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Multiplicative partition of true diversity yields independent alpha and beta components; additive partition does not

ANDRÉS BASELGA¹

Departamento de Zoología, Facultad de Biología, Universidad de Santiago de Compostela, c/ Lope Gómez de Marzoa s/n, 15782 Santiago de Compostela, Spain

The need for a measure of beta diversity independent of alpha diversity was stressed long time ago (Wilson and Shmida 1984), in order to ensure a “useful application of a measure [of beta diversity] to systems with different alpha diversities.” It should be noted that this requirement refers to the independence of beta diversity

of mean alpha diversity, and not to the independence of beta diversity with regard to differences in alpha diversity between sites. The latter issue was addressed by several authors (Harrison et al. 1992, Lennon et al. 2001, Koleff et al. 2003, Baselga 2007) because beta diversity measures that are dependent on the variation in alpha diversity consider spatial turnover and nestedness patterns as being equivalent (Baselga et al. 2007). However, the dependence of beta diversity on the mean value of alpha diversity is even more critical because it compromises the comparability of beta diversity

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¹ E-mail: andres.baselga@usc.es

measures among systems with different mean alpha diversity.

Focusing on the latter issue, Jost (2007) showed that different formulations (multiplicative, additive, and others) are required to partition the different diversity indices (i.e., species richness, Shannon, Gini-Simpson) into independent alpha and beta components. Jost writes that “when these new alpha and beta components are transformed into their numbers equivalents (effective numbers of elements), Whittaker’s multiplicative law ($\alpha \times \beta = \gamma$) is necessarily true for all indices.” I follow Jost (2007) in using the term “true diversity” for diversity measured in terms of species counts, since species richness is its own numbers equivalent. Thus, when referring to true diversity, the only way to obtain independent alpha and beta components involves using the multiplicative partition. Although the rationale behind this assertion is not explicit in Jost’s paper, it runs as follows. By using this multiplicative law for groups of communities sharing the same proportion of species, we will obtain the same value of beta diversity regardless of the number of species in these groups. In other words, beta diversity will be computed to be equal for (1) a set of two communities with $\alpha = 10$ and 5 species in common and for (2) a set of two communities with $\alpha = 100$ and 50 species in common. This is because multiplicative beta diversity depends on the proportion of shared species. Thus, if we replicate the species composition of the analyzed communities, the beta value should not change if it is independent of richness. Ricotta (2008) termed this requirement the “replication principle,” proposing it as a test for the independence of a beta diversity measure with regard to richness. Ricotta showed that additive beta diversity based on species counts suffers the major drawback of being dependent on species richness, in contrast to multiplicative beta. The dependence of additive beta on species richness was also recently noted by Zeleny (2009) and Manthey and Fridley (2009) in a different context.

Veech and Crist (2010; referred as VC throughout the text) proposed an evaluation of the assumed independence of multiplicative beta diversity on alpha diversity, going beyond theoretical discussion and aiming to provide empirical evidence for the dependence or independence of beta diversity measures. In a simulation procedure, they compared the performance of the additive and multiplicative partition of true diversity. Veech and Crist concluded that neither additive nor multiplicative beta diversity is independent of alpha diversity, and that the dependence of multiplicative beta is even greater than that of additive beta. Here, I evaluate their simulation procedure and provide new approaches. All computations were performed in R (R Development Core Team 2006). I will show that (1) the patterns of dependence between multiplicative beta and alpha are the outcome of the particular conditions of VC’s simulation procedure, which imposed severe

restrictions on the possible values of alpha and gamma, and therefore beta; (2) when these restrictions are eliminated, multiplicative beta is completely independent of alpha but additive beta is not.

The number of communities does matter

The first drawback of the VC simulation is its failure to specify the number of communities (N). As they acknowledge in their paper, N is not consistent across the simulated cases (pairs of alpha and gamma). For example, a possible pair of values in VC simulation is $\gamma = 1000$, $\alpha = 10$. This combination is only possible for $N > 100$ (i.e., you cannot obtain a $\gamma = 1000$ with a lower number of communities when mean $\alpha = 10$). Another possible pair of values yielded by the VC simulation routine could be $\gamma = 100$, $\alpha = 10$, and this is only possible for $N > 10$. However, N should be a fixed parameter because for a given value of gamma (which is the first variable sampled by the VC procedure) the distribution of possible alpha values is determined by N . For example, for $\gamma = 1000$ the maximum value of alpha is always 1000 (all the communities have identical composition) but the minimum value of alpha is $1000/N$ (i.e., 200, 20, 2 for $N = 5, 50, 500$, respectively). Therefore, to ensure that the simulation procedure randomly takes into account all the possible combinations of alpha and gamma, it is strictly necessary to set a defined N .

Fig. 1 shows the pair-wise relationships between alpha, beta and gamma derived from three simulations for $N = 5, 50$, and 500. This simulation procedure (Procedure 1; see R script in Supplement) follows VC in that gamma was set equal to a random number between 10 and 1000 drawn from a uniform distribution, but differs in that alpha was set equal to a random number between γ/N and gamma drawn from a uniform distribution. Thus, the only difference is the fixed N . The number of replications (pairs of gamma and alpha) was set to 10 000. As reported by VC, multiplicative beta showed a pattern of dependence on alpha diversity, although the pattern was quite different depending on N . The most conspicuous result was, however, that multiplicative beta showed no pattern when plotted against gamma, whereas additive beta showed clear patterns of dependence on both alpha and gamma.

The order of simulation routines does matter

A second and more critical drawback of the VC simulation is the assumption that different routines are equivalent, in that the order in which alpha and gamma distributions are generated has no influence in the outcome. I have tested this assumption by performing a new simulation procedure that began by setting the value of alpha randomly (Procedure 2; see R script in Supplement). Fig. 2 shows the pair-wise relationships between alpha, beta, and gamma derived from three simulations for $N = 5, 50$, and 500. In these new simulations, alpha was set equal to a random number

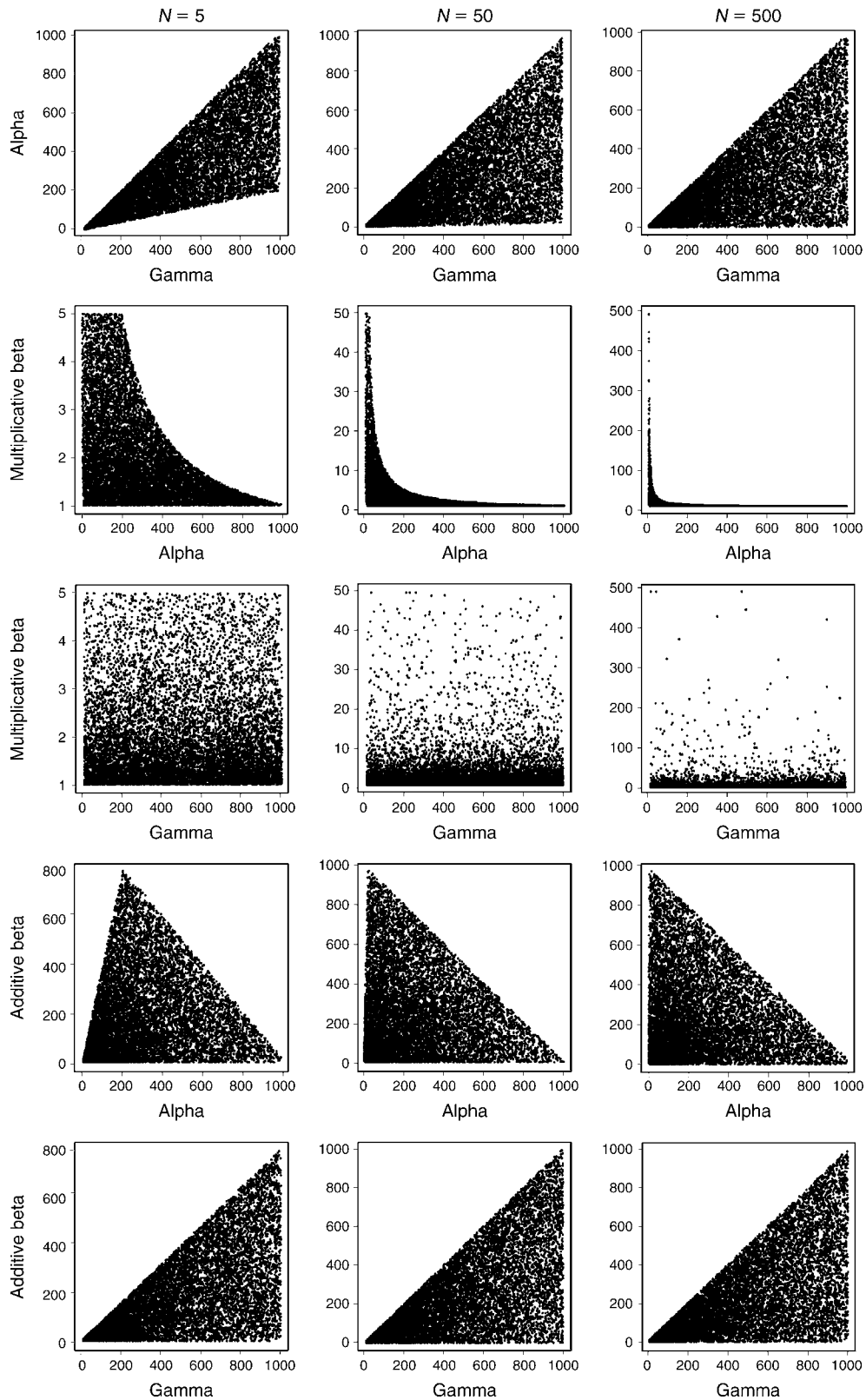


FIG. 1. Pair-wise relationships between alpha, gamma, and multiplicative or additive beta diversity as simulated by Procedure 1. See *The number of communities does matter* for details.

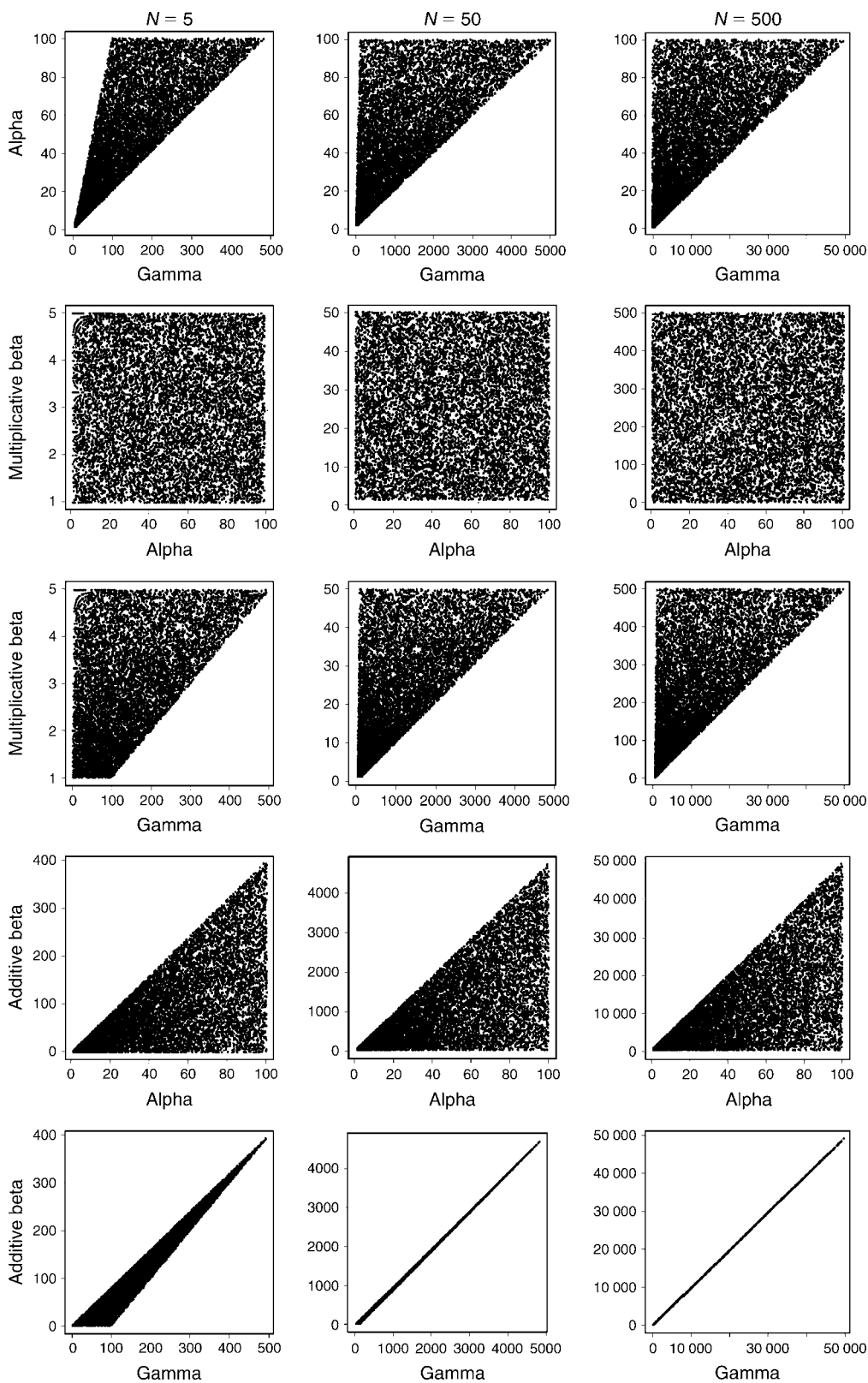


FIG. 2. Pair-wise relationships between alpha, gamma, and multiplicative or additive beta diversity as simulated by Procedure 2. See *The order of simulation routines does matter* for details.

between 1 and 100 drawn from a uniform distribution, and gamma was set equal to a random number between alpha and $\alpha \times N$ drawn from a uniform distribution. The number of samples (pairs of alpha and gamma) was set to 10 000. The most striking result of these new simulations was that, in contrast with Procedure 1, no pattern of dependence appeared between multiplicative beta and alpha. Instead, a pattern of dependence between multiplicative beta and gamma was found. Dependence of additive beta diversity on both alpha and gamma was found again, but using Procedure 2 the pattern is extremely marked in the case of gamma. Therefore, it seems clear that dependence patterns of multiplicative beta diversity are related to the simulation procedure selected. Multiplicative beta seemed to be dependent on the variable (alpha or gamma) determined second during each simulation. When random values of gamma are set first, and thereafter random values of alpha (consistent with the selected gamma and N values) are set, then multiplicative beta shows dependence on alpha. However, when random values of alpha are set first, and thereafter random values of gamma (consistent with the selected alpha and N values) are set, then multiplicative beta shows dependence on gamma.

Reasons for the dependence patterns

At this point, elements are available to interpret the results reported here as well as those published by VC. Firstly, the influence of the order of simulations on the dependence patterns results from the arbitrary limits of the distribution of the variable set in first place in the simulation (gamma or alpha). Secondly, the higher the number of communities, the higher the influence of the former arbitrary limits.

The limits of the first distribution are arbitrarily selected. In the first set of simulations, Procedure 1 bounds gamma between 10 and 1000. Each value of gamma is then randomly associated with any of all the possible values of alpha consistent with the specified N . For this reason, not all possible values of gamma consistent with the specified N are available for certain values of alpha, since we have arbitrarily limited gamma to be between 10 and 1000. For example, for $N = 5$ and gamma = 1000, one possible value is alpha = 1000 (as any other value between 200 and 1000). However, for alpha = 1000, the only possible value of gamma in this simulation is 1000, hence the dependence pattern between multiplicative beta and alpha in Procedure 1. However the limit of gamma and the forced low value of multiplicative beta are arbitrary and not caused by a real association between alpha and multiplicative beta. There is no reason to exclude the possibility of a value of alpha = 1000 associated with any value of gamma > 1000. In fact, it is much more unlikely to observe five different communities with exactly the same set of 1000 species. The shape of the pattern depends on N because below

the limit of $\alpha = \text{maximum gamma}/N$, for any given alpha all the possible values of gamma are permitted by the simulation procedure. Thus, no dependence pattern appears below 200, 20, and 2 for $N = 5, 50,$ and 500, respectively (Fig. 1). However, for values of alpha > maximum gamma/ N , the possible values of gamma are increasingly restricted with increasing alpha. Thus the distribution of multiplicative beta is artificially bounded to decreasing low values.

In Procedure 2, alpha is bounded between 1 and 100. Thereafter each value of alpha is randomly associated to any of all the possible values of gamma consistent with the specified N . Using this method, not all the possible values of alpha consistent with the specified N are available for some values of gamma, since we have arbitrarily limited alpha to be between 1 and 100. For example, for $N = 5$ and alpha = 100, one possible value is gamma = 500 (among many others between 100 and 500). However, for gamma = 500, the only possible value of alpha in this simulation is 100, hence the dependence pattern between multiplicative beta and gamma in Procedure 2. However, this is again an arbitrary constraint of the simulation. As found in Procedure 1, the pattern depends on N because below the limit of $\alpha = \text{maximum alpha}$, for any given gamma all the possible values of alpha are permitted by the simulation procedure (no pattern appears below gamma = 100). Since gamma = 100 is a different proportion of maximum gamma for $N = 5, 50,$ and 500, respectively, the dependence patterns exhibit different shapes (Fig. 2). For values of gamma > maximum alpha, the possible values of alpha are increasingly restricted to high values with increasing gamma. Thus the distribution of multiplicative beta is artificially bounded to increasing high values.

An appropriate test for each question

The problem generated by the arbitrary limits of distributions cannot be solved if one aims to test the independence of beta simultaneously on alpha and gamma. Once the range of the first variable is fixed and all the possible values of the second variable are included, then, unavoidably, all the possible values of the first variable are not available for some values of the second one. But this difficulty is only an apparent one. If one wants to test the independence between beta and alpha, the correct procedure is to consider a range of possible values of alpha, and then include in the simulation all the possible values of gamma consistent with the distribution of alpha. This is Procedure 2. On the other hand, if one wants to test the independence between beta and gamma, the correct procedure is to consider a range of possible values of gamma, and then include in the simulation all the possible values of alpha consistent with the distribution of gamma. This is Procedure 1. In sum, each simulation is appropriate to test for the dependence of beta on only gamma

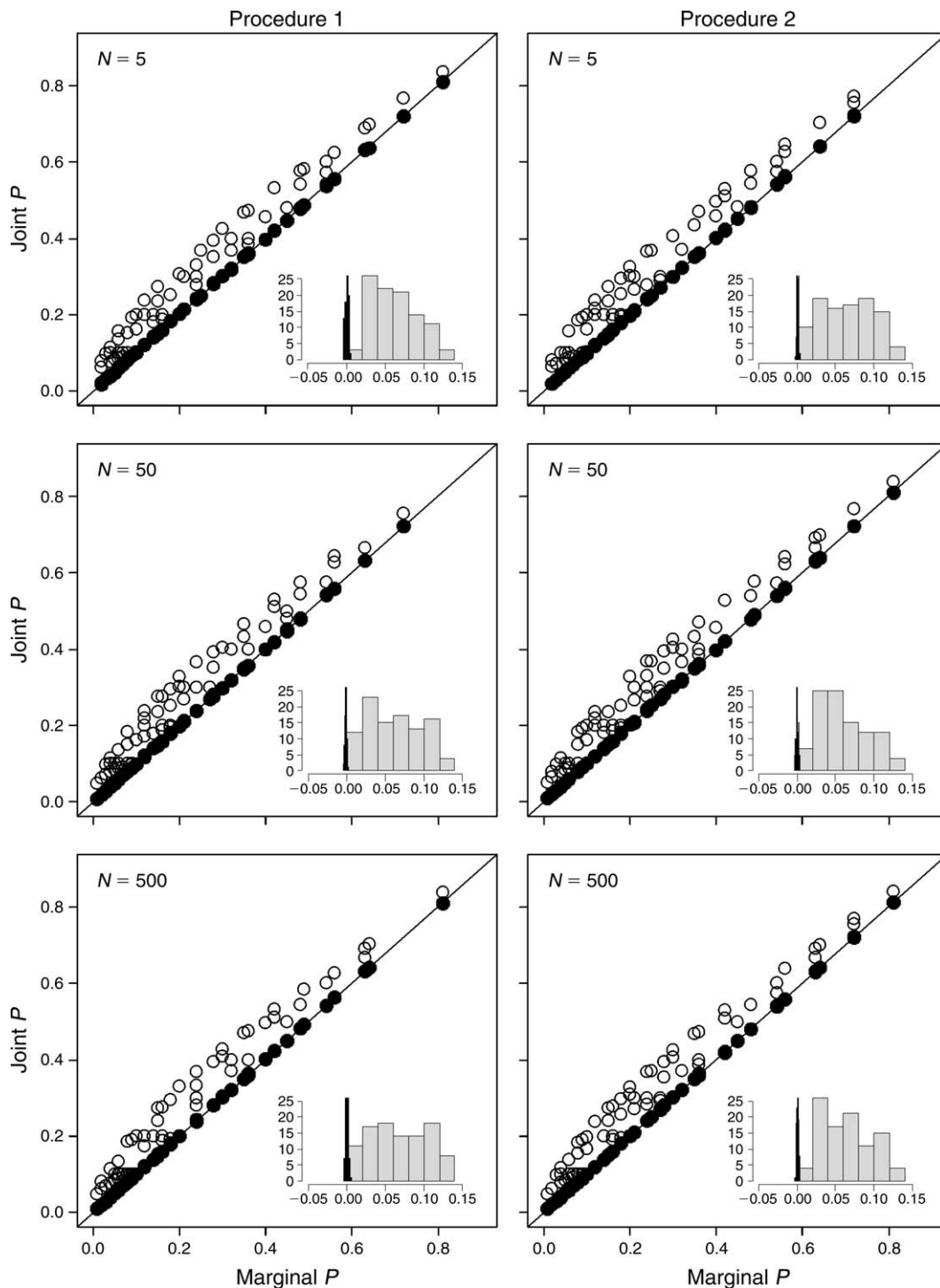


FIG. 3. Relationship between joint probabilities (P) and the products of marginal probabilities for multiplicative (solid circles) and additive beta diversity (open circles). Marginal and joint probabilities were computed for random events involving pairs of beta and gamma values in Procedure 1 and pairs of alpha and beta values in Procedure 2. The diagonal lines mark the 1:1 relationship (perfect fit between joint P and the product of marginal P). Histograms show the distribution of differences between joint P and the product of marginal P for multiplicative beta diversity (black) and additive beta diversity (gray).

(Procedure 1) or alpha (Procedure 2), but not on both. In both cases, multiplicative beta passes the test, as no pattern of dependence was detected between beta and alpha (Fig. 2) or gamma (Fig. 1). In contrast, additive beta is shown to be dependent on alpha and gamma, as previously known (Ricotta 2008).

In my opinion, the plots shown in Figs. 1 and 2 are conclusive. However, for comparability with VC results, I computed the marginal and joint probabilities of random events involving pairs of multiplicative beta or additive beta and gamma or alpha to assess their dependence. Thus, for Procedure 1, I selected two random probability, P , values between 0.1 and 0.9 (i.e., $P(G)$ and $P(B)$) and computed the quantile of gamma corresponding to $P(G)$ (G), as well as the quantiles of multiplicative beta and additive beta corresponding to $P(B)$ (B_M and B_A , respectively). The joint probabilities of gamma $< G$ and multiplicative beta $< B_M$ ($P(G, B_M)$), as well as gamma $< G$ and additive beta $< B_A$ ($P(G, B_A)$), were computed empirically as the proportion of pairs in which gamma was lower than the selected quantile of gamma, and beta was lower than the selected quantile of beta. If the measure of beta is independent of gamma, the joint probability of a pair of random events ($P(G, B_M)$ or $P(G, B_A)$) should be equal to the product of the marginal probabilities ($P(G)P(B)$). For Procedure 2, the same was done but using a random probability $P(A)$ corresponding to a quantile of alpha, instead of $P(G)$. As can be observed in Fig. 3, when assessing the independence of beta with regard to alpha or gamma using the appropriate procedure, joint probabilities are almost equal to the products of marginal probabilities for multiplicative beta (mean absolute difference < 0.0017 , maximum absolute difference < 0.0047 in all simulations). Moreover, differences have an unbiased distribution centered at zero (see histograms in Fig. 3). On the contrary, for additive beta, joint probabilities are markedly different from the products of marginal probabilities (mean absolute difference between 0.062 and 0.069, maximum absolute difference between 0.12 and 0.13 in all simulations). Differences have a positively biased distribution (see histograms in Fig. 3). In sum, multiplicative beta diversity is methodologically independent of gamma and alpha diversity, whereas additive beta diversity is intrinsically dependent on both gamma and alpha diversity (Figs. 1 and 2, respectively).

Conclusion

The empirical tests demonstrated that multiplicative partition of true diversity yields independent alpha and beta components, but additive partitioning does not. As stressed by Jost (2010), this conclusion is not particular for species richness but can be generalized to any diversity measure. The appropriate partitioning for different diversity measures (Shannon, Gini-Simpson) is that which is equivalent to the multiplicative partition-

ing of its number equivalents (Jost 2007). Therefore, the point raised here is independent of the inclusion of incidence or abundance measures in the diversity index, and should be taken into account prior to other considerations, such as the effect of sample size and undetected species (Chao et al. 2005, 2006) or discrimination between turnover and nestedness patterns (Baselga et al. 2007, Baselga 2010). As a conclusion, using the additive partition of true diversity, one would always find a correlation between alpha and beta diversity patterns derived from the intrinsic dependence between both measures. In contrast, using multiplicative partitioning, one can assess if there is any relationship between alpha and beta diversity patterns. If found, this relationship could be analyzed as a meaningful biological pattern (Jost 2010). As reported previously by Wilson and Shmida (1984), alpha and beta diversity patterns are the result of different ecological and biogeographical processes. Thus, if we are to understand the mechanisms underlying biodiversity we need to assess alpha and beta patterns using truly independent measures. These measures are provided by the multiplicative partitioning of true diversities, or the equivalent formulations for other diversity measures (Jost 2007).

LITERATURE CITED

- Baselga, A. 2007. Disentangling distance decay of similarity from richness gradients: response to Sojininen et al. 2007. *Ecography* 30:838–841.
- Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19:134–143.
- Baselga, A., A. Jiménez-Valverde, and G. Niccolini. 2007. A multiple-site similarity measure independent of richness. *Biology Letters* 3:642–645.
- Chao, A., R. L. Chazdon, R. K. Colwell, and T. J. Shen. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters* 8:148–159.
- Chao, A., R. L. Chazdon, R. K. Colwell, and T. J. Shen. 2006. Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics* 62: 361–371.
- Harrison, S., S. J. Ross, and J. H. Lawton. 1992. Beta-diversity on geographic gradients in Britain. *Journal of Animal Ecology* 61:151–158.
- Jost, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88:2427–2439.
- Jost, L. 2010. Independence of alpha and beta diversities. *Ecology* 91:1969–1974.
- Koleff, P., K. J. Gaston, and J. K. Lennon. 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* 72:367–382.
- Lennon, J. J., P. Koleff, J. J. D. Greenwood, and K. J. Gaston. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70:966–979.
- Mantley, M., and J. D. Fridley. 2009. Beta diversity metrics and the estimation of niche width via species co-occurrence data: reply to Zeleny. *Journal of Ecology* 97:18–22.
- R Development Core Team. 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (<http://www.r-project.org>)

- Ricotta, C. 2008. Computing additive beta-diversity from presence and absence scores: a critique and alternative parameters. *Theoretical Population Biology* 73:244–249.
- Veech, J. A., and T. O. Crist. 2010. Diversity partitioning without statistical independence of alpha and beta. *Ecology* 91:1964–1969.
- Wilson, M. V., and A. Shmida. 1984. Measuring beta diversity with presence absence data. *Journal of Ecology* 72:1055–1064.
- Zeleny, D. 2009. Co-occurrence based assessment of species habitat specialization is affected by the size of species pool: reply to Fridley et al. (2007). *Journal of Ecology* 97:10–17.

SUPPLEMENT

R scripts for conducting the simulations described in the main text (*Ecological Archives* E091-135-S1).