

METHOD

The units of biodiversity

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Abstract

Biodiversity is a central concept in ecology and biology. Its underpinnings are multifaceted and complex and involve multiple spatiotemporal scales, and many ways of measuring relevant characteristics. Its comprehensive understanding requires a framework on which to organize concepts and associated metrics. The analysis of biodiversity is based on combinations of two types of units: study units (i.e., the inferential domain in time and space that characterizes sampling) and measurement units (i.e., metrics). We provide an integrated framework for the units of study derived from three aspects of organisms: their spatiotemporal relationships (geography), their evolutionary relationships (phylogeny), and their ecological relationships based on their requirements and effects (niche). We systematize the units of measurement based on four types of data (identity, abundance, phylogeny, traits), two properties of those data (magnitude and variability), and three approaches for their measurement (total, pairwise, nearest neighbor). Together, they define 14 basic elements that can be combined in many ways and be subject to various mathematical operations. The result is 130 different metrics, including those in the literature and those developed herein. We propose standardized symbols for these metrics and provide formulas using standard notations for their parameters. Importantly, we show how our framework can be used to align study units and measurement units with questions concerning the causes and consequences of biodiversity. We provide case studies on bats in Peru and trees in the eastern United States to ecological gradient theory, niche theory, and theory about relationships between biodiversity and productivity, and we discuss which metrics might be most appropriate in tests of island biogeography theory and the dilution effect of pathogen transmission. Our key recommendations are that researchers should: (1) harmonize study unit properties with explicitly defined questions, (2) couple metric properties with underlying processes, and (3) compare metrics with similar properties. By providing an overarching framework that clearly delineates units of study and units of measurement, we hope to ensure that appropriate data are applied to particular scientific questions, especially those of a comparative nature, thereby leading to robust conclusions of theoretical import or practical use in management or conservation.

KEY WORDS

assemblage, biodiversity, dispersion, divergence, ensemble, equability, functional trait diversity, local guild, phylogenetic diversity, regularity, taxonomic guild

INTRODUCTION

Much of science involves the quantification of patterns and processes as a prelude to understanding their causes and predicting future states. What we measure, how we measure it, and the scale at which we measure it combine to constrain our observations, the identification of their causes, and ultimately higher-level understanding. By necessity, ecology is rife with measurements and involves the continued pursuit of more accurate, effective, and useful quantifications of complex aspects of the natural world. In ecology, utility typically comes from two intertwined goals: a better understanding of the causes of ecological patterns and the use of that understanding to better manage the world's resources. Biodiversity is of particular concern, as most of the ecosystem services that enable human well-being are derived from biological interactions. We are interested in the mechanistic bases for biodiversity (i.e., how it arises and is maintained, and the identity of processes that lead to its spatiotemporal dynamics), such as ecological and evolutionary patterns or processes, and their consequences for ecosystem or biosphere functionality. Current human-induced rapid environmental changes are threatening our ability to sustainably manage biodiversity so as to provide critical ecosystem services (Willig & Scheiner, 2011). Consequently, understanding patterns of biodiversity is, arguably, a central question in ecology, evolution, and conservation biology (Scheiner & Willig, 2011a).

A necessary task for reaching that understanding is the creation of a comprehensive operational framework on which to organize concepts and associated metrics (Pickett et al., 2007). Although true for understanding any natural system, it is especially critical for biodiversity because its conceptual underpinnings are multifaceted and complex, involve multiple spatiotemporal scales, and are associated with many ways of measuring relevant characteristics. Indeed, a fundamental attribute of ecological patterns is that they can be characterized at multiple, interacting spatial and temporal scales, as well as at different levels of the taxonomic hierarchy.

The urgency of the biodiversity crisis has fueled the recent explosion of proposed metrics to characterize phylogenetic and functional biodiversity (e.g., Mammola et al., 2021; Tucker et al., 2017). This deluge of metrics that attempts to capture related aspects of biodiversity

has prompted our efforts to develop an organizational framework to simplify the task of identifying metrics that match the concepts ecologists, conservation biologists, or natural resource managers endeavor to understand. In tackling this critical need, we address wider issues about the essence of biodiversity and how various concepts that underlie it can be integrated with theories about ecological or evolutionary processes (Scheiner & Willig, 2011b). The analysis of biodiversity is based on combinations of two types of units: study units (i.e., the inferential domain in time and space that characterizes sampling) and measurement units (i.e., metrics). Most of the literature focuses on the latter, with the former relegated to either a brief mention or only implicit consideration. Nonetheless, units of study have multiple aspects, just as do the units of measurement.

A spectrum of metrics is necessary to understand the interrelationships among study units of biodiversity and the mechanisms that give rise to their variation at different spatial and temporal scales. Errors in understanding may arise because of (1) a mismatch, or at least ambiguity, regarding the spatiotemporal scales at which biodiversity is measured and the scales at which generative, dynamic mechanisms operate, (2) the scales at which consequences of biodiversity manifest (Godsoe et al., 2023), or (3) an incongruity between what a metric measures and the concept researchers are attempting to understand. An explicit and comprehensive framework reduces these ambiguities, invites closer scrutiny, and guides future research. In particular, synthetic analyses will be facilitated by the use of a common framework of concepts and metrics.

This article is organized into three sections. In the first, we provide a framework for the units of study. In the second, we systematize the units of measurement. The alignment of both kinds of units to theories to test hypotheses is critical for framing particular questions and for guiding approaches for answering them. In the third, we present five case studies to demonstrate how these frameworks can be used to align study units and measurement units with ecological or evolutionary questions concerning the causes and consequences of biodiversity. We use a set of ecological or evolutionary questions as examples to demonstrate how to select the appropriate units of study and units of measurement to effectively address these questions (Table 1, Box 1). These examples are meant to be illustrative, not

TABLE 1 Examples of ecological and evolutionary questions, how they could be addressed by different units of study or units of measurement, and related theoretical and empirical publications.

Question	Units of study	Units of measurement	Theory	Empirical example
1. How do various components of biodiversity vary along environmental gradients?	Ensemble	Species richness, abundance variation, pairwise phylogenetic diversity, pairwise functional trait diversity	Fox et al. (2011)	Scheiner et al. (2017a) (Case study 1)
2. How does competition shape trait diversity in communities?	Ensemble	Abundance combined with nearest-neighbor functional trait variation	Hutchinson (1959)	Istock (1966) (Case study 2)
3. Is community invasibility related to overall biodiversity or competitive interactions?	Local guild	Species richness, abundance variation, abundance combined with nearest-neighbor functional trait variation	Elton (1958)	Tilman (1997)
4. What are the causes for the relationship between productivity and biodiversity?	Local guild	Species richness, nearest-neighbor functional trait diversity	Naeem et al. (2012)	Liu et al. (2024) (Case study 3)
5. Does host biodiversity affect pathogen abundance and transmission?	Local guild	Species richness combined with abundance variation and total function trait variation	Ostfeld and Keesing (2000)	Keesing and Ostfeld (2021) (Case study 5)
6. Do the magnitude or variability in functional traits affect temporal dynamics of communities?	Assemblage	Abundance magnitude, total functional trait diversity	May (1973)	McGrady-Steed and Morin (2000)
7. Is species filtering from regional species pools to local communities affected more by phylogenetic relationships or functional traits?	Assemblage	Nearest-neighbor magnitude phylogenetic diversity, nearest-neighbor magnitude functional trait diversity	Weiher and Keddy (1995)	Marteinsdóttir and Eriksson (2013)
8. Are global hotspots of biodiversity congruent for species richness, phylogenetic diversity, and functional trait diversity?	Assemblage	Species richness, total magnitude phylogenetic diversity, total magnitude functional trait diversity	Davies and Cadotte (2011)	Qian et al. (2023)
9. How does the pattern of biodiversity change over island existence?	Assemblage	Species richness combined with total phylogenetic diversity	Whittaker et al. (2008)	Weigelt et al. (2016) (Case study 4)
10. How does the pattern of biodiversity change during island colonization?	Community	Species richness combined with total functional trait diversity	MacArthur and Wilson (1967)	Simberloff and Wilson (1970)
11. Is phylogenetic diversity a good proxy for functional trait diversity?	Taxonomic guild	Total phylogenetic diversity, total functional trait diversity	Blomberg et al. (2003)	Pavoine et al. (2013)

definitive or exhaustive. The outcome of this effort is three primary recommendations:

1. For study units, it is important to understand their spatial, temporal, and biological properties so that they match the question being addressed.

- For measurement units, it is important that the properties of metrics match the processes under study.
- When comparing metrics that are based on different types of data, it is important that their properties and measurement methods are in alignment so that like is being compared to like.

BOX 1 Glossary

Abundance: the representation of a species in a sampling unit based on the number of individuals, biomass, cover, or similar measures.

Assemblage: a group of related organisms living in the same place.

Alpha diversity: mean biodiversity (variability) measured at a specified grain within a focus.

Beta diversity: the effective number of units within a focus; differences in unit composition along an environmental gradient or among units in a landscape.

Biodiversity: the spatial, temporal, and/or compositional makeup of the individuals, populations, species, and/or communities in a defined set.

Clade: a group of organisms that consists of a common ancestor and all of its descendants.

Cladogram: a branching treelike diagram showing evolutionary relationships among ancestors and descendants.

Community: a group of populations that coexist in space and time and interact with each other directly or indirectly.

Divergence: the amount of evolutionary differentiation of a particular species from other species in a set.

Dispersion: the difference in functional trait values of a particular species from all other species in a set.

Ensemble: members of a clade that live in the same place and use biotic or abiotic resources in a similar way.

Equability: the extent to which species in a set are equally different from each other in functional trait values.

Evenness: the extent to which the species in a community are equally abundant.

Extent: a component of scale indicating the coarsest spatial or temporal scale that encompasses all of the sampling units.

Focus: a component of scale indicating which grains are aggregated or summed.

Functional group: a set of organisms that uses biotic or abiotic resources in a similar way.

Gamma diversity: total biodiversity (variability) measured at a particular extent.

Grain: a component of scale (resolution) indicating the standardized unit to which all data are adjusted before analysis, often equal to the area or duration of the sampling unit.

Guild: a group of organisms that use biotic or abiotic resources in a similar way, including the environmental conditions within which they can function.

Identity: the category, group, or species to which an organism is assigned.

Local guild: a group of organisms living in the same place that use biotic or abiotic resources in a similar way.

Measurement unit: a metric that captures aspects of biodiversity.

Niche: the range of ecological conditions in which a species will persist.

Numbers: the abundance of a particular species.

Phylogenetic diversity: the extent to which species within a set are closely or distantly related.

Phylogeny: the pattern of relationships among taxa based on evolutionary ancestry.

Realized niche: the environmental range within which a species is found.

Regularity: the extent to which species within a set are equally phylogenetically divergent.

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

Scale: the spatial or ecological context of a set of data, measured as grain, extent, and focus.

Species: a group of organisms given the rank of species; the basic unit of biological classification.

Species density: the number of species per unit area, volume, or duration.

Species richness: the number of species.

Study unit: the inferential domain in space and/or time that characterizes sampling.

Taxon (pl. taxa): a group of organisms that share a common ancestor.

Taxonomic guild: a group of organisms that both share a common ancestor and use biotic or abiotic resources in a similar way.

UNITS OF STUDY

We base our schema for units of study (Figure 1) on three aspects of organisms: their spatiotemporal relationships (geography), their evolutionary relationships (phylogeny), and their relationships with the environment based on their requirements and effects (niche). Another way to think of these aspects is that they address various issues about (1) “where” and “when” (geography), the location and time during which potential interactions between individuals and species occur; (2) “who” (phylogeny), the ancestor–descendant relationships of the interactors; and (3) “what” and “how” (niche), the physiological and ecological processes that determine patterns of interactions. Ultimately, all of these descriptors are used to address theoretical explanations for patterns and processes (issues of “why”). Although we recognize that the study units of biodiversity range from genes to ecosystems to the biosphere, for ease of exposition we only consider the most commonly used units of study in our examples, contemporaneous populations of species that co-occur in space (i.e., a community or its constituent

assemblages, ensembles, or local guilds). Nonetheless, the same schema can be extended in space or time to include units other than species and can be applied to other levels of the biological hierarchy (e.g., genera). Thus, the unit of study can be anything from a few cubic centimeters of soil (e.g., Joergensen & Emmerling, 2006), a 50-ha patch of a tropical forest (e.g., Chave et al., 2003), or the entire globe (e.g., a study of global diversity of parrots, Kosman et al., 2019). The time duration of inference of that unit could be the instance of measurement, a short period of time such as a year or a decade, or a geological age (e.g., Jablonski, 1993). Although any of these can be a unit of study, what is important is that it be explicitly and precisely delimited to ensure that it matches the questions being posed (see case studies in the third section).

Elements of the schema

Our schema derives from that of Fauth et al. (1996). Although our terminology generally follows theirs, we incorporate three modifications. First, we relabel their “resources” as “niche,” which we use in the broadest possible sense to represent all aspects of an organism’s environment. Second, we added “taxonomic guild,” a group of species constrained by resource use and phylogeny (Gurevitch et al., 2021). Third, we use “clade” rather than “taxon” to emphasize that we are referring to monophyletic groups.

Geography concerns the spatial and temporal extent of a unit of study, typically referred to as a community. We focus this geographic extent on local groups of species, as those are the most common units of study and the geographic scale at which many ecological interactions happen. As has been long recognized, the spatial boundaries of a community are arbitrary in practice. Nevertheless, the spatial extent of a community or its constituent units (e.g., guild, ensemble) should be defined by the biology of its species (e.g., the foraging or movement extent of individuals, the distances among mated individuals). As a result, the geographic extent of study units can be different for organisms that differ greatly in size or mobility, such as microbes versus annual plants versus large herbivores.

Phylogeny reflects the evolutionary relationships of species and emerges from considerations of deep time. Just as with the geographic boundaries of a community, the choice of phylogenetic boundaries can be somewhat arbitrary (e.g., whether to restrict considerations to a class, order, or family). Nonetheless, the choice of clade (i.e., phylogenetic boundary) should be explicit and justified based on the nature of tested hypotheses and

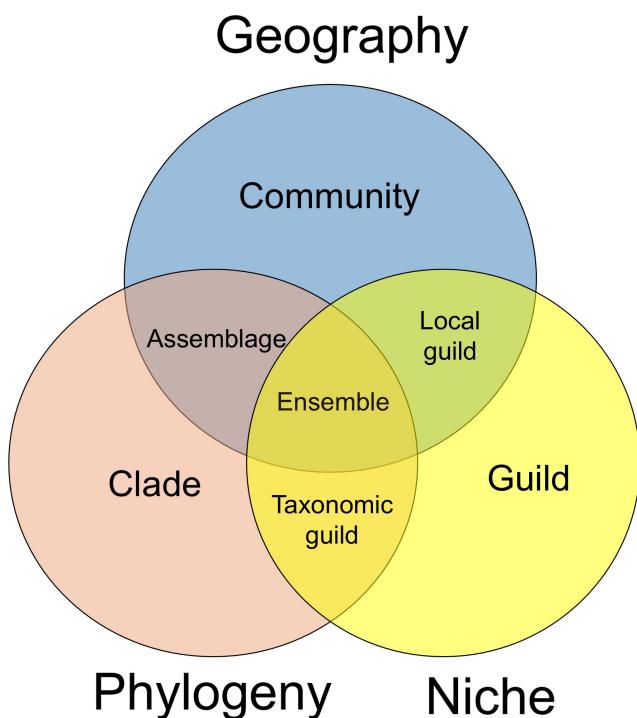


FIGURE 1 A schema of study units based on three aspects of species: their spatiotemporal association (geography), their evolutionary relationships (phylogeny), and their ecological requirements and effects (niche). Each of those aspects defines a different unit of study: community, clade, and guild, respectively. The intersections of those units define additional, more proscribed units that are subsets of two or more larger units. See Box 1 for definitions.

explored mechanisms. For example, different families or subfamilies of bats in the neotropics typically occupy different guilds, which can guide the hierarchical levels one might consider when evaluating hypotheses about functional or phylogenetic biodiversity of this clade (Questions 1, 7, and 8, Case study 1).

The concept of the niche includes consideration of the environmental factors that affect persistence of a species as well as their interactions with competitors, predators, parasites, and mutualists. As with many terms in ecology, niche and guild have a variety of definitions (Blondel, 2003; Chase & Leibold, 2003) and are associated with complementary underlying concepts. Niche space defines the environmental context of a species, whereas a guild reflects the functional role of a species (i.e., a circumscribed volume in niche space that includes a species and others that are similar to it). This definition of “guild” is similar to that of Wilson (1999): “a group of species that are similar in some way that is ecologically relevant, or might be.” Our definition is an expansive one that includes resource use (Root, 1967), the environmental conditions within which a species can function (e.g., temperature range, Hutchinson, 1959), and its demography and dispersal patterns (Holt, 2009). Traditionally, guilds are generally categorical constructs (e.g., herbivore versus carnivore). Our expansion emphasizes that guild attributes reflect continua (e.g., the relative amount of herbivory or carnivory performed by a species) and that a particular species or individual can perform a variety of types of roles (e.g., be both an herbivore and a carnivore, as in bat species that consume fruits, nectar, and insects). The volume in niche space that delineates a guild can be small or large (e.g., only annual, herbaceous, autotrophic plants versus all photosynthetic species). It can delineate a narrow but “long” volume that otherwise cuts across other axes (e.g., all seed eaters including insects, birds, and mammals, Brown et al., 1979). Thus, a particular species can belong to many guilds simultaneously, and to some extent, guild is a human construct that is used to impose order on complex and multifaceted phenomena. Consequently, how a guild should be defined is a conceptual as well as an operational question that depends on the ecological and evolutionary processes at issue (Questions 3, 5, 6, and 7, Case study 5).

The niche of a species, or the guilds of which it is a member, defines the functional traits that are relevant to any particular study that in turn become the basis for measuring functional biodiversity (see the next section). We use the term “functional traits” and the term “functional trait diversity” instead of the more common usage of just “function” to emphasize what is measured in practice, and what is measured likely is not an effective proxy

of all functions performed by a species. Truncating these terms to just “traits” or “trait diversity” would be an even more accurate label for what is measured, as function is typically inferred (Streit & Bellwood, 2023); however, “functional diversity” is too strongly embedded in the literature to take this course of action.

What is measured

Although ecologists purport to study and characterize communities, complete communities that comprise all co-occurring species in a local area (e.g., microbes, plants, fungi, invertebrates, vertebrates; Question 10) are never analyzed in reality, either because of logistical constraints or because of the nature of posed questions. Instead, the unit of study in ecology is typically an assemblage, an ensemble, or a local guild (Figure 1). Moreover, the meaning of results from such studies is constrained by the nature of the selected unit. For example, a study of a bird “community” is typically a study of an assemblage—the members of a single clade occupying the same space—as it might consist of all members of the order Aves, which represents a variety of herbivores, granivores, insectivores, and carnivores while excluding other granivores (e.g., ants) or carnivores (e.g., foxes) that are outside of the focal clade but within the community. Alternatively, a study might be narrower and only include syntopic seed-eating heteromyid rodents, making the unit of study an ensemble. This is not merely a semantic issue but affects the inference space of the research and constrains the breadth of understanding associated with particular mechanisms. For example, studies of biodiversity often focus on the role of interspecific interactions within an ensemble (e.g., granivorous rodents at a desert site; Question 2) in determining its composition, richness, or structure. Nonetheless, the presence or abundance of rodents may be affected strongly by interspecific interactions with other granivorous taxa (e.g., birds or ants) outside of the focal ensemble (e.g., Brown & Davidson, 1977). Thus, conclusions about the mechanistic basis for the number of rodent species and their abundances will depend on whether the suite of interactions is limited to that within an ensemble or includes taxa in the local guild from other ensembles (Questions 2 and 3).

A key issue for a particular ensemble is the extent to which it includes all members of the specified clade. If a clade is species rich and includes members that belong to different guilds, different ecological and evolutionary processes might apply if the ensemble includes nearly all species in the clade compared with an ensemble that includes just a small percentage of species in that clade

(Case studies 1, 2, and 3). Similarly, different processes might apply if ensembles consist of taxa that are all closely related (e.g., congeners) rather than distantly related (e.g., confamilials). If the focus of a study is a single, local “community,” it is likely that the vast majority of the constituent ensembles will contain only a small proportion of the potential species from the focal clade because of the requirements that the species (1) co-occur in time and space and (2) occupy similar positions in niche space. All things being equal, the greater the phylogenetic distances among the species in an ensemble, the greater the likelihood that homologous or analogous structures (phenotypes) do not represent the same functions, making the notion of proximity in niche space more difficult to measure, define, or interpret. Moreover, these two requirements represent ways of identifying suites of species whose local interactions reciprocally affect population dynamics (Question 6).

Although ecological studies of biodiversity never involve entire communities, evolutionary studies can focus on entire clades. For example, evolutionary studies of trait diversification typically include all extant members of a clade regardless of their geographic location or guild affiliation (e.g., Aristide et al., 2015) and may even include extinct members. By contrast, ecological studies that focus on a particular guild will always be constrained by geography (local guild, e.g., Brown et al., 1979), phylogeny (taxonomic guild, e.g., Tran, 2014), or both (ensemble, e.g., Batalha et al., 2011; Stroud & Losos, 2019).

Both ecological and evolutionary processes affect the identity and abundances of species within study units as well as the variation among those units. Communities, local guilds, ensembles, and assemblages are ecological process units that are defined by only within trophic-level interactions (local guild or ensemble; Questions 1–5, Case studies 1, 2, 3, and 5) or by both within trophic-level and among trophic-level interactions (assemblage or community; Questions 6–10, Case study 4) that are circumscribed by space and time (Figure 1). Similarly, clades, taxonomic guilds, ensembles, and assemblages are evolutionary process units that comprise species with a shared evolutionary history that can be recent or distant depending on the group of species. Notably, ensembles and assemblages represent hybrid units that reflect both ecological and evolutionary processes. Indeed, most ecological studies of biodiversity are based on assemblages rather than ensembles or local guilds, despite how they are characterized with regard to underlying processes. Consequently, the conclusions of such studies regarding those processes may be in error because part of the local guild was ignored or because members of the clade that belong to different guilds were included. Critically, a thorough re-examination of past

studies is warranted to assess whether the unit of study and the underlying processes match and to understand the consequences of these mismatches for ecological understanding and management recommendations.

A particular research question may involve combinations of study units. For example, a study of plant–pollinator interactions could focus on an ensemble of plants and a local guild of pollinators (e.g., insects and hummingbirds) that reside within a single community (Question 3). A study of biodiversity patterns along an environmental gradient could focus on a set of related ensembles (Question 1). Whether the study includes only the same types of units as in Question 2 (e.g., granivorous rodents), or combinations of types of units as in Question 1 (Case study 1), may have implications for the nature of ecological and evolutionary processes under consideration. Moreover, consideration of the units of study may provide important concerns that constrain conclusions. For example, expectations for co-evolution of plants and pollinators (Agrawal & Zhang, 2021) might differ if one of the units was an ensemble (members of a single clade) and the other a local guild (members of disparate clades). If plants and pollinators were each members of a single clade, then we might predict a pattern of co-speciation and that pattern would not be possible if one side included multiple clades that do not have a common evolutionary history. Importantly, a comprehensive review of research in community ecology that properly addresses issues of comparable study units may facilitate the recognition of general patterns that are obfuscated by meta-analyses that represent many cases of differently ill-matched study units.

Grain, extent, and focus

Study units can be partitioned hierarchically into parts that compose wholes, thereby addressing questions about how diversity is distributed within and among study units. Those wholes and parts define the extent and grain of the study, respectively. Clearly identifying the grain, extent, and focus (units of analysis) matters because relationships among causes and effects can change as those units, or the scales of those units, change (Scheiner, 2011; Scheiner et al., 2000). Those units may have large spatial grains and extents (e.g., a biome, a biogeographic province), increasing the likelihood that many or at least some of the species that inhabit the study unit do not interact with each other. The absence of such interactions suggests that the term “community” would most likely be inappropriate for describing such a group of species. Studies at such large foci should make clear that the reference is to a spatial unit that contains multiple communities, ensembles, or

local guilds. Alternatively, units of study may represent small grains or extents (e.g., a 9-m² plot for hardwood trees, Case study 3), increasing the likelihood that at least some of the species that interact to reciprocally affect abundances are not included in the study unit. Studies at such small foci should make clear that the reference is to a spatial unit that contains only parts of communities, ensembles, or local guilds. In these cases, larger and smaller spatial extents only make sense when defined based on the perception or grain of the studied species (e.g., a 9-m² plot of bacteria may represent an ensemble, whereas a 9-m² plot containing frugivorous birds does not represent an ensemble or assemblage). Importantly, a taxonomic guild (Figure 1) is indifferent to geographic scale but is relevant when addressing evolutionary questions such as trait diversification in a widely distributed clade (Question 11).

We typically refer to the biodiversity of these wholes and parts as γ -components and α -components, respectively, with β -components referring to the variation among the parts (Whittaker, 1972). Examples of such hierarchies are those looking at the biodiversity of communities, ensembles, or assemblages within landscapes (e.g., Crist et al., 2003; Kristiansen et al., 2011; Sweeney & Cook, 2001) or exploring the biodiversity of communities, ensembles, or assemblages along spatial or environmental gradients (e.g., Gross et al., 2000; Willig & Gannon, 1997; Willig & Presley, 2019). All of these represent geographic partitions. The closest equivalent partition for phylogeny considers the ratios of genera to species or focuses on supraspecific taxa (e.g., Holland & Jain, 1981; Macheroum et al., 2021; Passy et al., 2017). We are unaware of any non-geographic partitioning of the trait space for functional traits. Critically, the potential subunits of a cladogram or trait space may not be defined clearly, making its partitioning different from that of biodiversity within and among geographic units (Chao et al., 2024; Scheiner et al., 2017a, 2017b; Tucker et al., 2017). For example, when partitioning the phylogenetic information contained in a cladogram, should you use a level in the standard taxonomic hierarchy (e.g., species or genera) to define units and subunits? When partitioning trait space, would you first do a cluster analysis, and would such a procedure make the analysis circular? These are issues that need to be explored.

UNITS OF MEASUREMENT

Ecologists must confront a plethora of ways to measure biodiversity (Magurran, 1988; Magurran & McGill, 2011; Peet, 1974). We use the phrase “unit of measurement” to refer to the metric or metrical formula (e.g., species

richness as quantified by the number of species) rather than what is measured (e.g., prey item size as measured in grams). Choosing a metric can be challenging, often resulting in the use of a particular metric because it is commonly cited in the literature or can be calculated easily via a software package, rather than because it is the most suited metric for the data, questions, or hypotheses of interest. In addition, nearly all commonly used metrics are composites: they consist of more than one component of biodiversity (e.g., richness and evenness). This composite nature is often hidden by the way the metrics are described or calculated, making determination of the most appropriate metric for a particular task more challenging.

In this section, we have four goals that combine to create an organizational framework for measuring biodiversity. The first goal is to provide a typology of the metrics of biodiversity that encompasses three commonly considered categories of data: abundances, phylogenies, and traits (i.e., functions). Our typology derives from that of Tucker et al. (2017) for phylogenetic metrics but goes beyond it by further refining their schema and applying it to trait-based metrics. The second goal is to update the summary of phylogenetic-based metrics of Tucker et al. (2017) and the summaries of trait-based metrics of Weiher (2011) and Mammola et al. (2021), as well as to propose new metrics that arise from considerations of the new typology. The third goal is to harmonize these metrics via a common system of notation that exposes their conceptual bases and their mathematical similarities or differences. The fourth goal is to propose a standardized set of symbols for many of the metrics so that their properties are obvious.

A typology of biodiversity metrics

Because biodiversity comprises a number of interrelated concepts, it requires a variety of types of data that can be combined into particular metrics. Our proposed typology begins by identifying basic components (two properties of data and three methods of measuring that data), defining a set of elemental metrics from those components, and illustrating how those elements can be combined to produce commonly used metrics or new metrics based on different elements that are analogous to those of existing metrics. The identities, abundances, phylogenetic relationships, and functional traits of species represent the foundational data on which biodiversity metrics are based. Each of the latter three types of data (i.e., abundance, phylogeny, functional traits) evinces two properties, magnitude and variability, that can vary independently over space or time, although they may be

correlated. To be clear about the data referenced for each combination of type and property, we adopt the nomenclature (Table 2) of Scheiner et al. (2017a).

Magnitude quantifies the extent to which each of the species in a group manifests some property. For abundance, magnitude (numbers) is typically the number of individuals of a particular species and can be either absolute abundance or relative (proportional) abundance (abundance of a species compared with the total abundance of all individuals regardless of species identity). For other properties of species (e.g., frequency of occurrence, biomass, geographic range size), analogous measures can be used to quantify magnitude (e.g., relative frequencies of occurrence, relative biomass, or relative geographic range size). For phylogeny, magnitude quantifies the evolutionary differentiation (i.e., divergence) of a particular species from other species (Figure 2a). For functional traits, magnitude quantifies the difference between trait profiles (vectors of trait values) of a particular species from other species (i.e., trait dispersion; Figure 2b).

TABLE 2 The three types of data and their two properties combine to define six types of data (Scheiner et al., 2017a).

Data type	Magnitude	Variability
Abundance	Numbers	Evenness
Phylogeny	Divergence	Regularity
Functional trait	Dispersion	Equability

Variability quantifies the extent to which magnitudes differ among species in a group. For abundance, variability (evenness) reflects similarity in the (relative) number of individuals of each species. For phylogeny, variability (regularity) is the extent to which species are equally divergent. For traits, variability (equability) is the extent to which species are equally different from each other in trait values. These properties are derived from those of Pavoine and Bonsall (2011) and Tucker et al. (2017). Our magnitude property encompasses both their richness and their divergence properties, whereas our variability property encompasses their regularity property. In those papers, the same terms are used for magnitude and variability with regard to phylogenetic and trait data. By contrast, we use different terms for each to emphasize the use of a particular property and data type.

These four data types about species (identities, abundances, phylogenetic relationships, and functional traits) differ in three other regards. First, for identity, abundance, and phylogenetic data, there is a single “correct” species assignment, count, or phylogeny, respectively, although their estimation may have errors. By contrast, for trait data, the value of the metric is dependent on which traits are selected for analysis, and there is no single correct set for inclusion. Critically, which traits to include should depend on the ecological or evolutionary processes that are being addressed or on the anticipated effects of biodiversity on ecosystem processes (Questions 1 and 4, Case studies 1 and 3); selected traits should be related to the axes in niche space that are under

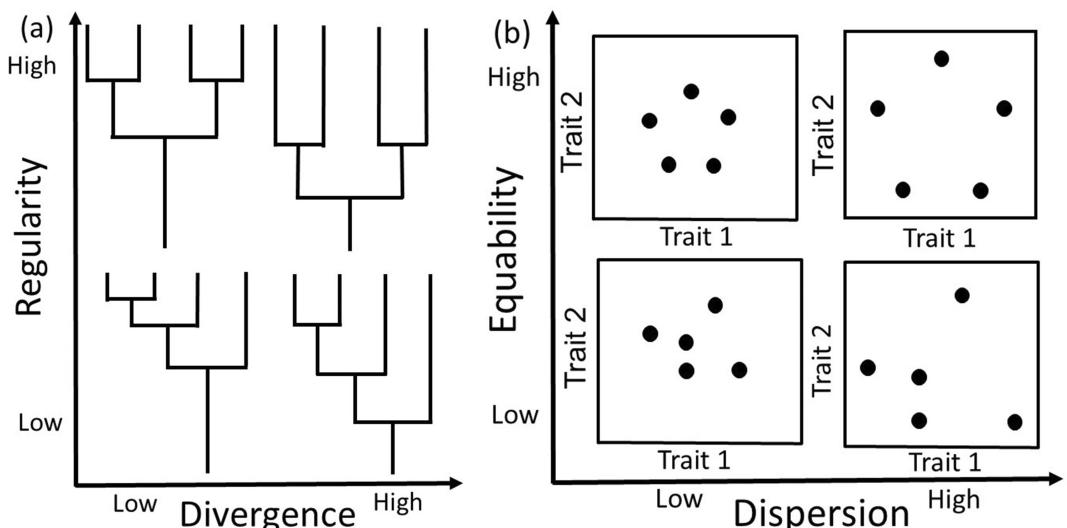


FIGURE 2 (a) Four phylogenies showing how magnitude (divergence) and variability (regularity) can vary independently. A phylogeny with higher divergences has longer branch lengths toward the tips. A phylogeny with higher regularity has more symmetrical or similar-length branches. (b) Four assemblages showing how magnitude (dispersion) and variability (equability) can vary independently. Species with higher dispersions have greater distances among the species in trait space. Species with higher equability have more similar distances among the species. See Box 1 for definitions.

consideration (Questions 2, 3, and 7, Case study 2). Second, trait values can differ among individuals within species. Third, abundances are additive across a hierarchy of wholes and parts, whereas phylogenies and traits are not, precluding the use of some mathematical operations with those data types.

Our typology considers three methods for measuring phylogenetic and trait data that are based on relative distances between and among species: total, pairwise, or nearest neighbor. For trait data, total metrics are based on the mean distance in trait space of each species from all others; pairwise metrics are based on the distances between all possible pairs of species (Case study 2). (For some metrics of magnitude, total and pairwise measures are equivalent, although they are never equivalent for metrics of variability.) Nearest-neighbor metrics are based on only the smallest pairwise distance for each species, although a particular species might have the same minimal distance with more than one other species. For phylogenetic data, total metrics are based on measures of the total proportional branch lengths from root to tip of each species (Case studies 1, 2, and 3). Most commonly, shared branch lengths are divided by what are called “fair proportions” (Isaac et al., 2007), although other divisions are possible (Cadotte & Jonathan Davies, 2010). Both pairwise and nearest-neighbor metrics are based on the lengths of branches from one tip of the phylogeny to another, with the former comprising all pairwise lengths and the latter including only the shortest length. Both differ from total metrics in that they do not include shared root branches. For example, in Figure 2a, the single root branch in each of the phylogenies would not be included in any pairwise or nearest-neighbor metric. Thus, for total metrics, the sum of the values for each species equals the total branch length; that equality generally does not hold for pairwise or nearest-neighbor metrics.

TABLE 3 Thirteen metrics of biodiversity derived from combinations of basic elements (plus identity).

Data type	Magnitude			Variability		
	Total	Pairwise	Nearest	Total	Pairwise	Nearest
Abundance	M(A)	${}^qE(A)$ ${}^qE(A)^N$ qRE
Phylogeny	M(P_{tl}) AvPD	$M(P_{pw})$ MPD J PSV	$M(P_{nn})$ MNTD	${}^qE(P_{tl})$ ${}^qE(P_{tl})^N$ $C(P_{tl})$	${}^qE(P_{pw})$ ${}^qE(P_{pw})^N$ $C(P_{pw})$	${}^qE(P_{nn})$ ${}^qE(P_{nn})^N$ $C(P_{nn})$
Trait	M($T_{tl/pw}$) KW		M(T_{nn})	${}^qE(T_{tl})$ ${}^qE(T_{tl})^N$	${}^qE(T_{pw})$ ${}^qE(T_{pw})^N$	${}^qE(T_{nn})$ ${}^qE(T_{nn})^N$ $C(T_{nn})$ FNEve

Note: Metrics that are in **bold** are newly proposed; metrics in *italics* are implied based on previously proposed metrics. See Appendix S1: Table S2 for the formulas for each metric, along with the name, alternative symbols, the quantities that each measure, and the source reference.

Two different classes of variability metrics exist, those based on Hill numbers and those based on the SD. The former metrics provide easily interpreted results in units of the effective number of species or the effective number of groups (for β -components of biodiversity, Tuomisto, 2010), whereas the latter metrics have better mathematical properties: combining with (dividing by) the mean (magnitude) to produce a CV and standard variance partitioning methods.

Leinster and Cobbold (2012) provide a list of preferred properties for biodiversity metrics based on consideration of (1) effective numbers, (2) modularity, (3) replication, (4) symmetry, (5) the effect of absent species, (6) the effect of identical species, (7) monotonicity, (8) the extent to which metrics simplify when abundance, phylogeny, or trait values are not included (naive model), and (9) the range of the metric. Some of those properties (e.g., effective numbers, data range) hold only for metrics that combine species richness with other elements, meaning that not all metrics satisfy all of the listed criteria. Nonetheless, these criteria are useful for examining the properties of competing metrics. Our list of metrics is meant to be comprehensive, rather than prescriptive or proscriptive. Herein, we take no position on whether all of the properties of Leinster and Cobbold (2012) are required for any particular metric to be informative or useful.

A summary of biodiversity metrics

We begin our summary of biodiversity metrics by defining 14 basic elements defined by data type, measure of magnitude, and measure of variability (Table 3), plus identity. All biodiversity metrics can be derived from combinations of these 14 basic elements, representing a comprehensive

organizational framework for understanding biodiversity measurement. To aid in the selection of appropriate measures, we use a consistent set of symbols for biodiversity metrics and for the variables in their formulas (Box 2); where there is a previous, common symbol for a given metric, we provide it in the text alongside the first appearance of our suggested notation. The most common type of identity is “species,” but other units are possible (e.g., genus, genotype). When the units are species, then identity biodiversity equals species richness (S). Each of the 14 basic elements can be measured in more than one way (e.g., the four different metrics for equability based on nearest-neighbor distances). After combining those elements in various ways, the result is a daunting 130 different metrics (Appendix S1: Table S1). That number does not include all metrics already in the literature, although it does include all of the commonly used ones, as well as many new metrics that are introduced herein.

Ecology may or may not need so many ways to measure biodiversity. Regardless, our purpose is to show that each of these metrics is a combination of 14 basic elements, and even these basic elements reduce to just three categories (four data types, two properties, and three measurement methods; Table 3). They represent a spectrum of potential metrics that provide options to appropriately measure biodiversity for potential questions of interest to ecologists, evolutionary biologists, or conservation scientists. Organizing the metrics in this comprehensive fashion accomplishes four goals. First, the organizational schema identifies metrics that are based on the same types of data, properties, or measurement methods. If one wishes to compare phylogenetic diversity and functional trait diversity for a group of species, it does not make sense to compare a measure of pairwise divergence for phylogenetic diversity to a measure of nearest-neighbor equability for functional trait diversity (Case study 1). Our framework (Table 3, Appendix S1: Table S1) facilitates the identification of metrics that share approaches (e.g., nearest-neighbor distances) across dimensions of biodiversity. It also highlights how different diversity concepts might focus on different properties and types of data.

Second, our organizational schema distinguishes among different combinations of elements. For example, a measure of abundance-weighted functional trait biodiversity (Appendix S1: Table S1D: ${}^qDA(T_{tl})$) combines elements of identity, numbers, and total equability:

$${}^qDA(T_{tl}) = \left(\sum_{i=1}^S n_i \left(\frac{d_i}{\sum_{i=1}^S d_i n_i} \right)^q \right)^{1/(1-q)} .$$

When all species are equally abundant (for each i , $n_i = n$), ${}^qDA(T_{tl}) = n {}^qD(T_{tl})$, and when all are equally

distant (for each i , $d_i = d$), ${}^qDA(T_{tl}) = \sum_{i=1}^S n_i = N = \bar{n}S$, where \bar{n} is mean abundance. By contrast, a measure of trait-weighted abundance biodiversity [${}^qDT_{tl}(A)$] combines elements of identity, total dispersion, and evenness:

$${}^qDT_{tl}(A) = \left(\sum_{i=1}^S d_i \left(\frac{n_i}{\sum_{i=1}^S d_i n_i} \right)^q \right)^{1/(1-q)} .$$

When all species are equally abundant, ${}^qDT_{tl}(A) = \sum_{i=1}^S d_i = \bar{d}S$, where \bar{d} is the mean total distance between species, and when all are equally distant, ${}^qDT_{tl}(A) = d {}^qD(A)$. Therefore, if all species are only equally abundant or equally distant, then ${}^qDA(T_{tl})$ and ${}^qDT_{tl}(A)$ result in different values. In particular, if all species are both equally abundant and equally distant, then ${}^qDA(T_{tl}) = N$ and ${}^qDT_{tl}(A) = \bar{d}S$. Recognizing that these two metrics combine different basic elements, and thus measure different properties, prevents confusion or inappropriate comparisons, especially among studies done by different researchers.

This organizational framework, combined with standardized formulas for the metrics, identifies why certain metrics are likely to be correlated with each other. For example, Morelli et al. (2018) found a positive correlation between functional evenness (FEve) and functional divergence (FDiv) in a set of bird assemblages (Question 11). Both are compound metrics that involve weighting by the same abundance values, predisposing the metrics to be correlated positively. If the question to be addressed is whether variability in trait distances is related for total or nearest-neighbor values, it is better to evaluate the correlation of their basic elements— ${}^qE(T_{tl})$ and ${}^qE(T_{nn})$ —than to do so with compound variables that comprise potentially confounding factors such as species abundances. In the next section, we explore a case in which the use of a compound metric results in erroneous conclusions about patterns (Question 4, Case study 3).

Third, the organizational schema exposes possible metrics that have not yet been defined or described but that are analogous to other metrics that use different types of data. Imagine Table 3 and Appendix S1: Table S1 without any of the metrics in italic or bold font. That is how we began this compilation. The metrics in italics are those that are implied by previously published metrics (e.g., a metric for Hill diversity implies a related evenness metric by dividing by S , such as ${}^qE(T_{tl})$, Table 3). The metrics in bold are those that were suggested by analogy with existing metrics. For example, metrics for divergence based on total or pairwise measures suggested metrics based on nearest-neighbor divergence, which were done via simple substitutions of data types. Once we began this process, it became straightforward to continue

BOX 2 A proposed set of standardized symbols for metrics of biodiversity and their parameters

We propose a consistent symbology for many metrics of biodiversity. The system is designed to convey information about the content of the metric; that is, the symbol is more than just an arbitrary designation. The system is applied primarily to metrics that are based on Hill numbers (Hill, 1973). The Hill function is:

$${}^qD = \left(\sum_{i=1}^S x_i^q \right)^{1/(1-q)},$$

for $\sum_{i=1}^S x_i = 1$. The function is undefined when $q = 1$, requiring a limit formulation:

$${}^1D = \lim_{q \rightarrow 1} {}^qD = \exp\left(-\sum_{i=1}^S x_i \log x_i\right).$$

For the sake of brevity, the formulas in Appendix S1 only show the general formula. We also use these symbols for metrics that rely on standard mathematical operations (averages, SDs, and CV). We developed this system in assembling the metrics so as to highlight similarities and differences among them. Especially as new metrics were being described, we discovered that previous symbols, including ones in our previous papers, were inadequate for creating a unique symbol for each metric. In addition, no single, standard symbol existed for some metrics. The proposed system conveys the three data categories as follows:

1. Type of data: A , abundances; P , phylogenetics; and T , functional traits.
2. Property as determined by a mathematical function:

Magnitude: M , mean; Σ , sum.

Variability: σ , population SD; C , coefficient of variation; D , Hill diversity; and E , Hill evenness.

For Hill functions, the superscript q represents an exponent (typically 0, 1, or 2).

For metrics of Hill evenness, the superscript N normalizes to a scale of [0,1].

For trait data, the subscript I represents an operation performed on individuals within species.

3. Type of measurement for phylogenetic or trait data denoted as a subscript: tl , total; pw , pairwise; nn , nearest neighbor.

If the symbol for a data type is inside parentheses, the function is performed on that parameter. If the symbol is outside the parentheses, that parameter is a weighting factor. For example, ${}^qDT_{pw}(A)$ is Hill diversity of abundance data weighted by pairwise trait data; ${}^qDA(T_{pw})$ is Hill diversity of pairwise trait data weighted by abundance data; and ${}^qD(AT_{pw})$ is Hill diversity of both abundance and pairwise trait data. Not included here, because we do not list their formulas, are symbols designating ecological hierarchies (α -, β -, and γ -components of biodiversity). For clarity, those should be added as subscripts of the mathematical function (e.g., ${}^qD(AT_P)_\beta$).

We urge the use of a consistent set of symbols to make it easier to understand the nature of a metric, especially if the formula for that metric is not explicit in a source publication. We are well aware that getting authors to do so will be difficult. In one case, one of our own metrics was used in an article with a notation that differed from the one in the original publication. As the original publication listed several different metrics, it was not obvious which one was being used. We implore editors and reviewers to be critical in encouraging consistency of usage.

In a similar fashion, we propose a standardized set of symbols for the parameters used in diversity metric formulas:

S : the number of species.

n_i : the number of individuals of species i .

N : the total number of individuals.

τ : the time depth of the cladogram.

q : the exponent of the Hill function.

B_i : the set of all branches on the cladogram.

B : the number of branches on the cladogram.

L : the total length of all branches on the cladogram.

S_i : species i .

$b(S_i)$: the set of branches in the path from the root to the tip of the i th species.

L_i : the total proportional branch length share of species i .

L_b : the length of the b th branch segment.

N_b : the total number of individuals of all species that share the b th branch segment on the cladogram.

L_{ib} : the proportional share of the b th branch segment of species i .

Φ_{ij} : the total branch length between species i and j .

φ_{ij} : the total relative branch length between species i and j , $= \Phi_{ij}/L$.

$\varphi_{i \text{ min}}$: the shortest relative branch length between species i and all other species.

c_i : the sum of the branch lengths from the root to the tip of species i .

c_{ij} : the sum of the branch lengths from the root to the most recent common ancestor of species i and j .

d_{ij} : the distance between species i and j in trait space in which the axes have been standardized to a [0,1] interval.

d_i : the mean distance of species i to all other species in standardized trait space.

$d_{i \text{ min}}$: the smallest distance between species i and all other species in standardized trait space.

$\mu_{l \text{ min}}$: the length of the l th branch connecting two species in a minimum spanning tree constructed from phylogenetic or functional-trait distances.

δ_i : the distance of species i from the abundance-weighted centroid of the species trait-space distribution.

Δd : the sum of abundance-weighted standard deviances from the centroid of the trait-space convex hull.

$\Delta|d|$: the sum of abundance-weighted absolute deviances from the centroid of the trait-space convex hull.

\overline{dG} : the mean distance from the centroid of the trait-space convex hull.

d_{kl} : the standardized trait-space distance between individuals k and l ignoring species identity.

The use of such standardized symbols avoids confusion that arises when the same symbol is used for different concepts (e.g., using “ d ” for both branch length and trait-space distance). For the most part, the symbols used are those typically found in previous publications, except where the same symbol was being used for different concepts. Where possible, subscripts are used to distinguish between related parameters (e.g., min for metrics involving nearest-neighbor divergences or distances). Formulas are presented in as atomistic a fashion as possible (e.g., denominators show full summations rather than a composite sum). Doing so makes it easy to see the components of each formula, avoids confusion, and limits the number of needed symbols. We urge other researchers to adopt this usage to explicitly identify the relationship of any new metric to current metrics.

until all 81 cells in Table 3 and Appendix S1: Table S1 contained at least one metric. Even if a cell already contained a metric, others were added if they were based on combinations of basic elements that were not considered previously or if based on different concepts of magnitude or variability. In general, metrics are presented in their original form. Our only systematic deviation from that practice is that all of the variance-based metrics of Tucker et al. (2017) were converted to SDs to make the units comparable for magnitude and variability (Appendix S1: Table S4).

Fourth, our organizational schema facilitates identifying and developing new metrics. For example, the most commonly used metric of evenness, ${}^qE(A)$, is not independent of richness; standardization methods exist to create new metrics that do not suffer from this critique (Chao & Ricotta, 2019; Jost, 2010). The creation of new evenness metrics for phylogenetic and functional trait data (Table 3) raises similar concerns, and our

organizational schema facilitates the identification of situations in which similar adjustments can improve extant metrics. Alternatively, basic elements might be combined in new ways, or different types of basic elements might be developed (e.g., innovative ways of measuring variability).

Other issues

The effective number of species for a particular metric is the number of equally abundant, divergent, or dispersed species that a set would contain while still possessing the same value for that metric as obtained in a particular instance (Jost, 2006). They are obtained by multiplying species richness by a measure of evenness, regularity, or equability based on the Hill function, resulting in a value in the interval (1,S] (Jost, 2010). Some, but not all, of the variability metrics in Appendix S1: Table S1 represent

effective numbers (Figure 3). Those that are not effective numbers include weightings. However, if those weightings are based on relative values so that they are in the interval [0,1], the metrics would represent effective numbers. Most mathematical models of ecological processes describe competition, mutualism, or predation in terms of absolute values, whereas biodiversity as expressed by effective numbers is based on relative values. A critical need exists to bridge these two approaches for analyzing ecological processes as they relate to understanding how species interactions affect changes in biodiversity within a particular system (Questions 2, 3, and 5, Case studies 2 and 5).

There are other approaches for measuring biodiversity such as Kosman's assignment-based measure of magnitude (Kosman, 1996, 2014; Kosman & Leonard, 2007). This magnitude measure is calculated based on pairwise distances for trait data or phylogenetic data using an algorithmic approach, rather than a formula. The assignment-based measure of magnitude is more suitable to the case of association among traits than the corresponding estimate of the mean pairwise distance ($M(T_{tl/pw})$) (=MFAD). Another algorithmic metric is functional richness (FRic, Cornwell et al., 2006).

Considerations about the characteristics of the data

Identity information is generally anchored to "species." Although a variety of species concepts exist (Nathan & Cracraft, 2020), our schema is agnostic with respect to them. Nonetheless, the species concept that underlies a study has implications for understanding the nature of

the ecological or evolutionary process(es) under consideration (Question 9, Case study 4). When species richness is measured in a spatially constrained unit (i.e., a community, assemblage, ensemble, or local guild), species density ($S/\text{area sampled}$) is measured, even though the term "species richness" is used more commonly. For comparisons of samples based on different areas or sampling efforts, some type of rarefaction technique may be necessary to standardize estimates (e.g., Chao et al., 2014; Gotelli & Colwell, 2001).

Abundance data can be based on counts of individuals or on characteristics that are related to their prevalence (e.g., biomass or frequency of occurrence) in a study unit. Different types of units may necessitate the use of different types of data. For a plant ensemble that consists entirely of herbs, counts of individuals may be appropriate. However, if the ensemble includes herbs, shrubs, and trees that differ in size by orders of magnitude, biomass may be more appropriate, especially if biodiversity is being linked to ecosystem function. Similarly, biomass may be most appropriate for a local guild of seed eaters that includes disparate taxa such as birds, rodents, and ants. In general, the use of abundance data is meaningful only for assemblages, local guilds, or ensembles because abundance is meaningful only with respect to a defined geographic area (Questions 2, 3, and 5, Case studies 2 and 5).

For phylogenetic and trait data, meaningful comparisons may require rescaling. For phylogenetic data, phylogenetic trees generally should be chronograms so that branch lengths are scaled equally. Moreover, it is important to scale to the same time depth, thus the inclusion of a shared root in the cladograms of Figure 2a (Questions

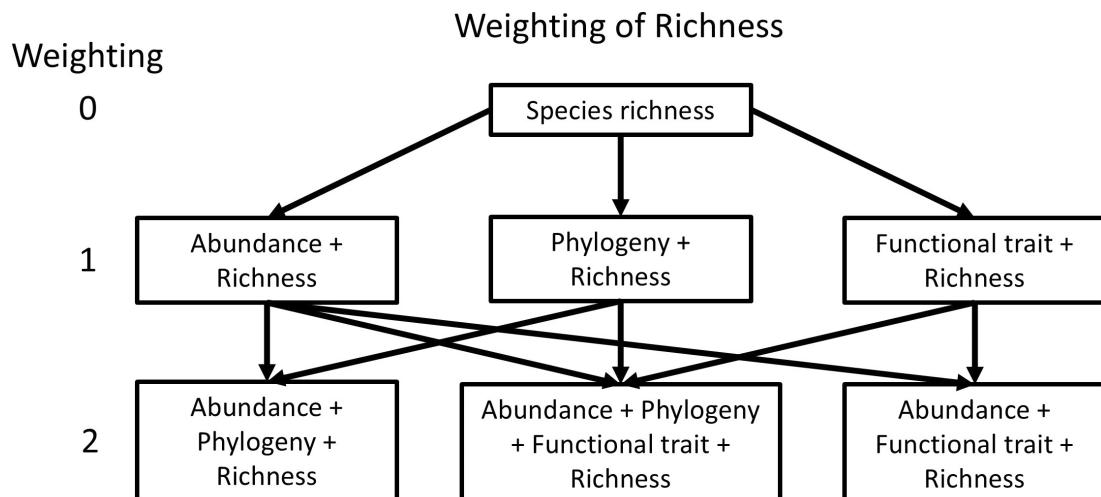


FIGURE 3 The ways in which the effective number of species can be measured using various weightings of species richness (S), either by combining richness with just one other element, abundance (A), phylogeny (P), or traits (T), or by combining multiple elements of richness and abundance with phylogeny or traits. Metrics that combine these elements can be found in Appendix S1: Table S1.

1 and 8, Case study 1). It is possible to use non-ultrametric trees, such as those based on the amount of genetic change. However, when comparing biodiversity among groups of species, care must be taken that the same amount of genetic change represents similar amounts of evolutionary divergence, as is likely if the groups of species are all from a single clade of reasonably closely related species.

How to perform such scaling for functional trait data is not straightforward. For example, if comparisons are among taxonomic guilds, a meaningful comparison might be among clades that encompass the same set of taxonomic levels. For example, for angiosperms and bats, the most meaningful comparisons are likely among families because families typically comprise species that represent a single guild (e.g., bats—vespertilionids are generally aerial insectivores; desmodontids are generally sanguinivores; glossophagids are generally nectarivores; noctilionids are generally piscivores) or life form (e.g., plants—Fagaceae are generally trees, Cyperaceae are generally herbs). However, such a comparison begs the question: Is it meaningful to compare functional trait diversity among taxa when the nature of the traits and the functions with which they are associated differ among taxa? Are traits involving carbon uptake in plants functionally equivalent to feeding traits in bats? Are metrics based on such disparate suites of traits useful for comparing the functional biodiversity of such ensembles? One potential solution is the use of self-referential measures, such as comparisons of rank-order changes in relative growth rate.

Trait data can be categorical or continuous, and functional trait diversity metrics can be characterized by two concepts: uniqueness and combinatorics (see fig. 1 of Scheiner et al., 2017b). For each concept, maximal diversity depends on the nature of the data. For the uniqueness concept, if data are categorical, functional trait diversity is greatest when each species in a group has a unique set of trait attributes. If the data are continuous, biodiversity is greatest when the species are as far apart from each other as possible in multidimensional trait space—both mean trait dispersion ($M(T_{\text{tl/pw}})$) and Hill pairwise equability (${}^qE(T_{\text{pw}})$) are maximized when the species are evenly distributed on the surface of the multidimensional hypersphere defined by the traits. For the combinatorics concept, if data are categorical, biodiversity is greatest when a group contains species that represent every possible combination of trait attributes. If the data are continuous, biodiversity is greatest when species dispersion is as compact as possible (i.e., when all species have the same number of neighbors at the nearest distance) while equalizing the minimum distances between species (i.e., when nearest-neighbor distances have an evenness (${}^qE(T_{\text{nn}})$

of one)). If some traits are categorical and some continuous, two approaches can be used. One is to make categorical data continuous through the use of an appropriate distance measure (e.g., Gower's distance, Gower & Legendre, 1986). Alternatively, continuous data can be made categorical by using the trait data to define functional groups (e.g., Chao-Hill diversity, Chao et al., 2021). Such functional groups might be inappropriate, though, for an analysis of local guilds that include species from different clades, resulting in incommensurate traits (e.g., granivores that include birds, rodents, and ants; Question 3).

Nearly all functional trait diversity metrics use a single trait value to represent a species. However, individuals within species can differ in their trait values. This variation can be captured with metrics based on individuals instead of species (Appendix S1: Table S5) or through the estimation of trait probability density (TPD) functions (Carmona et al., 2019). The latter has been applied to a few metrics but might be appropriate for many others listed here.

One limitation of the use of functional trait data is that even the most complete data sets (e.g., the TRY database for trees, Kattge et al., 2020) are characterized by missing trait data. As a proxy, a measure of phylogenetic diversity could be used under the assumption that evolutionary divergence is expected to be positively correlated with trait divergence (e.g., Barrufol et al., 2013; Vilà et al., 2013). However, if this assumption is incorrect or if the correlation between phylogenetic divergence and trait divergence is weak, subsequent interpretations would be compromised and inaccurate (Question 11). Alternatively, one can impute missing values using phylogenetic information. Additionally, some distance measures (e.g., Gower) can be estimated with missing data when the distance for a given pair of species is calculated using only those traits that are available for both species, and some metrics have been shown to be robust to missing data (Stewart et al., 2023).

General remarks

We emphasize that we are not advocating the use of any particular metric. Rather, our goal is to be comprehensive so that researchers can identify the metrics that are most appropriate for the questions or hypotheses under investigation. This task is especially important for metrics that are composites of two or more elements because the combination of elements is not always obvious in metric descriptions. For example, it can be unclear if a particular metric measures abundance biodiversity weighted by phylogenetic data or phylogenetic diversity weighted

by abundance data. Such a distinction ensures that comparisons among biodiversities with different data types (e.g., phylogenetic and trait) are done with metrics based on similar properties (e.g., both are based on nearest-neighbor distances; Question 7). Importantly, certain types of comparisons may not be informative. For example, Hill diversity metrics based on phylogenetic or trait data include species richness as a component; consequently, any correlation between the two Hill diversities may arise because of the confounding effects of richness (Question 4, Case study 3). Instead, the correlation should be done using normalized Hill evenness metrics that do not contain the shared element of species richness.

Our compilation is incomplete in several regards. First, we have undoubtedly overlooked some metrics despite our attempts to ferret them out from the literature. Second, we have not addressed all aspects of biodiversity. Our focus is exclusively on metrics relevant to species within spatiotemporally defined groups. Moreover, our compilation does not consider other types of measures, such as entropy (Jost, 2006). Third, all of the presented formulas assume the absence of sampling biases. Bias-corrected formulas for some of the metrics can be found elsewhere (e.g., Chao et al., 2014, 2015; Chao & Jost, 2012; Colwell & Coddington, 1994). Fourth, we do not deal with hierarchical data structures that give rise to metrics that reflect α -components (mean subsample) and β -components (among subsamples) of biodiversity. Formulas for hierarchical data structures exist for some of the metrics (e.g., Chao et al., 2012; Chiu et al., 2014; Kosman et al., 2024; Pavoine et al., 2016; Podani et al., 2018; Scheiner et al., 2017b; Tucker et al., 2017; Tuomisto, 2010).

ADDRESSING ECOLOGICAL AND EVOLUTIONARY QUESTIONS

Clearly delineating units of study and units of measurement ensures that appropriate data can be applied to scientific questions. In this section, we present several examples that demonstrate how the use of particular metrics or units of study could result in erroneous conclusions about patterns of biodiversity and the processes that drive them. In Table 1, we list a number of questions with units of study and units of measurement for those questions. In this section, we provide a detailed analysis of several of those questions to explore associated conceptual issues. More specifically, we demonstrate the need to use comparable metrics for different data types (ecological gradient theory; Question 1); situations in which total, pairwise, or nearest-neighbor metrics might be most

appropriate (niche theory; Question 2); situations in which composite metrics can be misleading (productivity and biodiversity; Question 4); how different types of data might be appropriate at different times during a process (assembly and evolution of communities on islands; Questions 9 and 10); and when composite metrics might be most appropriate (dilution effect theory; Question 5).

General considerations about processes and metrics

For ecological questions, functional trait dispersions can provide information about potential ecological interactions among species. Total trait dispersion metrics (e.g., $M(T_{tl/pw})$, KW) are related to average group-level interactions (e.g., diffuse competition), whereas nearest-neighbor trait dispersion metrics (e.g., $M(T_{nn})$ (=meanNN)) are related to interactions between each species and the other species in the group with which it is most similar. The amount of variability in pairwise trait equability (e.g., $^qE(T_{pw})$) indicates whether species interact with all others to the same extent, whereas the amount of variability in nearest-neighbor equability (e.g., $^qE(T_{nn})$) reflects whether species interact with nearest neighbors to the same extent.

For questions about the mode and tempo of evolution, phylogenetic divergences can be measured as either the total divergence of a particular species from its cladistic root, the sum of all pairwise divergences, or the divergence of a species from its most closely related species. As a result, both total and pairwise phylogenetic divergences provide information about clade-level speciation processes as they include patterns of diversification. One can use those metrics to address questions such as: “Are branching events concentrated at the base of the tree, at the tips of the tree, or evenly through time?” These questions are addressed with measures of the magnitude of total phylogenetic biodiversity, such as $M(P_{tl})$. Alternatively, one can explore the extent to which phylogenetic trees exhibit symmetry or asymmetry using measures of the variability of total branch lengths, such as $^qE(P_{tl})$. By contrast, nearest-neighbor phylogenetic divergences provide information about the recency of divergence between pairs of species. We can ask questions such as the following: “Have the most recent speciation events been concentrated in time?” using nearest taxon Hill regularity ($^qE(P_{nn})$). All of these metrics could then be applied to questions such as the following: “Following island colonization, does diversification happen quickly or gradually?” or “Following island colonization, does diversification happen evenly throughout the phylogenetic tree or is it concentrated within particular clades?”

Comparisons among datasets are typically of two types: (1) data collected in the same place(s) but for different taxa (e.g., multiple taxa along an environmental gradient) or (2) data collected for a single taxon from multiple places (e.g., bats in Costa Rica and in Puerto Rico). In these cases, one variable is kept constant (location or taxon), allowing for clear tests of hypotheses. By contrast, attempts to compare different taxa from different locations (e.g., bats in Costa Rica and birds in Puerto Rico) are problematic. Even comparisons involving species richness assume that the same species concepts are being used for each group. A comparison of species richness of tropical bats, temperate bacteria, and arctic angiosperms may not be meaningful or easy to interpret because of such considerations.

Case study 1: Ecological gradient theory

Ecological gradient theory (Fox et al., 2011; Scheiner & Willig, 2005) makes predictions about patterns of species richness along environmental gradients (Question 1). Case study 1 uses our own previously mistaken comparison of incompatible metrics. The third proposition of ecological gradient theory states that within an area of fixed size or a unit of time of fixed duration, the variance of an environmental factor increases with its mean. This proposition predicts that species richness will be positively correlated with trait dispersion and equability. The most appropriate units of study for such questions are local guilds or ensembles (Figure 1). For measurements of dispersion and equability, it is critical that they be independent of species richness, such as mean trait dispersion ($M(T_{tl/pw})$) or normalized Hill equability (${}^qE(T_{tl})^N$).

We used data from the Manu Biosphere Reserve (hereafter Manu, Patterson et al., 2006), which spans an extensive elevational range (340–3625 m above sea level [asl]) on the eastern slopes of the Andes in southeastern Peru (MacQuarrie, 1992). Previously, we examined variation in bat functional trait diversity (Scheiner et al., 2017b) and phylogenetic diversity (Scheiner et al., 2017a) along that elevational gradient. The bats at each elevation are an assemblage as they consist of a single clade that includes species in eight guilds. The extent of the unit of study in this instance is the elevational gradient, and the grain and focus are an elevational band. In contrast to the predictions of ecological gradient theory, trait dispersion and equability were correlated negatively with species richness, although those correlations were not statistically significant ($M(T_{tl/pw})$: $r = -0.29$, $p = 0.33$; ${}^qE(T_{tl})^N$: $r = -0.38$, $p = 0.21$).

Our mistake came in comparing patterns of functional trait diversity and phylogenetic diversity using

metrics with mismatched data types. In Scheiner et al. (2017a), we contrasted the pattern of change in phylogenetic regularity (${}^qE(P_{tl})$) along the gradient—greatest at low elevations, least at middle elevations, and increasing again at higher elevations—with the pattern of trait equability (${}^qE(T_{pw})$) in Scheiner et al. (2017b), with no variation along the gradient (Figure 4). This comparison is problematic because the functional trait diversity measures were based on pairwise distances, whereas the phylogenetic diversity measures were based on total divergences. In this instance, the elevational patterns for total equability (${}^qE(T_{tl})$) and pairwise equability (${}^qE(T_{pw})$) are nearly identical, indicating that use of an appropriate comparison would not have changed general conclusions. Nonetheless, this example demonstrates the ease with which researchers may not realize subtle characteristics of the metrics that they use or how those nuances could affect conclusions or interpretation of results. In this case, different mechanisms can be responsible for patterns of pairwise equability versus those for total equability.

Case study 2: Niche theory, stress, and competitive exclusion

Niche theory (Chase & Leibold, 2003; Hutchinson, 1959) predicts that species with extensively overlapping resource needs cannot co-exist, leading to either species exclusion—on ecological timescales (Question 2)—or interspecific divergence of traits—on evolutionary timescales. The most effective unit of study for addressing this question is the ensemble (Figure 1) because that unit includes all of the species that are competing with each other for similar resources and have analogous or homologous traits. Local guilds and taxonomic guilds also consist of species that use similar resources; however, the use of either of these is complicated by conceptual or practical limitations. Local guilds include species for which it may be difficult to identify homologous or analogous traits that can be measured to reflect similar characteristics of resource use, making estimation of functional similarity particularly challenging. By contrast, taxonomic guilds are not confined to species that co-occur and compete for resources, meaning that this concept does not define a group of species that interact in ways that could define their niche spaces. To evaluate how species sorting generates local communities from the regional pool (Leibold et al., 2004; Soininen, 2014), measures of the magnitude or variability of species trait dispersion and equability can be compared between regional pools and local ensembles. For these comparisons, one would not want to use abundance-weighted measures because the meaningfulness of abundance at a

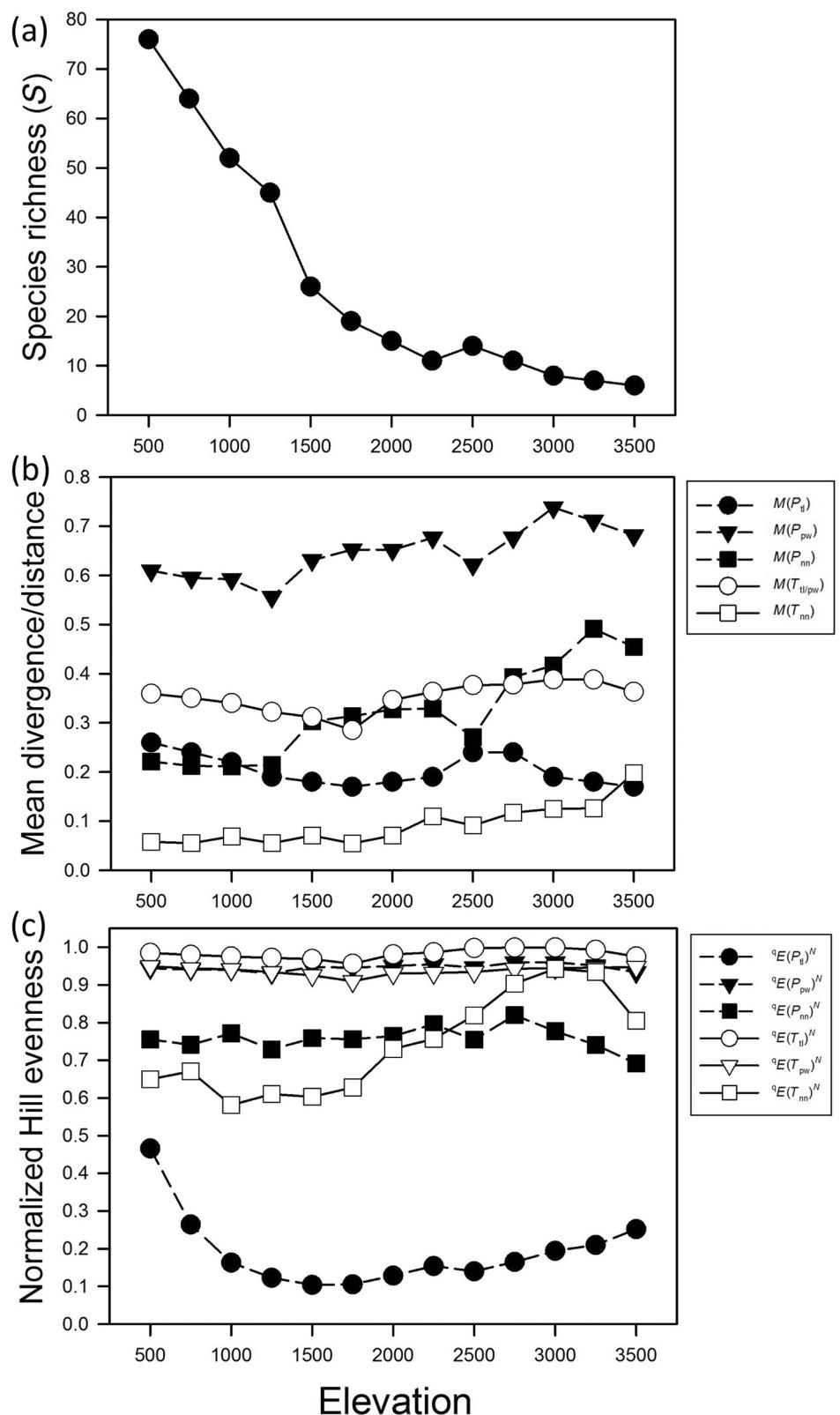


FIGURE 4 Diversity metrics as a function of elevation for a pool of 92 bat species at Manu, Peru. (a) Species richness, (b) means, and evenness (c) of standardized phylogenetic divergences (solid symbols) and trait-space distances (open symbols) based on total means (circles), pairwise means (squares), or nearest neighbors (triangles). Data are from Scheiner et al. (2017a, 2017b).

regional scale is unclear and challenging to quantify, and it is important to use the same measures at all scales in such a comparison. If the sorting process is happening at the level of the entire ensemble due to diffuse competition, the most appropriate measures of functional dispersion are those among all species in the ensemble, such as pairwise measures, mean trait dispersion ($M(T_{tl/pw})$), and Hill pairwise equability (${}^qE(T_{pw})$). Instead, if direct competition is more important, nearest-neighbor measures such as mean nearest trait dispersion ($M(T_{nn})$) or Hill nearest equability (${}^qE(T_{nn})$) should be used. Analogous measures can be used to evaluate patterns of evolutionary divergence, except in this case the appropriate units of study are ensembles or taxonomic guilds, which are sets of relatively closely related species.

Comparisons of aspects of functional trait diversity can also be made among groups of species along a resource gradient. For example, we can consider displacement or density compensation between strongly competing species, in which case measures that account for the abundances of nearest neighbors in trait space ($MA(T_{nn})$ and ${}^qEA(T_{nn})$) would be most appropriate. On a longer time scale, the focus would be on evolutionary divergences and regularities among species, but in this case, it is likely inappropriate to weight by abundance ($M(P_{nn})$ and ${}^qE(P_{nn})$), as abundances can vary greatly over evolutionary time. Alternatively, we could consider the total range of trait values exhibited by a group of species, predicting that an increase in environmental harshness should result in a decrease in the range of trait values (Swenson & Enquist, 2009; Weiher & Keddy, 1995). In this case, a measure of total divergence of the local guild or ensemble ($M(T_{tl/pw})$, KW) would be more appropriate than abundance-weighted measures.

For the Manu bat studies, we examined patterns of phylogenetic and trait divergence, regularity, dispersion, and equability for nearest neighbors (Figure 4). Bat species richness and richness within each guild decline with increasing elevation at Manu; however, the number of guilds remains relatively constant along the gradient, with six of the eight guilds present at all elevations (see Fig. S1 in Scheiner et al., 2017b). As a result, divergence ($M(P_{nn})$) and dispersion ($M(T_{nn})$) based on mean nearest-neighbor data increase with increasing elevation. This pattern holds for equability of trait values (${}^qE(T_{nn})$) but not for phylogenetic regularity (${}^qE(P_{nn})$). These patterns are the opposite of the prediction that environmental harshness will decrease the range of trait values, but likely reflect the inability of harsher, less productive environments to support multiple populations that are functionally similar (i.e., that rely on the same resource base). This results in fewer close competitors within each guild. The lack of close competitors due to harsh environments

being unable to support multiple populations of functionally similar species gave the appearance of increasing functional and phylogenetic diversity with elevation, but in reality, these patterns reflect a reduction in functional redundancy with elevation, thereby increasing values for nearest-neighbor metrics.

Case study 3: Biodiversity and productivity

Relationships between biodiversity and productivity (Question 5) have been the subject of extended debate and controversy (e.g., Mittelbach et al., 2001; Waide et al., 1999; Whittaker & Heegaard, 2003). Typically in such studies, biodiversity is measured as species richness (see references in Mittelbach et al., 2001). In all cases, the unit of study should, but rarely does, include all members of a trophic level (e.g., all primary producers). This relationship can be further probed by considering functional trait diversity. Often this is done by counting the number of functional types in a community (e.g., Fischer et al., 2018; Gherardi & Sala, 2015; Robinson et al., 2019), but this is a very crude metric of functional biodiversity. Instead, we could use a common metric of dispersion: functional attribute diversity ($\Sigma(T_{tl/pw})$ (= FAD), Appendix S1: Table S3). Unfortunately, this metric combines dispersion and species richness, confounding the ability to evaluate spatial patterns of functional biodiversity. To disentangle the effects of those two components of biodiversity, we should use a metric of functional trait biodiversity that is independent of species richness, such as mean trait dispersion ($M(T_{tl/pw})$).

Here, we demonstrate how one can be misled by failing to use independent metrics that isolate particular data types (e.g., functional traits). A study of trees in the eastern United States (Liu et al., 2024) addressed the question of which measures of biodiversity best predict productivity. We delve into the background analyses in that research to illustrate the importance of considering the appropriate metric. The data comprise 23,145 plots from the Forest Inventory and Analysis (FIA) Program of the USDA Forest Service (<https://www.fia.fs.usda.gov/>). The trees are a local guild as the study unit does not include all of the angiosperms that are located in each plot. The extent of the unit of study in this instance is the eastern United States and the grain is an individual FIA plot. Productivity was measured as the increase in the biomass of trees between censuses (growth). Here, we compare the relationships between productivity and two measures of functional trait diversity, mean trait dispersion ($M(T_{tl/pw})$), and functional attribute diversity ($\Sigma(T_{tl/pw})$). Liu et al. (2024) used a metric that weighted dispersion by abundance ($MA(T_{pw})$), which might be

considered to be more appropriate because it weighs the effects of common species more heavily (Storch et al., 2018). However, because $M(T_{tl/pw})$ and $MA(T_{tl/pw})$ were highly correlated (Pearson correlation, $r = 0.83$), we use the former for simplicity.

Mean trait dispersion ($M(T_{tl/pw})$) and functional attribute diversity ($\Sigma(T_{tl/pw})$) had opposite relationships with productivity for trees in the eastern United States, exhibiting negative and positive relationships, respectively (Figure 5a,b). The latter relationship was driven by the positive relationship of species richness and productivity (Figure 5c) because functional attribute diversity is confounded with species richness (Figure 5d). The negative relationship of the independent measure of functional trait diversity ($M(T_{tl/pw})$) to productivity is surprising, as it contradicts the theory that species with different functional traits will either use a wider variety of resources or respond in different ways to temporal

heterogeneity, leading to greater total productivity (Naeem et al., 2012). Liu et al. (2024) proposed four hypotheses for this discrepancy that are not mutually exclusive. Some of those hypotheses either challenge the theory itself or suggest that the way one measures functional trait diversity may be misleading. These challenges would not have been apparent without disentangling the different components of the units of biodiversity as illustrated here.

Case study 4: The theory of island biogeography

The theory of island biogeography (MacArthur & Wilson, 1967; Sax & Gaines, 2011; Whittaker et al., 2008) posits two different phases during the build-up of species on islands over ecological time, an initial colonization

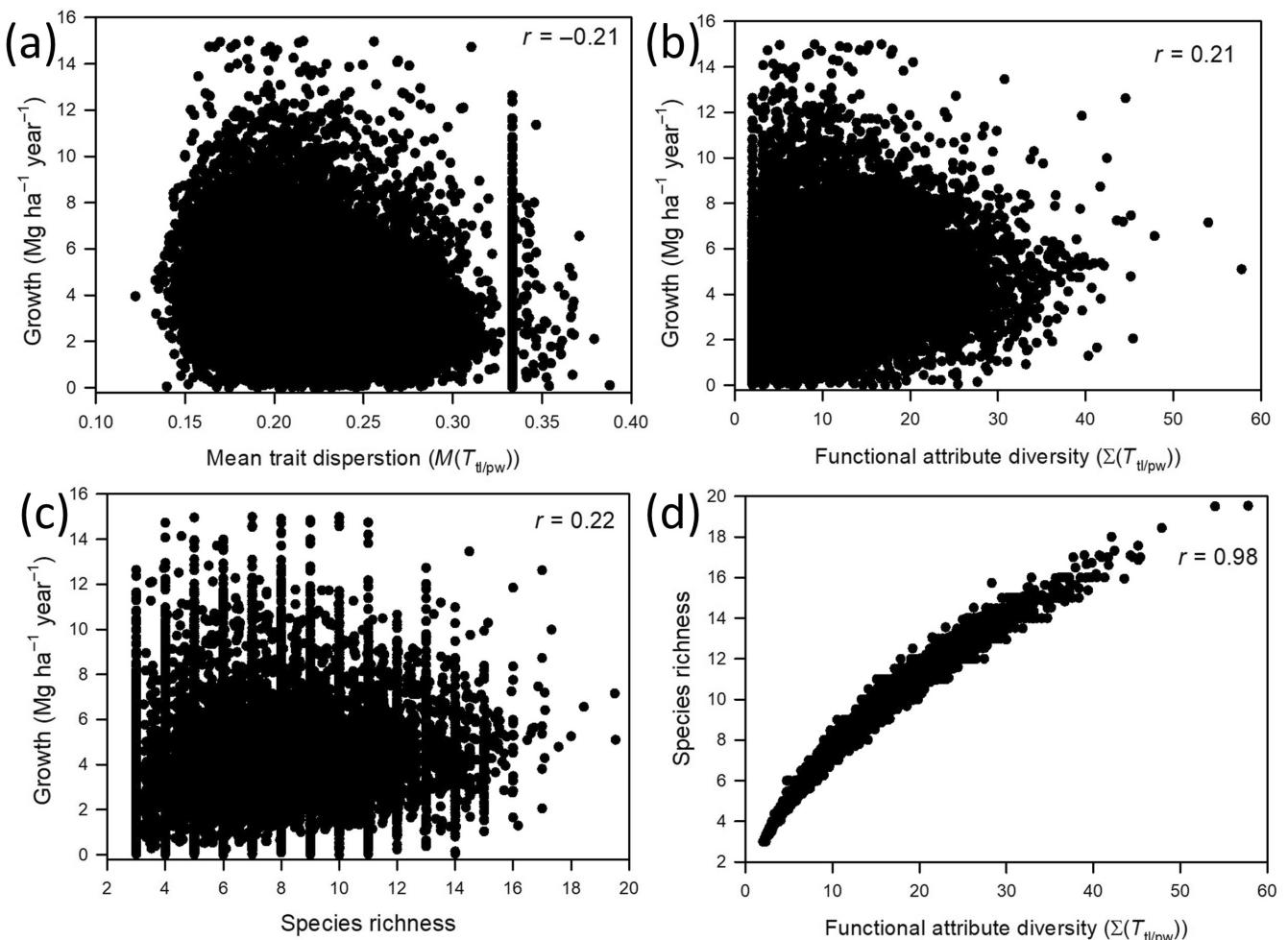


FIGURE 5 (a) The relationship between productivity, measured as the rate of growth in aboveground biomass, and functional trait diversity, measured as mean trait dispersion ($M(T_{tl/pw})$) for trees in the eastern United States. (b) The relationship between productivity and functional trait diversity, measured as functional attribute diversity ($\Sigma(T_{tl/pw})$). (c) The relationship between productivity and species richness. (d) The relationship between species richness and functional attribute diversity. Data are from Liu et al. (2024).

phase during which the species on an island should be a subset of the source pool determined primarily by inter-specific variation in dispersal ability (Question 10), followed by a phase of extirpation based on in situ inter-specific interactions (Question 9). In this context, the physical units of study are islands that differ in size or degree of isolation. The biotic units of study are the ensembles or assemblages on each island and the corresponding taxonomic guilds that comprise the source populations. During these phases, comparisons of functional biodiversity of ensembles or assemblages from different islands should use total trait divergences and equitabilities ($M(T_{tl/pw})$ and $^qE(T_{tl})$) because the focus is on ecological processes of colonization and competition. Over longer, evolutionary time and with increasing isolation, local speciation should decrease mean phylogenetic diversity relative to the source pool, as closely related endemics come to dominate on different islands if phyletic evolution gives rise to the new species or if allopatric speciation gives rise to new taxa and both persist on the same island, even if in different zones or habitats. In the case of allopatric speciation, if one of the sister species goes extinct, there would be little effect on phylogenetic diversity. Such a pattern could be observed by measures of pairwise divergence ($M(P_{pw})$) of ensembles.

Case study 5: Biodiversity, pathogen transmission, and the dilution effect

The dilution effect posits that pathogen transmission within a group of species decreases as the relative abundance of non-competent hosts increases (Dobson & Randolph, 2012; Ostfeld & Keesing, 2000). As noted by Keesing and Ostfeld (2021), the proper comparison should account for abundances, as well as richness of host species (Question 5). In this case, the local “guild” is defined by the group of potential host species for a pathogen within a host community, which can be taxonomically diverse (e.g., birds and mammals for influenza; mammal, birds, and reptiles for Lyme disease). Comparisons among communities would be of abundance-weighted species richness ($^qD(A)$). But we could go further and measure equability of those species based on traits such as infectivity or immunological competence. For example, if there is a trade-off in host species regarding infectivity by different hosts, species that are more distant in trait space are more likely to be less competent for the same pathogens. In that case, communities with species that have more equal numbers and are more evenly distributed in that trait space ($^qDA(T_{pw})$) should have lower transmission rates because of a greater opportunity for a pathogen to reside in lower-competence hosts. Host competence might have

a phylogenetic component, in which case $^qDA(P_{pw})$ would be an appropriate metric, especially if the traits that affect host competency have not been identified or measured.

CONCLUDING REMARKS

We have created a comprehensive framework that organizes biodiversity metrics based on units of study and units of measurement. This framework and the associated metrics enable a more deliberate metric selection process for testing ecological and evolutionary theories and for exploring patterns of biodiversity and their causes. The many choices of metrics, and the nuanced differences among them, make it imperative to be thoughtful about the choice of metrics, rather than blindly using the few most commonly found in the literature or those most easily calculated from software packages.

The ability to distinguish among metrics that represent the basic elements (Table 3) versus those that represent combinations of elements is foundational to the effective use of biodiversity metrics in both theoretical and applied research. Basic elements can be useful if the goal is to separate causes, as with our example of the relationship between productivity (tree growth) and functional diversity. In other cases, ecological and evolutionary theories depend on density- or frequency-dependent effects of species richness, such as the dilution effect on pathogen transmission. In these cases, composite metrics are most appropriate. Conservation efforts are typically focused on maximizing the number and types of species in a system of interest, suggesting that metrics representing the effective numbers of species may be most appropriate in such contexts. Our framework simplifies the identification of appropriate metrics.

Our efforts are initial steps in the systemization of measures of biodiversity. Our framework for units of study (Figure 1) is designed with species as the focal entity, although others are possible. While many of the metrics that we present can be applied to such other entities, our framework would require modification for those levels. For example, genes do not have niches and ecosystems do not have phylogenies. Even for species within communities, there are aspects of their biodiversity that are not captured by our framework, such as the spatial arrangement of individuals. Thus, we make no claim that our framework is all encompassing. For example, many of the metrics in Appendix S1: Table S1, while including a measure of effective numbers of species, are not effective numbers themselves because the weighting factors are not constrained to the interval [0,1]. Given the interest in maximizing the effective numbers of species that

can be conserved, development of weighted metrics that are effective numbers is warranted. Although hierarchical partitions into α - and β -components have been developed for some of the metrics, they have not been formalized for many others. Similarly, sampling-bias corrections have been developed for some but not all metrics.

Our key recommendations are that researchers should: (1) match study unit properties to the nature of scientific questions, (2) match metric properties to the processes under consideration, and (3) only compare metrics with similar properties. Our intention is not to reduce the use of biodiversity metrics to a simple set of guidelines for determining which study and measurement units relate to particular ecological or evolutionary processes or to particular types of questions. Rather, we hope that our characterization of metrics and the resulting framework will facilitate the better use of biodiversity metrics by ensuring that they match their hypotheses or applications.

AUTHOR CONTRIBUTIONS

The paper was conceived by Samuel Scheiner. The original draft was written by Samuel Scheiner and Michael Willig. All authors contributed to the further refinement of ideas and metrics, as well as to the amplification of the text.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data for bats at Manu Biosphere Reserve are available in Scheiner et al. (2017b) at <https://doi.org/10.1111/2041-210X.12696>; incidence data are provided in Table S3f, and trait data are provided in Table S4. The phylogenetic relationships are available from the supertree in fig. S1 of Bininda-Emonds et al. (2007) at <https://doi.org/10.1038/nature05634>; for the ten species that were not present in the supertree, the closest congener was used. The data for the trees of the eastern USA forests were downloaded from the Forest Inventory and Analysis (FIA) database version 9.0 (<https://research.fs.usda.gov/products/dataandtools/fia-datamart>) in November 2022; the data were further filtered as shown in Appendix S1: Table S7.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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