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An Empirical Comparison of Beta Diversity Indices in Establishing Prairies

Abstract

Whittaker (1960, 1972) first proposed the idea that species diversity has spatial components, with alpha diversity estimating diversity within individual stands (or communities) and beta diversity estimating the number of community types in an area (or in Whittaker's terminology, "differentiation of communities along gradients"). These two values combined make up gamma diversity. Beta diversity is important because it provides the conceptual link between local and regional diversity, more directly measures how soil types, disturbance, and dispersal affect diversity, and is helpful in understanding why species loss is sometimes smaller than predicted by theory (Wilsey et al. 2005). Many interesting and longstanding questions are applied across scales, such as how much diversity is found within islands vs. across islands? Is the number of habitat types (i.e., beta) within islands key to explaining diversity at larger scales or is it the greater population sizes found on large islands? Furthermore, a consideration of both alpha and beta is necessary for understanding how diversity arises and is maintained in diverse systems. For example, in the northern Great Plains, we have found that remnant prairies can contain over 120 plant species within a small area (Wilsey et al. 2005); this occurs because of high diversity at the neighborhood scale where 20–25 species are found per square meter (Martin et al. 2005), and from species accumulation across neighborhoods (i.e., beta).

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An empirical comparison of beta diversity indices in establishing prairies

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Whittaker (1960, 1972) first proposed the idea that species diversity has spatial components, with alpha diversity estimating diversity within individual stands (or communities) and beta diversity estimating the number of community types in an area (or in Whittaker's terminology, "differentiation of communities along gradients"). These two values combined make up gamma diversity. Beta diversity is important because it provides the conceptual link between local and regional diversity, more directly measures how soil types, disturbance, and dispersal affect diversity, and is helpful in understanding why species loss is sometimes smaller than predicted by theory (Wilsey et al. 2005). Many interesting and long-standing questions are applied across scales, such as how much diversity is found within islands vs. across islands? Is the number of habitat types (i.e., beta) within islands key to explaining diversity at larger scales or is it the greater population sizes found on large islands? Furthermore, a consideration of both alpha and beta is necessary for understanding how diversity arises and is maintained in diverse systems. For example, in the northern Great Plains, we have found that remnant prairies can contain over 120 plant species within a small area (Wilsey et al. 2005); this occurs because of high diversity at the neighborhood scale where 20–25 species are found per square meter (Martin et al. 2005), and from species accumulation across neighborhoods (i.e., beta).

Many different approaches to estimating beta have been forwarded since Whittaker introduced the concept, and many sampling and statistical issues have been discussed. To an empirical ecologist, the key question when deciding which approach to use is "Will we get different answers to a question depending on the beta measure that we use?" Here, I address this question by testing whether commonly used indices (multiplicative and additive measures) differ in their response to a common set of ecological treatments.

Whittaker proposed a multiplicative form for beta ($m\beta$) as $\beta = \gamma/\alpha$. A simple way to describe this equation is that alpha is species diversity within communities, and

beta is the number of community types in the region (Jost 2007). A major issue with the among- vs. within-community approach is that the scale at which α is sampled varies so that alpha is used to estimate point diversity in some studies (e.g., at the scale of a sampling station or quadrat) and is used to estimate something larger (e.g., an island in an island biogeography study) in other studies. This makes sense in that beta describes a general concept of species accumulation across lower levels of organization, but it creates a problem in that one person's alpha (e.g., an island) is another person's gamma (e.g., an island, if alpha is at the scale of neighborhoods within the island). The additive form of beta ($a\beta$), $\beta = \gamma - (\text{mean } \alpha)$, has become popular in recent years (Lande 1996, Veech et al. 2002, Crist et al. 2003) because it can easily be applied at different spatial scales to address these issues in an effective manner. The additive form has the following advantages over the multiplicative form: (1) alpha and beta are in the same units, and (2) it enables estimates of beta even when the boundaries between communities are hard to discern, and thus, (3) it more easily allows multiple levels of beta. With additive beta, one can ask questions about how beta changes with the scale of measurement, and it fits in well with other topics in the popular field of landscape ecology.

However, Jost (2007) and Riccota (2007) correctly point out that $a\beta$ is not mathematically independent of additive α . They recommend using multiplicative forms of beta, alternative forms of additive beta based on numbers equivalents (Jost 2007), or proportions of additive alpha and beta to gamma (α/γ and β/γ [or propB]; Riccota 2007). To provide a simple ecological example that illustrates their point about a lack of independence: imagine a relatively homogenous field of herbaceous plants surrounded by a very large regional species pool with a consistent amount of species turnover throughout. Three studies are conducted in this same field, each group uses a different sized quadrat to sample, and all have the same sample size. Let us assume that they all sample the field without error. The first uses the smallest-sized quadrat and finds a mean alpha of 20 and gamma of 30. The second uses a medium-sized quadrat and finds a mean alpha of 40 and gamma of 60. The third uses a large-sized quadrat and

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finds alpha of 60 and gamma of 90. Since the field is the same and it has a consistent amount of turnover throughout, the three groups should come up with the same estimates of beta diversity. This is true of multiplicative beta and proportion of beta using the additive partitioning, but not with the absolute measures of additive beta. That is, the first group finds a $m\beta$ of $30/20 = 1.5$, and a $propB$ of $(30 - 20)/30 = 0.333$, the second a $m\beta$ of $60/40 = 1.5$ and a $propB$ of $(60 - 40)/60 = 0.333$, and the third a $m\beta$ of $90/60 = 1.5$ and a $propB$ of $(90 - 60)/90 = 0.333$. This can be interpreted to mean that there are 1.5 community types in this field (Jost 2007). So far so good. However, $a\beta$ is not the same across studies, and alpha is not independent of beta and gamma, even though the field is homogenous and should give the same beta values. Making the calculations, the first group finds $a\beta$ of $30 - 20 = 10$, the second $60 - 40 = 20$, and the third $90 - 60 = 30$. Now, let's say that people later compare the results from these studies, perhaps in a meta-analysis. Comparing these $a\beta$ estimates would give the meta-analyst the false impression that beta ranges from 10 - 30 when it does not (they all accurately sampled the same field). However, the $m\beta$ and $propB$ would give an accurate description of the difference among the three studies. What about comparing multiple sites (giving multiple γ s) with the same sized quadrat or sampling scheme? If alpha varies across sites, then $a\beta$ is going to rise and fall with alpha in the same manner with the same problems previously described.

This dependence of beta on alpha is different from the dependence within sites that was discussed by Veech and Crist (2010). Within sites, the relationship between alpha and additive beta can be negative when raw values and not means are used, because the closer alpha is to gamma, the lower beta will be (Veech and Crist 2010). However, the partitioning approach advocated by Lande (1996) and reviewed by Veech et al. (2002) uses mean alpha, which should be positively related to beta when alpha varies across sites.

Data from a thought experiment are one thing, but what about a real-life example? We have been conducting a long-term restoration experiment in Iowa that consists of seed additions of 30 native prairie species to bare-ground plots in former brome (*Bromus inermis*) fields. Seed mixes were added independently to 120 plots within each of two sites in a manner that would provide multiple independent values of alpha, beta, and gamma. The experiment involved establishing treatments that vary species arrival order and disturbance history, over-seeding all plots with a common seed mix, and then sampling the resulting communities to test how treatments affected plant community assembly. An abbreviated set of results will be presented here to test whether conclusions vary depending on which beta measures are used. Beta was calculated using the most commonly recommended measures of diversity, species richness (Σp_i^0) Shannon's ($e^{H'} = \exp[-\Sigma \ln(p_i) \times p_i]$),

and Gini-Simpson's ($1 - \Sigma p_i^2$), where p_i is the relative abundance of each (i th) species in the sample or combined samples.

Experimental Design

The experiment was established between April 2005 and April 2006 using a split-plot design at two sites that differed in their net primary productivity with five early-emerging species treatments applied to main plots, and four history treatments applied to subplots. In 5×5 m main plots, seeds of early-emerging species were established as six single-species treatments at a rate of 11.5 kg/ha: (1) the perennial C_3 grass *Elymus canadensis*, (2) the perennial C_4 grass *Bouteloua curtipendula*, (3) the annual C_3 legume *Chaemaecrista fasciculata*, (4) the biennial C_3 forb *Rudbeckia hirta*, (5) a mix of all four species, and (6) controls with no early-emerging species added. Species were selected because they emerge early in the establishment period compared to other members of their functional groups. The key prediction is that species will admit members of other functional groups more readily than members of their own functional groups, and that this will lead to enhanced beta diversity among plots. In 2×2 m subplots within each main plot, the following history treatments were applied using a seed mix of 30 native prairie species: (1) early-spring seeding of both the early-emerging species and the seed mix, (2) early-spring seeding of the early-emerging species with the seed mix added the following year in the spring, (3) late-summer seeding of both the early-emerging species and the seed mix, and (4) late-summer seeding of the early-emerging species with the seed mix added the following year in the spring. These history treatments were predicted to lead to enhanced beta diversity due to priority effects (seed mix added at the beginning vs. the growing season after early-emerging species had established) and timing of disturbance (spring vs. fall for seedling emergence). Timing was predicted to affect the establishment of functional groups differently due to either increasing soil temperatures and day lengths (early spring seeding favoring C_4 plant species) or decreasing soil temperatures and day lengths (late summer seeding favoring C_3 species). The original design had 30 main plots at each of the two sites, and 4 subplots per main plot for 2 sites \times 6 species treatments \times 5 replicates \times 4 subplot treatments = 240 total. Thus, each of the 240 plots received a separate seed mix, and a total of 60 independent gamma and mean alpha values could be calculated at the subplot to main-plot level. One plot at one site had to be dropped due to an accidental mowing event, for 236 subplots total, and 59 gamma values.

Abundances of each plant species were estimated in the center of each subplot with point intercept sampling in mid-July of the second growing season (July 2007). All hits were counted per pin so that data would be more strongly correlated with biomass. Relative abundance was calculated as abundance of each species by the total

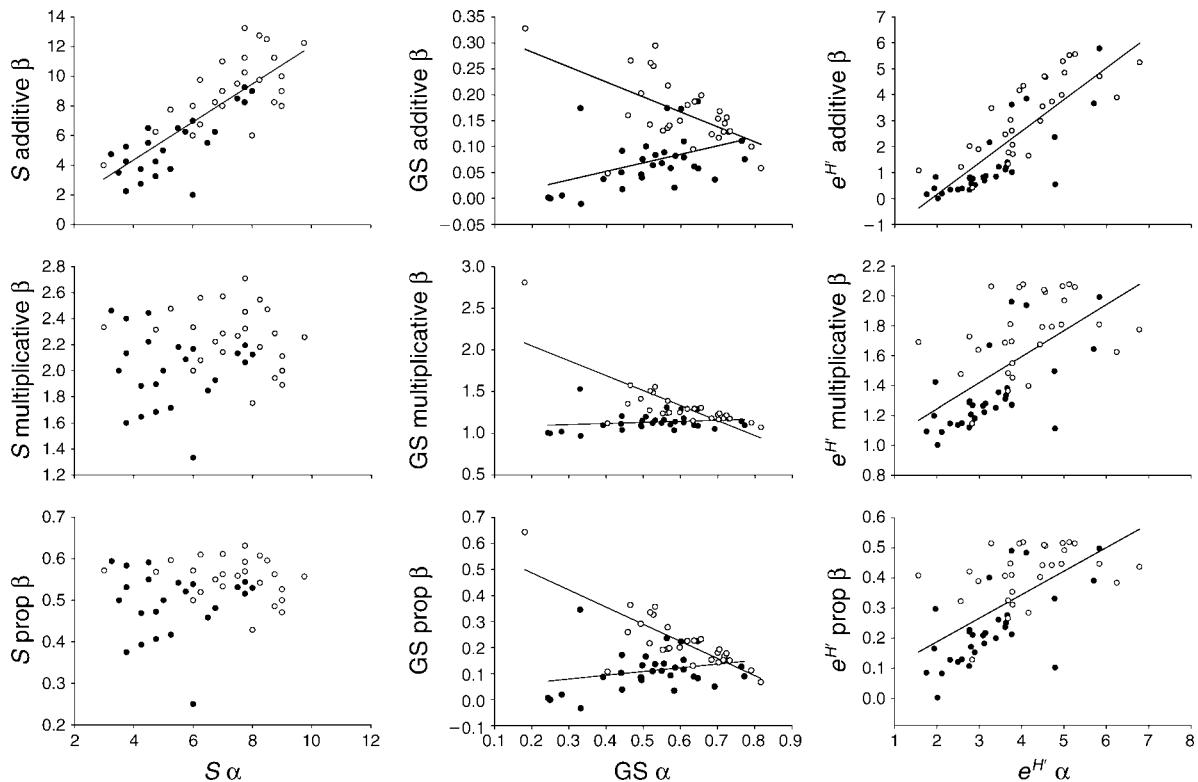


FIG. 1. Relationships between alpha diversity and additive (top panels), multiplicative (middle panels), and proportion of additive (prop, lower panels) beta using diversity measures of species richness (S , left-hand panels), Gini-Simpson's $1 - D$ (GS, middle panels), and Shannon's $e^{H'}$ (right-hand panels) at two sites (open and solid circles).

number of hits. Pins were dropped 20 times per plot from a 50×100 cm frame in a systematic manner. Occasionally, there were species in the plot that did not receive any hits. These were given a value of one hit and were included in the estimates of species richness.

RESULTS AND DISCUSSION

Relationships between alpha and beta depended greatly on which measure was considered (Fig. 1, Table 1). As in our thought experiment, and in accordance with a mathematical dependence between alpha and beta, the alpha and additive beta measures were strongly positively correlated for all measures considered except for the Gini-Simpson's index. Additive richness was strongly related to alpha values (slope = 1.3, $r^2 = 0.65$, $P < 0.001$). However, multiplicative richness and the proportion of additive beta were statistically independent of alpha (all P values > 0.05). Additive $e^{H'}$ (slope = 1.2, $r^2 = 0.67$, $P < 0.001$) was much more strongly related to alpha $e^{H'}$ than were multiplicative $e^{H'}$ (slope = 0.17, $r^2 = 0.38$, $P < 0.001$) and proportion of additive beta (slope = 0.08, $r^2 = 0.40$, $P < 0.001$). Interestingly, and as predicted by Jost (2007), the Gini-Simpson's index was not independent of alpha, and the slope depended on how close alpha was to 1. In the more mesic site, the relationship between alpha and the Gini index was *negative* (slope = -0.29 , $P < 0.001$, $r^2 = 0.34$).

This site had higher alpha values. At the more xeric site, the relationship was weakly *positive* (slope = 0.16, $P = 0.018$, $r^2 = 0.18$). Thus, values from both sites converged as alpha neared 1, and the ratio alpha/gamma approaches unity (Jost 2007). These results suggest that the Gini-Simpson's index should be avoided in beta diversity studies, contrary to what was recommended by Lande (1996) and Veech et al. (2002).

A very large amount of beta diversity was found when subplots were combined across history treatments regardless of the early-emerging species treatments (Table 1). Greater than half of the species richness and 17–49% of Shannon's diversity at this level was from beta, and there were on average about two different community types within each main plot as a result of history treatments. This is ecologically very interesting because it was associated with the proportions of native/exotic species and C_3/C_4 species across history treatments; this will be developed further for a future publication.

At the across-site level, there was less beta than at the across-history-treatment level ($m\beta$ and $prop\beta$), even though the sites were orders of magnitude further apart and on different soil types with different precipitation levels. However, notice that $a\beta$ for richness was much higher at the across-site level (20) vs. the

TABLE 1. Alpha, beta, and gamma species richness and diversity in experimental plots in two sites in Iowa, USA (a less-productive site, WRF, in Monona County, and a more-productive mesic site, Hort, in Story County).

Source	Species richness					Gini-Simpson's diversity ($1 - D$)					Shannon's diversity ($e^{H'}$)				
	α	a β	m β	prop β	γ	α	a β	m β	prop β	γ	α	a β	m β	prop β	γ
WRF subplot	11.5					0.59					4.5				
Control	5.9	6.5	2.1	0.51		0.53	0.07	1.13	0.11		3.2	1.3	1.3	0.22	
<i>Elymus</i>	5.5	6.1	2.1	0.51		0.49	0.06	1.09	0.07		3.1	1.3	1.4	0.25	
<i>Chaemaecrista</i>	6.1	7.1	2.1	0.51		0.54	0.10	1.22	0.17		3.6	1.9	1.4	0.29	
<i>Bouteloua</i>	5.4	5.5	2.0	0.50		0.61	0.07	1.11	0.10		3.6	1.4	1.3	0.24	
<i>Rudbeckia</i>	4.8	4.4	1.9	0.46		0.43	0.06	1.12	0.11		2.6	0.6	1.2	0.17	
Mix	5.7	6.3	2.1	0.52		0.53	0.07	1.12	0.10		3.4	1.1	1.3	0.20	
Hort subplot	16.5					0.77					7.5				
Control	8.4	9.8	2.2	0.53		0.66	0.16	1.24	0.19		4.7	3.9	1.8	0.44	
<i>Elymus</i>	8.5	11.0	2.3	0.56		0.74	0.12	1.17	0.14		5.4	5.1	2.0	0.49	
<i>Chaemaecrista</i>	7.8	8.7	2.1	0.52		0.65	0.16	1.26	0.20		4.6	3.7	1.8	0.43	
<i>Bouteloua</i>	6.6	8.4	2.3	0.55		0.51	0.19	1.38	0.27		3.5	2.2	1.6	0.37	
<i>Rudbeckia</i>	7.5	8.9	2.2	0.54		0.61	0.16	1.27	0.20		4.0	2.7	1.7	0.40	
Mix	5.4	8.1	2.6	0.61		0.48	0.19	1.38	0.30		3.2	2.2	1.7	0.38	
Sites mean	49	20	1.4	0.29		0.76	0.06	1.08	0.07		9.20	2.25	1.2	0.20	
Across-site γ	69					0.82					11.5				

Notes: Subplot means are alpha (α diversity in subplots), additive and multiplicative beta (a β and m β) and proportion of beta diversity (prop β) across four history treatments that varied timing of seeding and priority effects. Beta was calculated using the most commonly recommended measures of diversity: species richness ($\sum p_i^0$), Shannon's ($e^{H'} = \exp[-\sum \ln(p_i) \times p_i]$), and Gini-Simpson's ($1 - \sum p_i^2$), where p_i is the relative abundance of each (i th) species in the sample or combined samples.

across-history-treatment level (4.4 – 11.0) again due to the dependence of additive beta and alpha.

These empirical results suggest that it does matter which index is used in beta diversity studies. This statistical dependence of the absolute measure of additive beta on alpha creates problems with interpretation and I suggest that the raw additive beta measure should be avoided when there are differences in alpha (and gamma) between sites or samples. However, there are many studies in the literature that have analyzed the absolute measure of beta since the additive partitioning method was advocated (e.g., Polley et al. 2005, Hendrickx et al. 2007, Brudvig 2009). Ecologists may be reluctant to see these types of comparisons of a β across sites as a problem because alpha and gamma are important variables. They may intuitively sense that the sites that they are studying do indeed have different alphas and gammas. In fact, the first and most important step in any study is to compare alpha and/or gamma diversities. However, beta should provide a value that is not mathematically related to alpha or gamma (Jost 2007, Ricotta 2007). With beta values that are mathematically independent of alpha, we can compare sites with different levels of alpha diversities across scales, and we can more effectively compare and contrast different studies. The absolute measure of additive beta is only useful in comparing plots/sites when the alpha values do not vary across the units that are being compared (Jost 2007, Ricotta 2007). Sites/samples can be compared more effectively by not analyzing the absolute measure of beta, but instead by using the prop β , the m β , or by using ANCOVA or other statistical techniques that take into account this codependence (Veech and Crist 2010).

The Gini-Simpson's index should be avoided in diverse sites when its values approach 1. As Jost (2007) pointed out, this will be most problematic in the most diverse sites. For example, we commonly record α values of the Gini-Simpson index of 0.9 in diverse tallgrass prairie plots (Martin et al. 2005). In this situation, β can not exceed 0.1 regardless of how much species turnover there is. This problem can be remedied by using diversity measures (e.g., Shannon's or Simpson's $1/D$) that do not have an upper limit of one.

Finally, some flexibility is needed in deciding among the recommended indices used to estimate beta diversity. We will need to continue to interpret across study systems and to compare results to earlier time periods. The approaches in comparing beta diversity discussed here (proportion of additive beta or multiplicative beta indices), or using approaches not discussed (similarity-index-based ordination [Legendre et al. 2005] and rarefaction-curve-based approaches [Olszewski 2004]) are all valid ways to proceed. The general approach to use will depend on the objectives of the investigation. For example, if an experiment on diversity maintenance is designed to compare alpha and gamma diversity indices, then using the approaches discussed in this paper are logical ways to proceed. Converting "entropy" values to their numbers equivalents before interpreting them is helpful for the reasons pointed out by Hill (1973) and Jost (2007). If analyses of species composition differences or species-area curves are being conducted, then the logical choice is to use one of the latter choices that were not discussed here. We can then move beyond these discussions on how to calculate beta diversity to the important task of discerning what processes underlie observed patterns of beta.

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LITERATURE CITED

- Brudvig, L. A. 2009. Woody encroachment removal from midwestern oak savannas alters understory diversity across space and time. *Restoration Ecology* 18:78–84.
- Crist, T. O., J. A. Veech, J. C. Gering, and K. S. Summerville. 2003. Partitioning species diversity across landscapes and regions: a hierarchical analysis of α , β , and γ diversity. *American Naturalist* 162:734–743.
- Hendrickx, F., et al. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology* 44:340–351.
- Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54:427–432.
- Jost, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88:2427–2439.
- Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13.
- Legendre, P., D. Bocard, and D. R. Peres-Neto. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs* 75:435–440.
- Martin, L. M., K. A. Moloney, and B. J. Wilsey. 2005. An assessment of grassland restoration success using species diversity components. *Journal of Applied Ecology* 42:327–336.
- Olszewski, T. D. 2004. A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. *Oikos* 104:377–387.
- Polley, H. W., B. J. Wilsey, and J. D. Derner. 2005. Patterns of plant species diversity in remnant and restored tallgrass prairies. *Restoration Ecology* 13:480–487.
- Ricotta, C. 2007. Computing additive β -diversity from presence and absence scores: a critique and alternative parameters. *Theoretical Population Biology* 73:244–249.
- Veech, J. A., K. S. Summerville, T. O. Crist, and J. C. Gering. 2002. The additive partitioning of species diversity: recent revival of an old idea. *Oikos* 99:3–9.
- Veech, J. A., and T. O. Crist. 2010. Diversity partitioning without statistical independence of alpha and beta. *Ecology* 91:1964–1969.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30:279–338.
- Whittaker, R. 1972. Evolution and measurement of species diversity. *Taxon* 21:213–215.
- Wilsey, B. J., L. M. Martin, and H. W. Polley. 2005. Predicting plant extinction based on species–area curves in prairie fragments with high beta richness. *Conservation Biology* 19:1835–1841.