation (2), which measures the contribution of “differential convergence” to evolution. It is possible, as illustrated in Figure 2, for the same ancestral ensemble to give rise to the same descendant ensemble via different patterns of causal connection, each captured by different terms in our equation. Figure 2A shows evolution via differential divergence (fecundity selection); Figure 2B illustrates evolution via transformation (biased mutation); and Figure 2C, D depicts evolution via differential convergence (migration and mixed sexuality, respectively). This figure shows connection to be a linchpin in our framework.

As is the case with the Price equation, we have made very few assumptions about the entities themselves. The entities could

be genes, individuals, groups, or species, to name just a few possibilities. Biological systems are often organized hierarchically with subentities embedded within entities (e.g., individuals in social groups) and we may be interested in describing evolutionary change occurring simultaneously at different levels. The usefulness of the Price equation derives in part from its recursive structure, which allows it to be applied to hierarchically structured systems (Frank 1998). Price’s average term can be decomposed into a lower-level covariance term and a lower-level average term. Our equations are also recursive, but the average term in each case breaks down into *three* lower-level terms, each corresponding to the terms described above (see Appendix 3).

We also make few assumptions about the nature of a “connection” between entities. Above we have discussed connections mostly as parent–offspring relations. However, a connection can also represent the simple persistence of an entity (an entity at time t^a “connects” to itself at time t_d). Alternatively, a connection may represent other forms of influence between entities such as material or information flow. Consequently, the framework can also represent ecological change, cultural evolution, and many other processes. As with the standard Price equation, there is a cost associated with this high degree of generality. Our equations only represent change over a single time-step, and cannot (without further assumptions about the system) be iterated over many time-steps. (See Frank 1998 for a discussion of “dynamic sufficiency” and the Price equation.)

We now outline some examples of phenomena that our framework may shed new light on. The first example involves a different way to represent the intrinsic cost of sex. In Figure 1B, both asexual and sexual ancestors have two offspring each. Further, every offspring individual perfectly resembles its parent. Thus, the first two terms of equation (2) are zero. If sexual individuals have a character value of zero, and asexual individuals have a character value of one (as in Fig. 1B), then the frequencies of sexual individuals at times t^a and t_d are $s^a = 1 - \bar{X}^a$ and $s_d = 1 - \bar{X}_d^a$, respectively. The frequency change of sexual individuals is $s_d - s^a = -\Delta\bar{X} = \text{cov}(\tilde{C}_d^*, X_d) = -\bar{X}^a(1 - \bar{X}^a)/(1 + \bar{X}^a)$ in a case like Figure 1B. The covariance between the sexual character of the descendant and its relative number of parents measures the change in frequency of sexual individuals. This covariance is negative because all sexual offspring (with $X_d = 0$) have two parents (with $C_d^* = 2$), whereas all asexual offspring (with $X_d = 1$) have a single parent (with $C_d^* = 1$). Thus, we see that this covariance gauges the decrease in the frequency of sexual reproduction. Sex is costly because sexual offspring require two parents, whereas asexual offspring require only one parent. The cost of sex, understood in this way, also has a cultural analogue. If one cultural practice can only be copied from multiple individuals functioning as a unit, and a rival practice can be learned by observing fewer

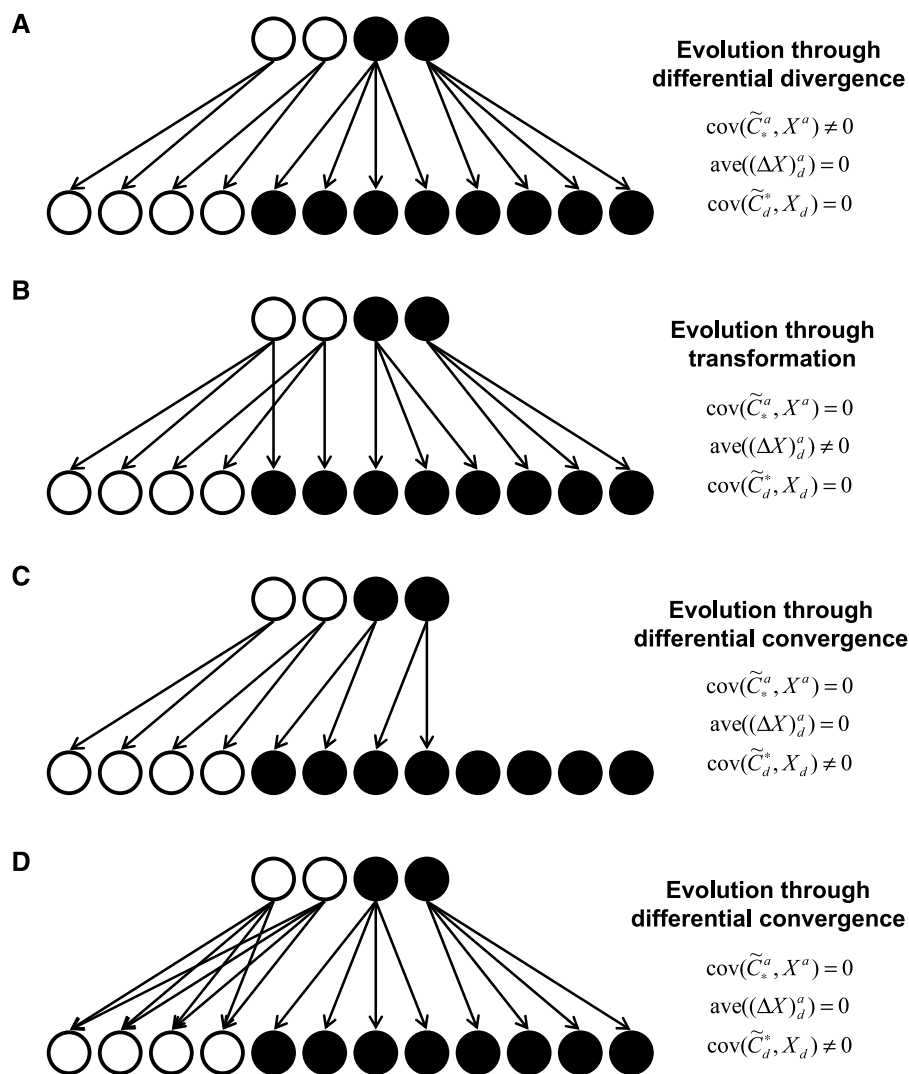


Figure 2. Statistical dependence on the pattern of connection. The same evolutionary outcome is shown four times. However, by changing the connections, evolution is explained solely by (A) fecundity selection, (B) biased mutation, (C) migration, or (D) mixed modes of reproduction. Distinct statistical terms from equation (2) wholly account for evolution in each case (shown to the right of each evolving population).

individuals, then the former practice is intrinsically costly in an evolutionary sense.

A second example involves an application outside of evolutionary biology. Fox (2006) used the Price equation to gauge how the loss of species affects change in ecosystem function between two sites (separated in space, time, or both). In the Supporting information, we use equation (1) to partition the effects of both loss and gain of species on ecosystem function. Once again, we discover structural symmetry in this new context. Of course, a framework that incorporates species gain will be especially relevant to ecosystem restoration and the study of invasive species.

Thus, our equations find applications both inside and outside evolutionary biology. The new covariance term not only makes

certain symmetries clear, but also enlarges the set of phenomena covered by a simple statistical equation. Migration is clearly an important source of change in biological populations, whether considering a collection of conspecifics or a multispecies community assemblage. Additionally, our equations draw associations between ostensibly distinct processes. In the same way that viability selection and fecundity selection are grouped together as “selection processes” by the first covariance term, the third covariance term unites migration and mixed reproductive modes as kindred processes of differential convergence. By accommodating arbitrary patterns of connection between evolving entities, our framework extends the range of applicability of Price-style statistical partitions to cover new cases of genetic evolution, ecological transformation, and cultural change.

ACKNOWLEDGMENTS

We thank J. Fox, S. Otto, and two anonymous reviewers for helpful comments.

LITERATURE CITED

- Fox J. 2006. Using the Price equation to partition the effects of biodiversity loss on ecosystem function. *Ecology* 87:2687–2696.
- Frank S. 1995. George Price's contributions to evolutionary genetics. *J. Theor. Biol.* 175:373–388.
- . 1998. *Foundations of social evolution*. Princeton Univ. Press, Princeton, NJ.
- Henrich, J. 2004. Cultural group selection, coevolutionary processes and large-scale cooperation. *J. Econ. Behav. Organiz.* 53:3–35.
- Okasha S. 2006. *Evolution and the levels of selection*. Oxford Univ. Press, Oxford, UK.
- Page K., and M. Nowak. 2002. Unifying evolutionary dynamics. *J. Theor. Biol.* 219:93–98.
- Price G. 1970. Selection and covariance. *Nature* 227:520–521.
- . 1972. Extension of covariance selection mathematics. *Ann. Hum. Gen.* 35:485–490.
- Queller D. 1992. A general model for kin selection. *Evolution* 46:376–380.
- Rice S. 2004. *Evolutionary theory: mathematical and conceptual foundations*. Sinauer, Sunderland, MA.
- Wade M. 1985. Soft selection, hard selection, kin selection, and group selection. *Am. Nat.* 125:61–73.

Associate Editor: S. Otto

Appendix 1

DERIVATION OF EQUATION (1)

In this Appendix, we first generate Price's terms within our "connectivist" framework. Along the way, we produce something resembling the Price equation, but with an extra term. The statistical resolution of this extra term yields equation (1).

Using the parameters and variables defined above, the following clearly holds:

$$0 = \sum_{i=1}^{n^a} C_*^i (X^i - \bar{X}^a) / n^a - \sum_{i=1}^{n^a} C_*^i (X^i - \bar{X}^a) / n^a. \quad (\text{A1})$$

Because $\sum_{i=1}^{n^a} C_*^i (X^i - \bar{X}^a) / n^a = \sum_{i=1}^{n^a} (C_*^i - \bar{C}_*^a) (X^i - \bar{X}^a) / n^a = \text{cov}(C_*^a, X^a)$, the first term is equivalent to Price's covariance term. We then add and subtract $\sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i X_j / n^a$:

$$0 = \text{cov}(C_*^a, X^a) + \sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i X_j / n^a - \sum_{i=1}^{n^a} C_*^i (X^i - \bar{X}^a) / n^a - \sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i X_j / n^a. \quad (\text{A2})$$

As defined above, $C_*^i = \sum_{j=1}^{n_d} C_j^i$ and $\sum_{i=1}^{n^a} C_*^i = C_*^*$. Thus, we have

$$0 = \text{cov}(C_*^a, X^a) + \sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i (X_j - X^i) / n^a - \sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i X_j / n^a + \{C_*^* \bar{X}^a / n^a\} \quad (\text{A3})$$

Because $\sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i (X_j - X^i) / n^a = (1/n^a) \sum_{i=1}^{n^a} C_*^i \sum_{j=1}^{n_d} C_j^i (X_j - X^i) / C_*^i = \text{ave}[C_*^a(\Delta X)^a]$, Price's average term is in place. If we then add and subtract $\sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i \bar{X}_d / n^a$

$$0 = \text{cov}(C_*^a, X^a) + \text{ave}[C_*^a(\Delta X)^a] - \sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i X_j / n^a + \sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i \bar{X}_d / n^a - \sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i \bar{X}_d / n^a + \{C_*^* \bar{X}^a / n^a\}. \quad (\text{A4})$$

As defined above, $\sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i = C_*^*$ and $\bar{X}_d - \bar{X}^a = \Delta \bar{X}$. Using these definitions, we have the following after some rearrangement:

$$\{C_*^* / n^a\} \Delta \bar{X} = \text{cov}(C_*^a, X^a) + \text{ave}[C_*^a(\Delta X)^a] - \sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i (X_j - \bar{X}_d) / n^a \quad (\text{A5})$$

Equation (A5) resembles the Price equation, but there is an extra term. Because $\sum_{j=1}^{n_d} C_j^* (X_j - \bar{X}_d) / n_d = \text{cov}(C_d^*, X_d)$, this extra term is resolved as follows:

$$\{C_*^* / n^a\} \Delta \bar{X} = \text{cov}(C_*^a, X^a) + \text{ave}[C_*^a(\Delta X)^a] - \frac{n_d}{n^a} \text{cov}(C_d^*, X_d). \quad (\text{A6})$$

Dividing both sides of equation (A6) by C_*^* / n^a yields equation (1).

Appendix 2

CONNECTION-BASED EQUATION

To derive equation (2), we multiply the numerator and denominator of the right-hand side of equation (1) by n^a . Given that $n^a \text{ave}[C_*^a(\Delta X)^a] = \sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i (X_j - X^i)$, we have

$$\Delta \bar{X} = \frac{n^a \text{cov}(C_*^a, X^a) + \sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_j^i (X_j - X^i) - n_d \text{cov}(C_d^*, X_d)}{C_*^*}. \quad (\text{A7})$$

This can be broken up as follows:

$$\Delta \bar{X} = \frac{\text{cov}(C_*^a, X^a)}{C_*^a/n^a} + \frac{\sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_{j,i}^i (X_j - X^i)}{C_*^a} - \frac{\text{cov}(C_d^*, X_d)}{C_d^*/n_d}. \quad (\text{A8})$$

The average change over any connection is

$$\text{ave}[(\Delta X)_d^a] = \frac{\sum_{i=1}^{n^a} \sum_{j=1}^{n_d} C_{j,i}^i (X_j - X^i)}{C_*^a}. \quad (\text{A9})$$

Thus, using the definitions of \tilde{C}_*^a and \tilde{C}_d^* from the main text, we have equation (2)

$$\Delta \bar{X} = \text{cov}(\tilde{C}_*^a, X^a) + \text{ave}[(\Delta X)_d^a] - \text{cov}(\tilde{C}_d^*, X_d). \quad (\text{A10})$$

Appendix 3

RECURSIVENESS

We will sketch recursiveness for the case of equation (2). Suppose the ancestral and descendent entities are made up of p^a and p_d “subentities,” respectively. Let the character value of subentity r in ancestral entity i be given by $x^{i,r}$ and the character value of subentity s in descendant entity j be given by $x_{j,s}$. Let $c_{j,i}^{i,r}$ indicate a connection between subentity r in ancestral entity i and

subentity s in descendant entity j . So

$$c_{j,i}^{i,r} = \begin{cases} 1 & \text{if subentity } r \text{ in ancestor } i \text{ connects to subentity } s \text{ in descendant } j \\ 0 & \text{if subentity } r \text{ in ancestor } i \text{ does not connect to subentity } s \text{ in descendant } j. \end{cases}$$

We assume that the only way for two subentities to be connected is for their “housing” entities to be connected ($c_{j,i}^{i,r} = 1$ only if $C_j^i = 1$). We also assume that the character of each entity is the average character of its subentities (e.g., $X^i = \sum_{r=1}^{p^a} x^{i,r}/p^a$). We define $c_{d,e}^{a,b}$ to be the subconnection indicator variable; $c_{d,*}^{a,b}$ and $c_{d,e}^{a,*}$ to be the ancestral and descendant subentity connectedness, respectively; $\tilde{c}_{d,*}^{a,b}$ and $\tilde{c}_{d,e}^{a,*}$ to be relative values of $c_{d,*}^{a,b}$ and $c_{d,e}^{a,*}$; $x^{a,b}$ and $x_{d,e}$ to be ancestral and descendant subentity character; and $(\Delta x)_{d,e}^{a,b}$ to be the deviation in character between an ancestral subentity and a descendant subentity to which it is connected. Given these definitions and assumptions, we see that

$$\Delta \bar{X} = \text{cov}(\tilde{C}_*^a, X^a) + \text{ave}_{(a,d)}[\text{cov}_b(\tilde{c}_{d,*}^{a,b}, x^{a,b}) + \text{ave}_{(b,e)}[(\Delta x)_{d,e}^{a,b}] - \text{cov}_e(\tilde{c}_{d,e}^{a,*}, x_{d,e})] - \text{cov}(\tilde{C}_d^*, X_d).$$

We include subscripts to indicate the “level” of the biological hierarchy relevant to the statistical functions (where a and d refer to entities, whereas b and e refer to subentities). If our subentities were comprised of sub-subentities, then $(\Delta x)_{d,e}^{a,b}$ could again be broken into three terms (two covariances and an average).

Supporting Information

The following supporting information is available for this article:

Appendix S1. Decomposition of the Effects of Species Shifts on Ecosystem Function.

Figure S1. The basic framework for species shifts.

Supporting Information may be found in the online version of this article.

(This link will take you to the article abstract).

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting informations supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.