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Musings on the Acropolis: Terminology for biogeography

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Abstract. Biogeography, like all science, is better served when its vocabulary usage is precise, organized and simple. In this light, I examine three intertwined sets of concepts concerning scale and diversity. First, I show how 'scale' consists of four components: sampling unit, grain, focus and extent. Using those more precise terms prevents potential ambiguities in communication. I also clear up a confusion in the usage of 'focus' that I promulgated in an earlier paper. Second, I explain how organizing our concepts concerning species richness relationships both disambiguates those concepts and leads to the development of new theories. Third, I explore the multitudinous ideas and terms that have collected under the general concept of 'diversity' and propose one scheme for simplifying current confusions. Biogeography is in a period of unification of its disparate threads of ecology, phylogeography and phylogenetics. In weaving together concepts of scale and diversity, I hope that this essay contributes to that unification.

"Rhetoric is the art of ruling the minds of men." (Plato)

Introduction

"Sticks and stones may break my bones, but words will never hurt me." (Child's rhyme)

On the contrary, words matter. They solidify concepts and ensure accurate communication. Improperly used, they can obscure and sow confusion. Ecologists are notorious for inventing complex lexicons, although we are probably no worse in this regard than many other disciplines and professions. Sometimes those lexicons make meanings precise, but only if used properly. My purpose here is to examine three intertwined sets of concepts concerning scale and diversity, with a goal of making our vocabulary usage more precise, organized and simplified.

While none of this is new, our continued misuse of terminology bears its repetition. This essay was conceived while at the Fifth International Biogeography Society meeting in Crete, listening to the talks and their misuses and ambiguities of rhetoric. Having come down with the 'flu a short time later, I spent an entire day in my hotel room writing this paper while gazing up at the Acropolis, hence the title of this piece. It is a hom-

age to those ancient Greek philosophers who gave us the foundations of our sciences.

More precise vocabulary

"It is the mark of an educated man to look for precision in each class of things just so far as the nature of the subject admits; it is evidently equally foolish to accept probable reasoning from a mathematician and to demand from a rhetorician scientific proofs." (Aristotle, Nicomachean Ethics)

Biogeography deals with patterns and processes that vary in time and space from seconds to epochs and micrometers to the entire globe. In referring to these ranges of time and space, we make one of the most common vocabulary errors in our discipline by talking about differences in 'scale.' Because 'scale' has multiple components (Table 1A), the use of the word 'scale' is often imprecise (Dungan et al. 2002). Most often what is meant is 'extent' – as in, "Studies at landscape and continental scales" – and this meaning is usually, but not always, obvious in context. The other frequent meaning of 'scale' is 'grain.' It is here that the use of 'scale' can sow confusion.

Consider the following: "The accuracy of species richness data differs when compiled at landscape and continental scales." That sentence

A.

Extent: the coarsest spatial or temporal dimensions that encompass all of the sampling units

Focus: the dimensions of the aggregated or summed grains

Grain: the dimensions to which data are standardized before analysis, often equal to the area, volume, or duration of the sampling unit

Sampling unit: the spatial and/or temporal dimensions of the collection unit

B.

Inventory diversity: the abundance of named objects in a specified unit or set of units

Differentiation diversity: how the composition of named objects differs among groups, i.e. units or sets of units

Pattern diversity: variation in the arrangement of groups of named objects in physical or mathematical space

Table 1. (A) The four components of scale. **(B)** The three classes of diversity; typically the objects under consideration are biological species. (Modified from Scheiner 1992; Scheiner et al. 2000).

could refer to the basic unit of analysis – the grain – or it may refer to the entire study – the extent. The causes of data inaccuracy that are being referred to in that sentence differ depending on which scale component is meant. If grain is meant, the sentence is contrasting plots within a single landscape that are typically very accurate as opposed to range maps interpolated over a latitudinal and longitudinal grid that are typically inaccurate for a given grid cell. If extent is meant, then the sentence is contrasting the less than complete coverage of plots within a landscape and the resulting inaccurate extrapolation from the samples to the entire landscape as opposed to the more accurate estimate of the total species richness of an entire continent using summed range maps. So, which of those two scales has less accurate data depends on whether one means grain or extent. Of course different particulars of data collection would alter that outcome, but you get my point.

Once we deal with data collection, two other scale components become relevant, focus and sampling unit. These components are rarely acknowledged and are typically unrecognized. We usually learn about scale by being presented with an area that has been completely gridded and sampled so that the focus is the same as the extent and the sampling unit is the same as the grain, thereby subsuming distinct concepts. In-

stead, consider an area incompletely sampled with plots and subplots; the data are averaged over subplots so that the plot is the unit of analysis (Fig. 1). Now the four scale components all differ.

A common failure is confusing focus with extent. Consider the following: "The relationship between productivity and diversity differs with the scale of the study." That sentence could mean that the relationship changes when the extent changes from landscapes to continents, or it could mean that within a single extent, the relationship changes with increasing numbers of plots – the focus. [That sentence could also be referring to differences in grain, yet a different ambiguity.] This example may seem contrived, but I recently ran into just this type of ambiguity in a manuscript that I reviewed that was examining the effects of scale components on richness estimates. Varying grain, focus and extent all had different effects that the authors would confound by speaking of the effects of scale.

Finally, I make a *mea culpa*. When we (Scheiner et al. 2000) first defined 'focus' and contrasted it with 'extent,' our definition of the latter was the same as in Table 1A, but our usage in a hierarchical setting (e.g., Fig. 4 in Scheiner et al. 2000) confounded 'focus' with 'extent'. To understand this more complex aspect of focus, consider the following instance. Assume that the sampling

units in Fig. 1 are 1/4 m^2 so that the grain is 1 m^2. From these samples we calculate the mean species richness of the 15 plots. Next, we take that mean value and aggregate it with 10 other samples (say different fields scattered across a landscape) and calculate the total species richness of those data. In that landscape-level analysis, the data that make up each data point have a grain (1 m^2) and a focus (15 m^2), but the total set of data points also has a grain (1 m^2) and a focus (10 m^2). Thus, the grain and the focus of the individual data points and the aggregate data will change as the data are manipulated. Separating these scale concepts allows better communication of these manipulations. In that previous paper we, unfortunately, used 'extent' when referring to the focus of the analysis at the landscape level. It was only because a co-author of a recent paper (Scheiner et al. 2011) pointed out inconsistencies in my use of those terms that I saw the discrepancy in the original usage and the confusion that I had caused.

More organized vocabulary

"The chief forms of beauty are order and symmetry and definiteness, which the mathematical sciences demonstrate in a special degree." (Aristotle, Metaphysics)

A fundamental relationship in ecology is that between species richness and the focus over space or time that it is measured. This relationship was originally termed a 'species–area curve', and that is probably the most frequently used phrase, although 'species–area relationship' is also common. Several years ago (Scheiner 2003), I pointed out that this single phrase referred to a multiplicity of types of relationships differing in sampling scheme, mode of aggregation and meaning of sampling units. I attempted to tame this confusion by organizing the relationships into a typology (Table 2), which to my surprise set off a debate about which was the true species–area curve (Scheiner 2003, 2004, 2009, Gray et al. 2004a, 2004b, Dengler 2009). This is not the place to rehash that debate; see those papers and Scheiner et al. (2011) for details. From that debate, however, we can draw three lessons.

The first lesson is the importance of organizing our vocabulary. Before I proposed my typology, the multiplicity of relationships hiding within a single concept was not clearly recognized. There is emerging evidence that the form of the relationship differs in a regular way between Type IV curves and Type II and III curves (Stiles and Scheiner 2007, Chiarucci et al. 2009, Williams et al. 2009, K.A. Triantis, F. Guilhaumon & R.J. Whittaker, unpublished) in part because the different types of curves are based on different diversity metrics (Tuomisto 2010c). Having a clear way to refer to these types makes easier such discoveries.

The second lesson is the importance of words in guiding our thoughts. The problem with
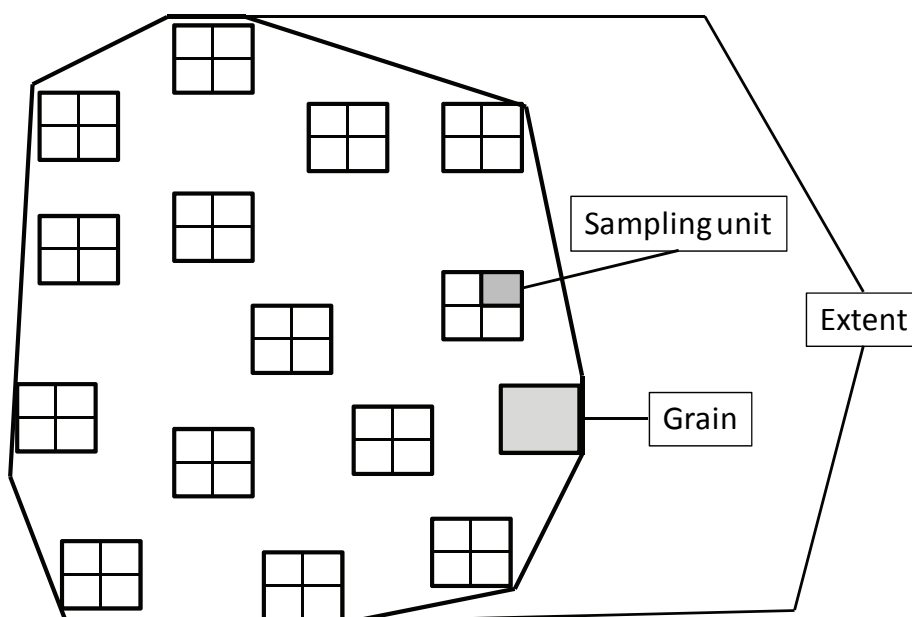

Figure 1. A sampling and analysis scheme that demonstrates the four components of scale. The data consist of surveys from an area that is sampled with scattered plots, each plot containing four subplots. The data from the subplots are aggregated at the plot level for analysis. The entire area is the extent, the sum of the sampled areas is the focus, the area of a plot is the grain, and the subplot is the sampling unit.

Type	Sampling scheme	Species density (species richness per unit area)	Construction spatially explicit	Grain	Focus	Extent
I	Nested	The number of species in a contiguous sample unit of specified size	Yes	A sample unit nested within the larger or longer one	Same as the grain	The largest or longest sampling unit
IIA	Contiguous	The number of species in a contiguous sample unit of specified size	Yes	One or more adjacent sampling units	The cumulative area or time of all sampling units	Same as the focus
IIB	Contiguous	The number of species in an aggregated sample unit of specified size	No	One or more aggregated sampling units	The cumulative area or time of all sampling units	Same as the focus
IIIA	Non-contiguous	The number of species in an aggregated sample unit of specified size	Yes	One or more neighbouring sampling units	The cumulative area or time of all sampling units	The maximum distance or time among sampling units
IIIB	Non-contiguous	The number of species in an aggregated sample unit of specified size	No	One or more aggregated sampling units	The cumulative area or time of all sampling units	The maximum distance or time among sampling units
IV	Independent units	The estimated number of species in a sample of a specified size	No	Independent space or time units	The cumulative area or time of all sampling units	The maximum distance or time among sampling units

Table 2. The six types of species richness relationships with a description of their features and scale parameters. See Table 1 for definitions of the scale components. From Scheiner et al. (2011).

the term 'species–area curve' is that the relationship could just as easily be over volume or time and 'species' is ambiguous in that it does not indicate what property of species is being measured. We (Scheiner et al. 2011) proposed substituting 'species richness relationship' (SRR), placing the emphasis on, and making explicit, the dependent variable. Although area is far and away the most common independent variable, by using our suggested term we will no longer automatically think of these relationships exclusively in terms of area. We recognize that doing so leaves the independent variable in the relationship unstated; see Scheiner et al. (2011) for a detailed explanation for this choice of terminology.

The third, and most important, lesson is that vocabulary is the precursor to concepts that are in turn the gateway to theory. Ecology is awash in theory (Scheiner and Willig 2011b), but ecologists often fail to recognize these linkages and relationships and the resulting conceptual framework. One way to arrive at such a framework is to recognize that highly specific theories (termed 'models' in our schema) can be unified under more general theories (termed 'constitutive theories') (Scheiner and Willig 2008, 2011a). Constitutive theories are a set of propositions that act as an instruction set for building models. Formulating those propositions requires one to think deeply about the processes underlying the object of one's models. In Table 3, I codify a constitutive theory of Type II and Type III SRRs based on the set of processes outlined in Scheiner et al. (2011). [A separate theory of Type IV SRRs can be built from the equilibrium theory of island biogeography (Sax and Gaines 2011, K.A. Triantis, F. Guilhaumon & R.J. Whittaker, unpublished).] I leave to others the task of relating this theory to the current multitude of SRR models. Such an endeavour will not only help organize and synthesize those

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Domain: Type II and III SRRs. The sampling units can be over space or time. The units can be contiguous or noncontiguous. The process of aggregation may or may not account for the spatial or temporal relationships of the sampling units.

Assumption: The system is at equilibrium.

Propositions for all Type II and III SRRs

1. As sampling increases to include more space or time, the number of individuals sampled may increase.
2. More individuals lead to more species.
3. As sampling increases to include more space or time, more environmental variation may be encountered.
4. If all individuals of all species are uniformly distributed, and if the sampling unit is smaller than the mean distance between individuals, then the SRR will have a positive relationship between space or time and species richness.
5. If the sampling regime encompasses large areas or long time durations, then those samples may derive from multiple species pools.

Additional propositions for spatially explicit or temporally explicit SRRs

6. Clustering in space or time of individuals of the same species will increase the rate at which species richness increases over space or time.
7. Competition can create overdispersed distributions. Such distributions will decrease the rate at which species richness changes over space or time.
8. The inclusion of multiple species pools will increase the rate at which species richness increases over space or time.

Table 3. The domain, assumption, and propositions of a constitutive theory of species richness relationships (SRRs) built from the continual aggregation of sampling units (Types II and III). See Scheiner *et al.* (2011) for a full explanation and justification of the propositions.

models clarifying assumptions and mechanisms, it will highlight other models not yet considered.

More simplified vocabulary

> "Beauty of style and harmony and grace and good rhythm depend on simplicity." (Plato, The Republic)

Metrics are to concepts as models are to constitutive theories. A single concept can be quantified with many metrics. Therefore, using the same word for both a concept and one of its many metrics sows confusion. We see this confusion with the concept of diversity. Blame, if such be given, needs be laid at the feet of Robert H. Whittaker, who codified diversity concepts while simultaneously using the same word for multiple metrics (Whittaker 1960), further leading us into the morass over the next decade and a half (Whittaker 1972, 1977). Thankfully, he also gave us a terminology to lead us out of that swamp.

The key is to divide diversity into three broad concepts: inventory diversity, differentiation diversity and pattern diversity (Table 1B). The first two terms were coined by Whittaker (1972), and the third by myself (Scheiner 1992), generalizing a concept first put forth by Pielou (1966). Calls for the use of this terminology have been made repeatedly (e.g. Scheiner 1992, Whittaker et al. 2001, Jurasinski et al. 2009), and done again here. One benefit of doing so is the recognition that the three diversity classes are related through a single, hierarchical framework [see Fig. 1 in both Tuomisto (2006) and Tuomisto (2010c)].

Inventory diversity, the first level of the hierarchy, is the least contentious. It consists of metrics such as species richness and the Shannon–Weiner index. However, we also have a dilemma. One way to quantify inventory diversity is by the use of numbers equivalents (Hill 1973):

where S is the number of species, p_i is the frequency of the ith species, and q is a parameter

$$^{q}D = \left(\sum_{i=1}^{S} p_i^q \right)^{1/(1-q)}$$

that determines how species frequencies are weighed. When q = 0, ^{q}D is species richness. When q = 1, log (^{q}D) is the Shannon–Weiner index. When q = 2, ^{q}D is the inverse Simpson's index.

The dilemma is that ^{q}D is called 'diversity', yet it is just one metric of inventory diversity. To further muddy the waters, diversity is the product of species richness and evenness, the extent to which the species within a sample have equal abundances. Diversity (measured as ^{q}D), richness and evenness are all components of inventory diversity. So, why should one component be privileged with the name 'diversity'?

I have no real solution. The use of 'diversity' to reference ^{q}D and its cognates is too deeply entrenched. Ecologists have only recently moved on a regular basis to using 'species richness' (or 'richness') to distinguish that concept. All that I can offer to thread this needle is to recognize two concepts: 'diversity *sensu lato*' and 'diversity *sensu strictu*'. The former is the general idea of diversity that includes all of the various types (Table 1B) as subcategories; the latter is ^{q}D. We would not actually want to use such awkward terminology, but it would allow us to be precise about which aspect of diversity we meant if not otherwise obvious from context.

We can simplify terminology related to diversity in one respect. Whittaker proposed a hierarchy of inventory diversity – point, α, γ, ε – depending on the extent of the sample. The problem is that those extents are vague and have been used in various ways or to mean different extents (e.g. Cody 1975, Shmida and Wilson 1985, Currie and Paquin 1987, O'Brien 1993, Whittaker et al. 2001) so that they no longer convey precise meaning. Hanna Tuomisto (2010a) wisely collapsed those into just two concepts. γ-diversity is the inventory diversity of a given sample, whatever the focus of that sample. α-diversity is the mean inventory diversity of a set of subsamples at a specified grain within a sample, again independent of any particular length, area, volume or duration. Used in this fashion, the researcher must specify the actual dimensions of any particular set of measurements, ensuring clear communication.

Differentiation diversity is the second level of the hierarchy. Rather than a dilemma, here we have a controversy; one however, that contains its own solution. The controversy comes from

Whittaker (1960) defining β-diversity five different ways, while using the same term and symbol for all of them. Which of those versions had ascendency has waxed and waned over the years. A reviewer of the manuscript that became Scheiner (1992) insisted that I was wrong in claiming that Whittaker had defined β-diversity as the mean similarity of a set of samples; in my reply I had to quote the actual sentence from Whittaker (1972). That reviewer insisted that β-diversity was species turnover along a gradient, the prevailing concept in the 1970s and 1980s.

Today the argument is over whether the relationship between γ-diversity, α-diversity and β-diversity should be multiplicative ($D_\gamma = D_\alpha * D_\beta$) (Whittaker 1960, Jost 2006, 2007, Baselga 2010, Tuomisto 2010b) or additive ($D_\gamma = D_\alpha + D_\beta$) (MacArthur et al. 1966, Lande 1996, Crist et al. 2003, Veech and Crist 2010). The virtue of the multiplicative relationship is that it leads to D_β being the numbers equivalent of samples or communities. So, $D_\gamma = D_\alpha * D_\beta$ is interpreted as the total diversity of a set of samples (D_γ) being equal to the mean diversity per unit (D_α) times the number (equivalent) of units (D_β). Tuomisto (2010b) nicely shows the mathematical relationships among all of the concepts labelled β-diversity by Whittaker, listing some 30 different names.

We can simplify our discussion by using 'differentiation diversity' when referring to the entire concept of species variation among units, and be specific in words and symbols when referring to a particular metric (Table 2 of Tuomisto 2010b). A further reason for using the multiplicative formulation is that it leads to a simple unification of other concepts within inventory diversity – richness and evenness – with differentiation diversity (Tuomisto 2010a, pers. comm.).

Pattern diversity is the final level of the hierarchy and is the easiest to deal with because it has attracted the least attention. This concept has been labeled level-of-abstraction 3 (Tuomisto and Ruokolainen 2006) and proportional diversity (Arita et al. 2008). Currently there are few metrics, the most well known belonging to one class – nestedness (e.g. Patterson and Atmar 1986, Wright and Reeves 1992, Cook and Quinn 1998,

Wright et al. 1998). The particular metric I put forth in Scheiner (1992) – mosaic diversity – has never been further developed and is probably inferior to more recent ones (Tuomisto and Ruokolainen 2006, Arita et al. 2008). Most important is to recognize a single, unified concept, whatever its name, to clearly separate current and future metrics, and to develop a unified theory from which we can draw a better understanding of that concept.

Conclusion

"Rhetoric, it seems, is a producer of persuasion for belief, not for instruction in the matter of right and wrong ." (Plato, Gorgias)

According to Homer, the Trojan War began when Eris, the goddess of strife, tossed the golden apple amidst the gods saying, "For the most beautiful one." I hope that my offering here is not such an object of discord. My goal here is not to provoke, but rather to show how a more precise, organized and simplified vocabulary can prevent confusion and advance the science of biogeography. Unification of ideas into theories begins with clarity of terminology. The building of the Parthenon on the Acropolis and the golden age of Greek philosophy occurred after the Greek city-states set aside their antagonisms and united to defeat the Persian invasion. Biogeography is seeing a similar golden age with the current unification of its disparate threads of ecology, phylogeography and phylogenetics. In weaving together concepts of scale and diversity, I hope that this essay contributes to that unification and that I am not judged to have corrupted the youth of biogeography and forced to drink from Socrates' cup.

Acknowledgements

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