

## Diversity partitioning without statistical independence of alpha and beta

JOSEPH A. VEECH<sup>1,3</sup> AND THOMAS O. CRIST<sup>2</sup>

<sup>1</sup>*Department of Biology, Texas State University, San Marcos, Texas 78666 USA*

<sup>2</sup>*Department of Zoology, Miami University, Oxford, Ohio 45056 USA*

**Abstract.** Diversity partitioning has become a popular method for analyzing patterns of alpha and beta diversity. A recent evaluation of the method emphasized a distinction between additive and multiplicative partitioning and further advocated the use of multiplicative partitioning based on a presumed independence between alpha and beta. Concurrently, additive partitioning was criticized for producing dependent alpha and beta estimates. Until now, the issue of statistical independence of alpha and beta (in either type of partitioning) has not been thoroughly examined, partly due to confusion about the meaning of statistical independence. Here, we adopted a probability-based definition of statistical independence that is essentially identical to the definition found in any statistics textbook. We used a data simulation approach to show that alpha and beta diversity are not statistically independent in either additive or multiplicative partitioning. However, the extent of the dependence is not so great that it cannot be overcome by using appropriate statistical techniques to control it. Both additive and multiplicative partitioning are statistically valid and logically sound approaches to analyzing diversity patterns.

**Key words:** additive partitioning; alpha, beta, and gamma; data simulation; diversity partitioning; multiplicative partitioning; statistical independence.

In a recent paper, Jost (2007) further develops the mathematical foundation for multiplicative partitioning of species diversity (also see Ricotta 2005, Jost 2006). Jost suggests that “existing definitions of alpha and beta must be replaced by a definition that partitions alpha and beta into independent components” (Jost 2007: 2427). Jost further states that “... we must develop a new general expression relating alpha, beta, and gamma, and the new expression must ensure that beta is free to vary independently of alpha” (Jost 2007:2428). In this paper, we follow Jost (2006, 2007) and refer to the Shannon and other abundance-based indices as entropies to distinguish them from “true diversity” metrics. Jost (2007) showed that any abundance-based entropy of any order,  $q$  (except  $q = 1$ ), can be converted into its true diversity or “numbers equivalent” (see Eqs. 1 and 2 in Jost 2007). According to Jost (2007), “Numbers equivalents permit the decomposition of any diversity index  $H$  into two independent components” (Jost 2007:2430). Throughout his paper, Jost stresses the “independence” of alpha and beta but never empirically demonstrates this property. The purpose of

this paper is to evaluate the statistical independence of alpha and beta in multiplicative and additive partitions of species diversity. To be clear, we recognize that Jost (2007) never explicitly refers to “independence” as “statistical independence”; nonetheless, the issue of “independence” in diversity partitioning deserves further examination.

We simulated hypothetical data to quantitatively examine Jost’s (2007) claim that the alpha and beta estimates [ $D(H_A)$  and  $D(H_B)$ ] obtained using true diversities are independent. Jost (2007) defines independence of alpha and beta (Property 1; Jost 2007:2428) as freedom to vary independently: “Alpha and beta should be free to vary independently; a high value of the alpha component should not, by itself, force the beta component to be high (or low), and vice versa...” and “alpha should not put mathematical constraints on the possible values of beta, and vice versa.” We believe that the definition of independence used by Jost (2007) needs to be clarified, particularly with regard to independence being a statistical property of alpha and beta. We show that both the multiplicative decomposition of gamma diversity into  $D(H_A)$  and  $D(H_B)$  and the additive decomposition into the entropies  $H_A$  and  $H_B$  produce estimates of alpha and beta diversity that are dependent on one another. Thus, advocating the use of true diversities over entropies cannot be justified solely on

Manuscript received 16 September 2008; revised 11 December 2008; accepted 12 January 2009. Corresponding Editor: A. M. Ellison. For reprints of this Forum, see footnote 1, p. 1962.

<sup>3</sup> E-mail: joseph.veech@txstate.edu

the grounds that the former gives statistically independent estimates of alpha and beta and the latter does not.

Alpha, beta, and gamma diversity are related by  $D(H_G) = D(H_A)D(H_B)$  (Jost 2007: Eq. 4) in the multiplicative decomposition. Jost (2007) used this general formula to show that the entropies,  $H_A$  and  $H_B$ , can be related to one another in either an additive or multiplicative way (Jost 2007: Eqs. 8a–g) depending on the particular index being partitioned. Jost (2007) states: “Suppose  $H_A$  has a numbers equivalent of  $x$  equally likely outcomes, and orthogonal  $H_B$  has a numbers equivalent of  $y$  equally likely outcomes. Then if  $H_A$  and  $H_B$  are independent and completely determine the total diversity, the diversity index of the combined system must have a numbers equivalent of exactly  $xy$  equally likely outcomes.” (Jost 2007:2430). The general formula relating  $D(H_A)$  and  $D(H_B)$  is multiplicative and thus bears resemblance to the well-known product rule for the probability of occurrence of two independent events,  $P(W \text{ and } Z) = P(W)P(Z)$ . However, Eq. 4 does not ensure that  $D(H_A)$  and  $D(H_B)$  are statistically independent and Eqs. 8a–g do not ensure that  $H_A$  and  $H_B$  are statistically independent. Their independence must be established empirically by thoroughly observing the variables (and events that they represent) or by fundamental knowledge of the variables (or events) involved. For example, we have fundamental knowledge that the event representing a coin flip with the outcome of heads or tails is independent of the event representing the flip of another coin. Fundamental knowledge does not exist for claiming the independence of alpha and beta [or  $D(H_A)$  and  $D(H_B)$ ] a priori.

Statistical independence of two variables is defined as *complete or mutual* independence of the events that the two variables represent. The events are *completely* independent if the occurrence of one has no influence on the occurrence of the other. In additive and multiplicative partitioning, alpha and beta diversity are mathematically linked to one another through a third variable, gamma diversity. The presence of this third variable allows us to deduce a priori that alpha, beta, and gamma [ $D(H_A)$ ,  $D(H_B)$ , and  $D(H_G)$ ] are not mutually independent because knowing the values of two of them completely determines the value of the third. Similarly,  $H_A$ ,  $H_B$ , and  $H_G$  are not mutually independent. Indeed, in practice, beta can only be determined by first calculating alpha and gamma. Thus, alpha and beta are not mutually independent because beta is calculated from alpha (and gamma).

To quantify the dependence between alpha and beta, we conducted a series of simulations. Each simulation involved generating 1000 “data sets” each representing a decomposition of gamma into alpha and beta components. For each data set, gamma was set equal to a random number between 10 and 1000 (these limits had no influence on the outcome described in this paper) drawn from a uniform distribution. Alpha was then set as a random proportion of gamma with a lower limit of

1 (in some instances alpha can be  $<1$  but this requires data sets that have samples with zero species). This simulation routine produces a random (or independent) association of alpha and gamma. Alternatively we could have first selected alpha as a random number (between 10 and 1000) and then selected gamma as a random number between alpha and 1000. Another alternative would have been to simultaneously select a pair of random numbers with the smaller number being assigned to alpha and the larger number being assigned to gamma. All of these simulation routines produce a random association of alpha and gamma.

After obtaining alpha and gamma, beta was determined as gamma/alpha to simulate  $D(H_B)$  (the true diversity of any order  $q$ ) derived from a multiplicative decomposition and as gamma – alpha to simulate beta (measured as species richness or the entropy for  $q = 0$ ) derived from an additive partition. Each simulation (or group of 1000 data sets) thus gave distributions of alpha, multiplicative beta, and additive beta. To be clear, this method of simulating gamma and alpha does not specify a value for  $N$  (the number of samples) and thus  $N$  is not necessarily fixed. For 50% of the simulated data sets (i.e., particular combination of gamma and alpha), the minimum possible value for  $N$  was 2, 90% of the data sets had a minimum  $N < 10$ . The minimum value of  $N$  was obtained as gamma/alpha rounded up to the next highest integer. There is no maximum value for  $N$ . Therefore, each group of 1000 data sets generally could have represented almost any  $N$ , including an  $N$  that was fairly constant.

After producing each group of 1000 data sets, we then expressed alpha, multiplicative beta, and additive beta as random events instead of random variables. To do this, we set  $i$ ,  $j$ , and  $k$  to numbers representing random percentiles ( $p_i$ ,  $p_j$ , and  $p_k$ ) in the distributions of alpha and beta respectively. Event  $A$  was defined as alpha  $< i$ , event  $B_M$  as multiplicative beta  $< j$ , and event  $B_A$  as additive beta  $< k$ . From probability theory, all events have probabilities that can be derived either analytically or through simulation. We derived the probability of each event as the proportion of the 1000 data sets obeying the event. For instance,  $P(A)$  was the proportion of data sets in which alpha was less than  $i$ . This probability can also be obtained directly as  $p_i$ ; similarly,  $P(B_M) = p_j$  and  $P(B_A) = p_k$ . We then empirically determined the joint probability of  $A$  and  $B_M$  as the proportion of the 1000 data sets in which both events ( $A$  and  $B_M$ ) occurred and the joint probability of  $A$  and  $B_A$  in the same way. The dependence of alpha and multiplicative beta was then assessed by comparing  $P(A)P(B_M)$  to  $P(A, B_M)$ ; similarly  $P(A)P(B_A)$  was compared to  $P(A, B_A)$ . If the joint probability equals the product of the two marginal probabilities then the two variables (alpha and multiplicative beta or alpha and additive beta) are mutually independent; if not then the two variables are dependent to some degree. We repeated the simulation process 100 times and then

TABLE 1. Mean products of the marginal alpha and beta probabilities [ $P(A)P(B)$ ], joint probabilities [ $P(A, B)$ ], and differences between the two for additive and multiplicative beta.

| Measure                            | Additive | Multiplicative |
|------------------------------------|----------|----------------|
| Gamma = random variable 10 to 1000 |          |                |
| Mean $P(A)P(B)$                    | 0.283    | 0.310          |
| Mean $P(A, B)$                     | 0.282    | 0.255          |
| Mean absolute difference           | 0.013    | 0.056          |
| Maximum difference                 | 0.033    | 0.140          |
| Gamma = 300                        |          |                |
| Mean $P(A)P(B)$                    | 0.283    | 0.253          |
| Mean $P(A, B)$                     | 0.205    | 0.167          |
| Mean absolute difference           | 0.078    | 0.085          |
| Maximum difference                 | 0.240    | 0.249          |

calculated the average and maximum absolute differences between  $P(A)P(B)$  and  $P(A, B)$  for each beta metric. The difference between  $P(A)P(B)$  and  $P(A, B)$  serves as an estimate of the dependence between alpha and beta; a greater difference indicates greater dependence.

We also conducted the same type of simulation for two random variables ( $W$  and  $Z$ ) known a priori to be completely and mutually independent. That is,  $W$  was set equal to a random number between 10 and 1000 from a uniform distribution.  $Z$  was also set equal to a random number between 10 and 1000 from a uniform distribution and without any regard for the value of  $W$ . That is,  $W$  and  $Z$  were not related by any mathematical equation.

The results of these simulations were informative. For multiplicative and additive beta, there was a surprising amount of agreement between  $P(A)P(B)$  and  $P(A, B)$  (Table 1). This indicates that multiplicative beta and additive beta have similar and relatively low levels of conditional dependence on alpha. Multiplicative beta (or beta measured by any true diversity) may actually be slightly more conditionally dependent on alpha in that the average difference between  $P(A)P(B_M)$  and  $P(A, B_M)$  is greater than the difference between  $P(A)P(B_A)$  and  $P(A, B_A)$  (Table 1). For multiplicative beta, there is also a bias toward  $P(A)P(B_M)$  almost always being greater than  $P(A, B_M)$  as evidenced by the average raw difference ( $0.310 - 0.255 = 0.056$ ) equaling the average absolute difference (Table 1). On the other hand, there is very little bias in  $P(A)P(B)$  for additive beta, average  $P(A)P(B_A)$  and  $P(A, B_A)$  are very similar (Table 1). It is important to note that in these simulations, gamma was a random variable and alpha was a random proportion of gamma. When gamma is fixed, rather than drawn at random, there is greater dependence between alpha and beta. We conducted the same simulations with gamma = 300 and found greater discrepancy between  $P(A)P(B)$  and  $P(A, B)$  (Table 1) with  $P(A)P(B)$  always being greater than  $P(A, B)$ . As expected, there was very little difference between  $P(W)P(Z)$  and  $P(W, Z)$  for the two unrelated random

variables,  $W$  and  $Z$ . On average the difference between the product of the marginal probabilities and the joint probability was only 0.004 with a maximum difference of 0.014 for 100 sets of simulations.

When evaluating the statistical dependence of alpha and beta diversity, it is important to remember that a third variable, gamma diversity, is involved. Additive and multiplicative partitioning, as applied to a set of samples, both specify a decomposition of gamma into alpha (within-sample diversity) and beta (among-sample diversity). Whether using entropies or true diversities, gamma is a known and constant quantity for a given data set. This a priori knowledge of the value of gamma suggests that alpha and beta are not *conditionally independent*. Beta is completely determined from gamma and alpha. Procedurally, gamma and alpha are calculated first and then beta is calculated as either gamma – alpha or gamma/alpha. Alpha and beta would be conditionally independent (as the random variables  $W$  and  $Z$  are above) if the value of alpha did not determine the value of beta (or vice versa) given a known gamma. Each of the three variables, alpha, beta, and gamma, are *pairwise independent*. This means that for each of the pairs (alpha, beta), (alpha, gamma), and (beta, gamma), neither variable would determine the other without knowing the value of the third variable not in the pair. Denny and Gaines (2000) and Tijms (2004) provide further discussion of these forms of independence in the context of probability theory.

The conditional dependence of alpha and beta can also be assessed empirically by examining the extent to which beta is free to vary for a given value of alpha (and vice versa). This seems to be the concept of independence described as Property 1 in Jost (2007) and Property 4 in Jost (2006). When gamma is fixed then the relationship between alpha and additive beta is completely described by the linear function (beta = –alpha + gamma); the slope is negative and equal to alpha and the  $y$  intercept equals gamma (Fig. 1A). The relationship between alpha and multiplicative beta is given by a power function (beta = gamma  $\times$  alpha<sup>–1</sup>) (Fig. 1A). Thus, when gamma is constant, alpha constrains beta to a single value determined by either a linear or power function. A given value of alpha can have only one value of beta. When gamma is not constant (as in a situation where species are gained or lost from a set of communities), then alpha does not constrain beta as severely, particularly at lower values of alpha (Fig. 1B, C). Additive beta is no more constrained by alpha than is multiplicative beta (Fig. 1B, C). In fact, intermediate and high values of alpha seem to constrain multiplicative beta to very low values (Fig. 1B). In the practical application of additive and multiplicative partitioning (gamma is known), alpha puts mathematical constraints on the possible values of beta, and vice versa. Therefore, neither type of partitioning provides alpha and beta components that obey Jost's independence property (Property 1). None-

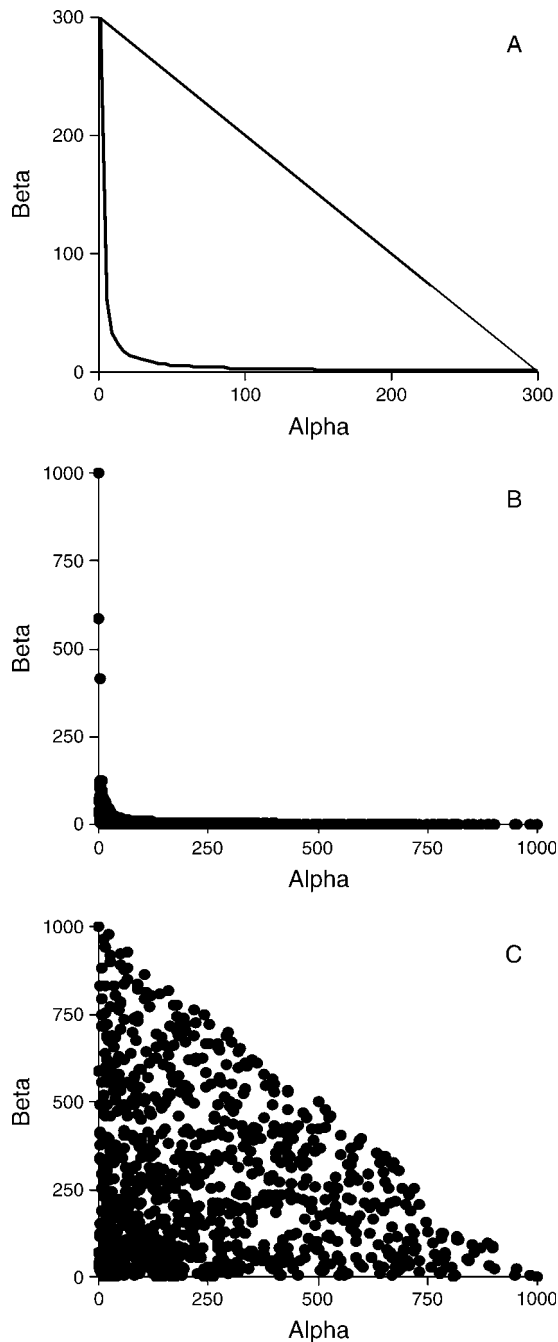


FIG. 1. The relationship between alpha and beta for (A) gamma fixed as a constant at 300 with alpha as a random proportion of gamma and beta as gamma/alpha (curved line) or beta as gamma - alpha (straight line). Gamma is a random variable between 10 and 1000, and alpha is a random proportion of gamma for (B) multiplicative beta and (C) additive beta.

theless, the statistical dependence of alpha and beta is not exceedingly great and does not prohibit the use of additive or multiplicative partitioning for measuring alpha and beta diversity.

However, we do agree with Jost that alpha and beta (as derived from additive or multiplicative partitioning) should measure different, although related, aspects of gamma diversity. Beta is intended to measure differentiation among samples (or communities) whereas alpha should measure within-sample diversity. According to Jost (2007), “If beta depended on alpha, it would be impossible to compare beta diversities of regions whose alpha diversities differed” (Jost 2007:2428). Later, he states: “if beta depends on alpha, the beta values between different hierarchical levels cannot be compared with each other (since each level has a higher alpha than the preceding level) nor with the beta values of other ecosystems” (Jost 2007:2436). However, the dependence between alpha and beta (measured as entropies or diversities) is not so strong that this difficulty cannot be overcome. The correlation between alpha and beta is rather weak (particularly for additive beta) when alpha does not vary substantially (Table 2).

In our simulations, alpha was allowed to vary. That is, for a given group of 1000 data sets, alpha could be any value between 1 and gamma. However, if we fix alpha (at any value) then an important difference emerges between additive beta and multiplicative beta. This difference can be explained analytically (without simulation). For any alpha and without knowing gamma, additive beta can vary from 0 to  $(N - 1) \times \alpha$ ; multiplicative beta can vary from 1 to  $N$ . In terms of probability,  $P(B_M = x | A = y) = P(B_M = x)$  when gamma is unknown and  $x = 1$  to  $N$ . In the absence of gamma, alpha provides no information as to the value of multiplicative beta. However, alpha does provide information as to the possible value of additive beta, specifically that additive beta cannot be greater than  $(N - 1) \times \alpha$ . Alpha and  $N$  constrain the range of additive beta; this constraint gets weaker as  $N$  and alpha increase (e.g.,  $N = 5$ ,  $\alpha = 10$ , additive beta can range from 0 to 40;  $N = 20$ ,  $\alpha = 40$ , additive beta can range from 0 to 760). However, we emphasize that alpha is

TABLE 2. The correlation of alpha with additive beta and multiplicative beta for different intervals of alpha.

| Interval | Additive beta | Multiplicative beta | Number of data sets |
|----------|---------------|---------------------|---------------------|
| 1–25     | 0.044         | –0.380              | 1106                |
| 26–50    | 0.084         | –0.107              | 813                 |
| 51–75    | 0.013         | –0.106              | 725                 |
| 76–100   | 0.035         | –0.061              | 597                 |
| 101–150  | –0.006        | –0.141              | 1053                |
| 151–200  | 0.006         | –0.102              | 873                 |
| 201–300  | –0.019        | –0.177              | 1374                |
| 301–400  | –0.050        | –0.161              | 1061                |
| 401–500  | –0.062        | –0.152              | 826                 |
| 501–600  | –0.101        | –0.180              | 618                 |
| 601–700  | –0.090        | –0.152              | 415                 |
| 701–1000 | –0.423        | –0.474              | 539                 |

Notes: Values are correlation coefficients. For each alpha interval, correlation coefficients are based on a linear regression of beta (additive or multiplicative) vs. alpha. A total of 10 000 data sets were randomly generated.

only setting a maximum potential value for additive beta. The minimum values for additive beta are not mathematically constrained by alpha. Thus, alpha is not forcing additive beta to be high as stated in Property 1 of Jost (2007).

For  $N = 5$  and 20, multiplicative beta ranges from 1 to 5 and 1 to 20 respectively for any alpha value. The range of multiplicative beta is constrained only by  $N$  and thus is constant over all alpha values. So in this sense, alpha and multiplicative beta are “free to vary independently” (Property 1 of Jost 2007), when gamma is unknown. But this does not mean that alpha and multiplicative beta are statistically independent. In practice, we always know gamma. Because gamma is a known value for a data set and is used along with alpha to calculate multiplicative and additive beta, neither beta is statistically independent of alpha. We agree with Jost (2007) that the absence of constraint by alpha on multiplicative beta is a desirable property (and one that additive beta lacks). It assures us that the nonindependence of multiplicative beta and alpha is not due to the potential for positive scaling between the two variables, but rather due to the third variable gamma. This potential positive scaling exists for additive beta and presumably contributes to the nonindependence of additive beta and alpha.

The independence of alpha and beta was also recently examined by Ricotta (2008). He suggested that “the foremost requirement for a meaningful index of beta diversity is that it has to be independent from species richness,” where “species richness” refers to alpha diversity. Ricotta (2008) defined independence of alpha and beta in terms of what he called the “replication principle”: alpha and beta are independent if species replication does not change the value of beta. Replication is simply adding an additional group of species to the data set such that the additional group has the same sequence of abundances and presence/absence (among the set of samples) as the first group. The expanded data set has additional species (and thus an increase in alpha) but differentiation among the samples has not changed and thus beta should not change either. The replication principle is an intuitively appealing way of defining independence because presumably any differences in beta estimates (among data sets that also differ in alpha) are due to real biological effects and not the artefactual effect of beta increasing or decreasing just because it is mathematically linked to alpha. Wilson and Shmida (1984) also defined independence of alpha and beta in this way, without using the term “replication.”

Using the replication principle to define independence, Ricotta (2008) recognized that multiplicative beta is independent of alpha but additive beta is not. Nonetheless, Ricotta then demonstrated that additive beta (measured as species richness) can be made to be “independent” of alpha (in the sense of satisfying the replication principle) by dividing beta by gamma. In

essence, this is a monotonic transformation of multiplicative beta (Ricotta 2008), but it does not establish the statistical independence between alpha and either additive or multiplicative beta. That is, beta/gamma as a variable is not *statistically* independent of alpha and so the effect of alpha on the variable must be removed (as described above) before comparing multiple beta/gamma values. Even when a beta metric satisfies the replication principle, it will still be conditionally dependent on alpha and, therefore, correlated with alpha if alpha appears in the formula for the beta metric. One widely used and accepted method of dealing with conditional dependence between two or more variables is to use each as a response variable in a multivariate analysis (e.g., MANOVA; Sokal and Rohlf 1995, Quinn and Keough 2002). Essentially, multivariate ANOVA treats the response variables as one and tests for an effect on this combined variable. For example, we might want to test for an effect of habitat patch connectivity on alpha and beta. If we have several sets of patches (varying in connectivity within the set) then alpha and beta could be modeled as a multivariate response to the main effect of connectivity.

The analyses presented in this paper do not examine the dependence between alpha and beta when beta is measured by entropies (e.g., Shannon and Simpson indices, others given in Table 1 of Jost 2007) other than species richness. Entropies are more constrained in the limits than species richness, with the Shannon index typically ranging between 1 and 5 and the Simpson index ranging from 0 to 1. Our method of simulating data sets (i.e., randomly selecting alpha and gamma values), without actually producing the hypothetical raw data that the values represent, is not amenable to analyzing other entropies because these are scaled differently than species richness, and require species-abundance distributions. However, we suspect that the beta estimates derived from these other entropies are statistically dependent on alpha.

Jost (2006, 2007) has brought attention to some important issues in the application of diversity partitioning, including making researchers aware of the value of using true diversities (numbers equivalent) to measure species diversity. We see value in these “new” metrics and the general partitioning approach advocated by Jost (2006, 2007). No metric for beta diversity will be statistically independent of alpha and gamma diversity if the beta is calculated directly from alpha and gamma. However, the statistical dependence is not overwhelming and can be handled (e.g., through multivariate analyses) to allow for statistically valid comparisons among multiple beta estimates.

#### ACKNOWLEDGMENTS

We thank A. Baselga and L. Jost for their comments, suggestions, and general insight on some of the issues explored

in this manuscript. H. Stevens helped us improve the clarity of the manuscript.

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