

## Commentary: Do we have a consistent terminology for species diversity? The fallacy of true diversity

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**Abstract** There is no single best index that can be used to answer all questions about species diversity. Entropy-based diversity indices, including Hill's indices, cannot account for geographical and phylogenetic structure. While a single diversity index arises if we impose several constraints—most notably that gamma diversity be completely decomposed into alpha and beta diversity—there are many ecological questions regarding species diversity for which it is counterproductive, requiring decomposability. Non-decomposable components of gamma diversity may quantify important intrinsic ecological properties, such as resilience or nestedness.

**Keywords** Alpha diversity · Beta diversity · Gamma diversity · Diversity partitioning · Hill index

In a recent *Views and Comments*, Hanna Tuomisto (2010) made substantial contributions to our understanding of biological diversity. Her pigeonholing metaphor provided a heuristic way of conceptualizing species diversity (Lakoff and Johnson 1980; Walker 2001; cf. Cachelin et al. 2010). Tuomisto assiduously highlighted the essential distinction between defining and measuring diversity, a distinction that is muddled in many areas of organismal biology (Wagner et al. 1998; Wagner 2010). Yet Tuomisto failed to emphasize that “the meaning of a theoretical concept does

not derive from its ‘definition’ (explanation) but from its status and use in the context of a theory and the associated experimental practice.” (Wagner 2010: 1359). In other words, any best measure of diversity will depend upon context, especially what specific biological question we are trying to answer. For instance, even though biodiversity and net primary productivity may be inextricably related (Tilman et al. 1996), neither is usually considered a surrogate for the other. Here, I expand on critiques of a single (universal) best measure of diversity expounded by Norton (1994) and Hoffmann and Hoffmann (2008), then suggest what value-added other definitions and measures of diversity might provide, and thereby advocate pluralism in defining and measuring biodiversity.

Biodiversity indices aggregate data and, in so doing, capture certain nuances of an ecological system, while smoothing over other nuances that we hopefully are not asking about. For example, ecosystem health and ecosystem services provide additional layers (Daily 1997)—layers beyond simply measuring alpha, beta, or gamma diversity—upon which we may want to quantify biodiversity (Norton 1994). Likewise, epidemiologists may ask whether there is diversity amongst different races of humans in the incidence of cancer (assuming races are real entities, which I do not). In the United States, cancer data are available per county, race, and type of cancer. Applying Tuomisto's framework, species would be equivalent to races and abundances equivalent to number of cancer cases per race per county. Yet, cancer epidemiologists do not invoke Tuomisto's indices of choice, the Hill indices  ${}^qD = \left( \sum_{i=1}^S p_i^q \right)^{1/(1-q)}$ , because they aggregate (i.e. eliminate) interesting variation, especially geographic variation near toxic hotspots. Simple graphical analysis (see Tufte 1983) provides a much richer portrait of both pattern and

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probable process of cancer diversity. Using Tuomisto's metaphor, two geographically adjacent counties may reside in different pigeonholes. Furthermore, phylogeny is not accounted for in measures of species diversity using entropy, including  ${}^qD$  (Rao 1982). This is why phylogenetic comparative methods exist (Felsenstein 1985; Garland et al. 1992; Martins and Hansen 1997). The Hill indices do not account for either geographic or phylogenetic structure, therefore, when either matter, it would be wise to invoke a different measure of diversity. The one fundamental disagreement that Tuomisto have is whether choice of species diversity index should depend upon the ecological question being asked.

Calling a diversity index 'true diversity' implies all other diversity indices are false. This is much like Ernst Mayr's coup of coining the term 'biological species concept', thereby implying that all other species concepts are somehow not biological, although some of them are quite reasonable, such as morphological, phylogenetic and evolutionary species concepts. While the term 'true diversity' is due to Lou Jost (2006), Tuomisto actively promotes this nomenclature and thereby inadvertently demeans other diversity indices without justification and without a specific biological question to be answered. The diversity index  ${}^qD$  used by Tuomisto and Jost should probably be called something less loaded, such as the Hill indices (Hill 1973) or, as a reviewer wisely suggested, 'effective species diversity'.

Tuomisto (2010) claims that, because there is a single unambiguous definition of geometric volume, there should also be a single unambiguous definition of species diversity. That premise is wrong insofar as Tuomisto chose to discuss definitions and measurement of volumes of a sphere. Ever since the famed Banach–Tarski decomposition (Banach and Tarski 1924), we have known that geometric volume, or even area, cannot be unambiguously defined. If mathematicians have not yet worked their way out of this conundrum to universally define area or volume, what chance do ecologists have to universally define species diversity? Such findings convince me to be a pluralist and even anarchist (sensu Feyerabend 1975) when it comes to devising and playing with multiple measures of species diversity.

Curiously, Tuomisto's true diversity,  ${}^qD$ , is not a single index, but rather a family of infinitely many diversity indices, indexed by the parameter  $q$ . Which value of  $q$  yields true diversity? For a single set of empirical data, can there exist uncountably many different values of true diversity, without making a mockery of the moniker 'true'? Allowing for an arbitrary value of  $q$  injects a modicum of pluralism into this approach. I really like this because I am a pluralist when it comes to measuring diversity. But it is

not obvious why advocates of  ${}^qD$  do not consider this to be too much pluralism. Whether rightly or wrongly, several other ecologists have at least argued for optimizing  $q$ , thereby having a single diversity index (Mendes et al. 2008).

Several diversity indices, such as square of coefficient of variation and its modifications (Martin and Gray 1971; Williams and O'Reilly 1998; Gorelick and Bertram 2007), do not arise from the Hill indices,  ${}^qD$ , nor from entropy-based methods. Yet these other diversity indices, such as coefficient of variation, have strong theoretical foundations and therefore should not be summarily dismissed as false diversity. Instead, they may provide viable measures of species diversity. Square of coefficient of variation equals variance divided by the square of the mean—dividing by the mean makes coefficient of variation scale-free. While there have been criticisms of coefficient of variation, e.g. it is sensitive to affine transformations and sample size (Bedeian and Mossholder 2000), sensitivities exist for anything but sufficient statistics. The square of coefficient of variation was devised as a way to measure hiring diversity amongst different sexes or races in different departments in a company. This was meant to insure more than just token diversity (Gorelick and Bertram 2010). This is essentially the same goal as measuring effective species diversity.

Why might someone use a different measure of species diversity than the one advocated by Tuomisto, Jost, and Hill, such as 'entropy-based diversity', 'probability-based diversity' and 'variance-based diversity' (sensu Moreno and Rodríguez 2011), even without caring about geographic or phylogenetic structure? Consider a framework with null models that yield expected values of random variables, in which we later collect observed values (instantiations) of these variables. A standard tack is to somehow compare observed with expected values, e.g. with Chi-square tests. The beauty of Shannon's index [which can be expressed as  $\log({}^1D)$ ] and square of coefficient of variation is that both arise naturally as weighted means of observed-divided-by-expected values of a vector, matrix, or higher-dimensional array (Reardon and Firebaugh 2002; Gorelick and Bertram 2010), thereby removing arbitrariness from these measures of species diversity. Shannon's index arises when observed-over-expected, which I designate by  $x$  in the following algebraic expressions, is weighted by  $x \cdot \log(x)$ . Square of coefficient of variation arises when observed-over-expected is weighted by  $(x - 1)^2$ , i.e. Euclidean distance from one. In both instances, the weighting equals zero when observed equals expected, which is sensible. The farther the observed value is from expected, the larger the magnitude of the weighting, as we also see with Chi-squared tests. The antithetical

fact arises that  $x \cdot \log(x)$  is negative when observed is less than expected and positive when observed is greater than expected, but this arises because Shannon's index  $H = -\sum x \cdot \log(x)$  was only designed for  $0 \leq x \leq 1$  (Boltzmann 1872; Shannon 1948), not for  $0 \leq x < \infty$ . An added benefit of using weighted means of observed-over-expected is that the weightings can be generalized to values that are always non-negative, such as  $|x \cdot \log(x)|$ ,  $|x - 1|$ ,  $|x - 1|^3$ , and  $(x - 1)^4$ , which each equal zero when observed equals expected ( $x = 1$ ) (Gorelick and Bertram 2010). Note, while  $|x \cdot \log(x)|$  is always positive (a good thing), its value increases as  $x$  goes from zero to  $1/e$  (a very peculiar thing). The family of weightings  $|x - 1|^n$ , where  $n > 0$ , has no such problems, with local and global minima at  $x = 1$ . Thus, modifications of coefficient of variation may be more sensible than entropy-based indices, including the Hill indices  ${}^qD$ , at least if we measure diversity by comparing observed with expected species abundances.

There are other advantages to using variance-based measures of diversity, such as coefficient of variation. Tuomisto (2010) and Jost (2006) chose the Hill indices because they insisted that gamma diversity be completely decomposable into alpha and beta diversity. While this decomposability simplifies the world, it does so at a cost. Consider decomposing variance of the joint distribution of two random variables,  $x$  and  $y$ ,  $\text{Var}(x, y) = \text{Var}(x) + \text{Var}(y) - 2\text{Cov}(x, y)$ . The covariance represents the non-decomposable piece, although suitable change of coordinates (spectral decomposition) can sometimes—but not always—render the covariance zero (Strang 1976). While there are other conceivable ways to decompose  $\text{Var}(x, y)$ , we usually insist that the parts have the same general structure as the quantity being decomposed. Thus, mutual entropy can be decomposed into marginal entropy and conditional entropy, with all three terms being some form of entropy. Evolutionary geneticists have a similar conundrum with genetic variance due to two or more genes, which can be decomposed into the sum of additive genetic variance due to each individual gene plus a non-decomposable variance known as epistasis. The non-decomposable piece—either covariance or conditional entropy or epistasis—tells us something interesting about the system. Could the same be true for decomposing gamma diversity? By requiring that gamma diversity be completely decomposable into alpha and beta diversity, are we neglecting an important non-decomposable piece of gamma diversity? Might this non-decomposable component of species diversity represent an emergent property of the system, such as ecological resilience, especially panarchy (Holling 2001; Walker et al. 2004), or ecosystem nestedness (Bascompte et al. 2003)? For measuring sociological diversity, where the independent variables

are race/sex and job descriptions, could this non-decomposable piece represent important and intrinsic social/organizational structure, which could again include nestedness? Could existence of covariance provide justification for using coefficient of variation as the measure of diversity, instead of the Hill indices,  ${}^qD$ ? The answer may be yes, depending on the biological question being asked. Imposition of complete decomposability is akin to imposition of the parallel postulate in classical geometry: sensible, sometimes useful, but too constraining, hiding many wonderful alternatives (Lobachevski 1840). If we care about non-decomposable interactions when measuring species diversity, then the Hill indices,  ${}^qD$ , are not true diversity because they can never measure important holistic aspects of ecosystems.

Tuomisto (2010) has written a lovely paper with much to offer; a paper that deserves to be well read and well cited. She superbly differentiated definition and measurement, seamlessly explicated a pigeonholing metaphor, and elegantly explained the derivation of  ${}^qD$ . I only object to her invocation of a single best index of true diversity for all questions of species diversity and especially object to the reason she invoked it, i.e. decomposability of gamma diversity. Indeed, I can do little better than quote from her utterly sensible concluding paragraph (Tuomisto 2010: 860):

“Making an informed choice of index for a particular study necessitates an understanding of which aspect of the data indices quantify, and which of them corresponds to what is needed to answer the ecological questions of interest.”

The fundamental disagreement that Tuomisto and I have is whether or not different methodologies should be invoked depending upon which biological questions are being asked. I have argued here that diversity indices should be chosen based on the specific ecological question being addressed, with no best nor true diversity index (Norton 1994; Hoffmann and Hoffmann 2008), especially if we wish to not sweep under the proverbial rug geographic structure, phylogenetic structure, nestedness, and non-decomposability. I suspect that ecology will more readily mature as a science if we have many ways of decomposing total (gamma) diversity. At the same time, I advocate borrowing tools from other fields that are asking isomorphic questions, such as sometimes using measures of human employment diversity for measuring species diversity, especially when both are trying to elucidate the effective number of species/sexes/races. Tuomisto and I both have the best interests of ecology at heart. However, I advocate pluralism, stopping the diversity index wars (Grusky and Charles 1998), and choosing the tools that make most sense to answer a given biological question,

appreciating emergent properties that may arise from non-decomposability.

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