Chapter 1
Phylogenetic Diversity and Conservation Evaluation: Perspectives on Multiple Values, Indices, and Scales of Application

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Abstract "Phylogenetic diversity" and its abbreviation "PD" have now become popular terms describing a fundamental aspect of biodiversity based on phylogeny. After more than 25 years of work on PD (following the 1992 paper in *Biological Conservation*), methods and applications have explored a wide range of taxonomic groups and geographic scales. PD provides a way to address biodiversity at the level of features or characteristics of species, based on its well-corroborated model linking phylogeny and feature variation. The quantification of feature diversity justifies PD as a measure of option value – the value of living variation in keeping options open for society. This justification for PD in biodiversity conservation gives attention to often-neglected arguments for the value to society of biotic diversity. These largely global option values are complemented by the "insurance" value of PD at the local ecosystem scale. Microbial applications of PD, particularly in human health studies, have successfully implemented a range of PD calculations, including PD dissimilarities among samples. Reduced microbial PD in the human body may indicate reduced resilience, and it is now associated with many human diseases. "Macrobial" ecology has been less successful in integrating PD into a consistent coherent approach. Here, the traditional recognition of many "diversity" indices has been extended to phylogeny. PD as a "biodiversity" measure is confounded with the multitude of phylogeny-based diversity indices describing various ecological factors. Greater integration among the different areas of PD application could better establish PD as a core biodiversity measure, with a shared toolbox providing a range of PD-related calculations.

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Background

My title echoes the title of the paper, "Conservation evaluation and phylogenetic diversity" (Faith 1992) which proposed "phylogenetic diversity" ("PD") as a natural phylogeny-based measure of biodiversity. The definition of PD provided in that paper was deceptively simple: the PD of a subset of species (or other taxa) from a phylogenetic tree is the total length of the branches spanning that subset on the tree. I say "deceptively" for two reasons. First, that simple definition corresponded to a not-so-simple framework to quantify the relative "feature diversity" of subsets of taxa, equating features with the units of biodiversity that we would like to count up. Second, feature counting meant that the simple definition of PD did not just define one simple "index." Instead, it established a basis for a whole family of associated calculations (the PD "calculus") that could be used for practical decision-making in biodiversity conservation. As I will discuss in this perspectives paper, these not-so-simple aspects of PD continue to be debated in the many studies that now apply, critique, and extend this popular approach.

As my title also indicates, the many published PD studies now range widely across taxonomic groups and scales of application. Prior to 1992, a handful of papers had used the term "phylogenetic diversity," largely descriptively. Following the Faith (1992) paper, there have been about 5000 papers in *Web of Science* with the key term "phylogenetic diversity." At the time of this writing, the 1992 paper is the most-cited paper ever in *Biological Conservation* from the more than 7000 papers in that journal spanning more than 40 years. While there are some partial reviews of this work, for example, by Porter and Hajibabaei (2018) in the genomics context, in a recent book (Pellens and Grandcolas 2016), and in Faith (2015, 2016, 2017) (see also Chap. 7), there appears to be no single review covering the full range of PD studies.

Some exciting areas of PD application have departed from organismal phylogeny. As examples, PD is now applied to conservation of "phylogenetic language diversity" (Gavin et al. 2013), and PD is used as an analogous biodiversity measure for hierarchies other than phylogenies (environmental hierarchies, e.g., Faith 2013, and functional trait hierarchies, "FD", Petchey and Gaston 2002). As I will discuss below, more communication is needed among all these different areas of PD application. This need includes better integration of the PD work in microbial and macrobial ecology.

As preparation for discussion in this chapter of the ongoing applications of PD, it is useful first to look back at PD's "prehistory" (the history of a term before it was invented; see Faith 2017). This reveals how PD naturally emerged from some important precursors, including early discussions about biodiversity's value, about "taxonomic distinctiveness," and about how phylogeny informs us about characters or features.

It is commonly thought that the development of methods for using taxonomy and phylogeny in biodiversity conservation was an "explosive radiation," given that several notable papers appeared at about the same time (e.g., May 1990;

Vane-Wright et al. 1991; Faith 1992; Weitzman 1992; Crozier 1992). The reality is that there was significant foundational thinking on this topic over the decade prior to the appearance of those papers. Foremost among this work was the “World Conservation Strategy” report by IUCN (1980). This single report foreshadowed later thinking on biodiversity option values, on ecological integrity, and on taxonomic distinctiveness (all relevant to this chapter) and also on the integration of distinctiveness and extinction threat (relevant to Chap. 4). These early IUCN influences complemented other foundations for PD, including early influential work in systematics that explored the links from phylogeny to features (discussed in Faith 1992).

As part of this Background section, I will discuss these precursors below, under the headings “Taxonomic Distinctiveness,” “The Link from Phylogeny to Feature Diversity,” “Option Values,” and “Insurance Value/Ecological Integrity.” With these in mind, the main body of this chapter then will explore some current challenges in applications of PD. Here, my discussion of microbial and “macrobial” ecology applications will complement the discussion of PD at the regional/global conservation scale, found in other chapters in this book (Chaps. 4 and 8).

Taxonomic Distinctiveness

The development of PD involved sorting out what we mean by “distinctiveness” as compared to “diversity.” For IUCN (1980), the reference to taxonomically “distinct” species implied differences among species, presumably in characters. IUCN referred to “the greater the gap between the nearest related family (or genus) and therefore the more distinct” and noted:

> The size of potential genetic loss is related to the taxonomic hierarchy because, ideally at least, different positions in this hierarchy reflect greater or lesser degrees of genetic difference, and hence difference in such variables as morphology…

Following IUCN, this basic argument about taxonomically distinct species appears to have inspired early work on related priority setting. Faith (1994a), for example, noted that several state agencies in Australia had been working on taxonomic distinctiveness and priorities during the late 1980s. Later important work focused specifically on quantitative measures of taxonomic distinctiveness (Weitzman 1992; Vane-Wright et al. 1991). The Faith (1992) reference to distinctiveness was more oblique, but it very much motivated the basics of an emerging PD calculus, as described below. PD was from the outset much more than a single index of biodiversity; it also provided a set of associated calculations that quantified distinctiveness and complementarity (gains and losses in biodiversity). Faith (1992) established an important perspective on distinctiveness and diversity by linking these to the implicit counting up of features of species. Distinctiveness of a species then was not a static quantity, but would depend on the context:

> Species that are taxonomically distinct will be expected to make a large contribution to some overall measure of diversity of any subset of the total set of species. This is apparent if species are replaced as the basic units (or attributes) of biological diversity by features of

> species. Taxonomically distinct species then contribute more to the diversity of a given subset because they contribute different “features”.

Thus, the Faith (1992) discussion of distinctiveness and features echoed the IUCN reference to “genetic difference” and morphology.

Faith (1992) referred to the contribution of the terminal phylogenetic branches to the total PD as the “length of a terminal branch (corresponding to the number of uniquely derived features for the terminal taxon)” (Faith et al. (2004) later described this as the “PD endemism” or the “unique PD contribution” of a species). More generally, this complementarity contribution is calculated as the gain in representation of feature diversity if another species or another area is added to the set (Faith (1992) simply called this “G” for gain). G is the increment in the PD estimate of the number of new features resulting from the addition of a new taxon to a subset.

Thus, we not only might calculate the total PD, say, of the mammal species represented in a set of protected areas but also use PD calculations to add and subtract and compare sets. This discussion reveals how “biodiversity” – here, an estimated total number of features – is related to companion calculations such as distinctiveness or complementarity that reflect *additional* features relative to some existing set. This family of calculations is important; to select a *set* of species that collectively captures maximal biodiversity, we cannot just select individual species that were designated at the start as individually “distinctive.” We must use dynamic distinctiveness or complementarity (a process nicely illustrated in examples in Faith 1992 and later papers).

This consideration is fundamental to conservation policy. I note that the World Conservation Conference (WCC 2012) proposed distinctiveness as an important conservation criterion, resolving to halt the loss of evolutionarily distinct lineages. However, any efficient program for preserving PD must utilize the dynamic forms of distinctiveness, within a program perhaps resolving to halt the loss of our evolutionary heritage.

The Link from Phylogeny to Feature Diversity

PD is one example of a general biodiversity framework (Faith 1994b, 2017) in which a process-based model is used to make inferences about the relative number of different “units” contained in any given set of objects. For example, the “ED” (“Environmental Diversity”) strategy infers the relative number of ecological traits among different sets of species, based on a process-based model related to adaptions to environmental gradients and “niche space” (see e.g., Faith 1994b, 2015, 2017). PD was based on the well-established idea that phylogenetic pattern is informative because shared features (the “units” of biodiversity) are accounted for by shared ancestry (Faith 1992, 1994a,b). This means that the basic PD calculation of gains and losses of feature diversity is based on summed phylogenetic branch lengths.

Phylogeny is informative about features generally. Not only do we not know, in general, the future value of different features (discussed in the next section), but also, we cannot even list the features for most species. Phylogenetic pattern provides one way to estimate and quantify this variation at the feature level. A species complements others in representing additional evolutionary history (Faith 1994a,b), as depicted in the branches of the estimated phylogeny.

As noted above, the degree of complementarity reflects the relative number of additional features contributed by that species. For example, given some subset of species that are well-protected, and two species in that taxonomic group that are endangered, the priority for conservation investment may depend on the relative gains in feature diversity (the complementarity values) expected for each species. We do not know in practice what all the actual features are, but we can make predictions about these relative gains and losses.

How well can phylogeny inform us about feature diversity? Faith (1992) did not propose an untested model or assumption for this link. In fact, the PD assumption that shared ancestry explains shared features had reasonable justification based on already accomplished tests. In this context, an established form of testing was noted by Faith (1992): the PTP (permutation probability test of Faith and Cranston (1991)) evaluates whether the shared-ancestry model explains the given feature/character data better than expected by chance (e.g., compared to randomized characters). Faith (1992) cautioned against relying on trees (or "cladograms") that do not pass PTP and so do not provide corroboration (Faith and Cranston 1992) of this shared-ancestry/shared-features model:

> Cladograms based on a small number of characters, or on characters that exhibit large amounts of homoplasy (convergences and reversals in the derivation of features), are probably less reliable, as indicated by recently developed statistical approaches for evaluating cladograms. (Faith and Cranston 1991, and references therein)

The PTP test of Faith and Cranston (1991) evaluates how well a set of observed characters or features all can be explained by shared ancestry on a single phylogeny. PTP counts up the total number of "steps" on the tree – if a shared feature is accounted for by shared ancestry, only one step is needed. The total count ("parsimony" value) is compared to parsimony value scores under a null model where the features are randomly assigned to species. A significant result supports the PD model. PTP therefore is not just any arbitrary test for "phylogenetic signal"; it specifically corresponds to evaluating the PD shared-ancestry model.

The nature of these tests is important. Because PD does not assume that every feature is accounted for by model (Faith 1992), it is not strictly falsifiable. However, the PTP test is well-established as a method for corroboration assessment (see Faith and Cranston 1991, 1992). Corroboration of a hypothesis is found when the apparent supporting evidence for the hypothesis could not have been found easily by chance alone. For a set of characters/features, the count of the number of shared features explained by shared ancestry is evidence for the PD model, and this provides corroboration when that count could not have been found easily by chance alone.

Since 1990, there have been many PTP tests using actual character data sets, over many different taxonomic groups. How well have these supported the PD model? While Faith (1990) documented a dramatic case where the characters failed the PTP test, most character sets have passed the test. For example, Slowinski and Crother (1998) examined PTP tests on 40 published and unpublished character data sets, and all but one character set passed. Wilkinson et al. (2002) surveyed existing tests and reached the same conclusion, noting:

> PTP is a relatively conservative test statistic. Over a range of numbers of taxa, characters, character states, and relative proportions of character states the Type 1 error rate is mostly <5%.

Thus, PTP tests often "reject the null hypothesis" and this rarely is an incorrect rejection. We can conclude that the shared-ancestry model linking PD to feature diversity is well corroborated based on many published PTP tests that corroborate the PD model.

From the outset, Faith (1992) also emphasized that PD should not be expected to magically make inferences about every favorite character or feature. While we have the intuitive, fundamental, link between shared ancestry and shared features, the history of phylogenetics shows that homoplasy ("extra steps" on the phylogeny, as for convergent evolution) also is common. Faith (1992) cautioned that "the diversity patterns for some features (namely those incongruent with the cladogram in implying extra steps) may be poorly predicted by phylogenetic diversity." Faith (1992, 1994a,b, 2015) suggested that alternative patterns and models (including the "ED" approach; see Faith 1994b) are more effective for inferences about such features (or ecological traits).

The early development of PD as a measure of biodiversity at the level of features recognized several important properties that are relevant to issues often raised in PD research and applications. First, while PD is the measure of biodiversity at the level of features, that inference of features allows many associated companion calculations. Indeed, any index conventionally defined at the species level (endemism, dissimilarity, expected loss, etc.) has a PD counterpart (Faith 1994b; see also Faith 2013, 2017). Second, PD drew upon a link between phylogeny and features that was already well tested and corroborated. Third, shared convergently derived ecological traits were highlighted as not well predicted by PD, and an alternative approach based on a shared-habitat/shared-traits model was proposed (Faith 1989, 1992, 1994b; see also Faith 2015, 2017).

Option Value

PD provides a useful calculus at the level of features for conservation decision-making, but why should we worry about conserving all that feature diversity? Faith (1992, 1994a,b) proposed that PD as a measure of feature diversity provided a fundamental current value of biodiversity – called "option value." This reflects the idea, as Faith (1992) described it, that "society may be able to benefit (e.g. economically) from features of these species in response to future needs." IUCN (1980) not only provided foundations for PD's recasting of distinctiveness but also provided a rationale for "option value." However, as described below, IUCN (1980) also reflected insights on such values from the previous decades.

The term "biodiversity" refers to the variety of life, and the earliest discussions of its values (in contrast to discussions of the value of individual species) logically reflect the value to society of such living variation. In fact, such discussions precede the actual invention of the term "biodiversity" (around 1985). Early discussions of the value of variety referred to "biotic diversity," for example. Faith (2017) sketched what he called the "prehistory" of the term "biodiversity" – basically the history of that term before it was invented.

A message emerging strongly in the 1970s was that the crisis of disappearing species could be thought of as a loss of biotic diversity and that this loss matters because it means a loss of options for future generations (e.g., Ehrenfeld 1970; Iltis 1972; Haskins 1974; Roush 1977; see also reviews by Mazur and Lee 1993; Farnham 2007). For example, back in 1972, the botanist, H. H. Iltis, argued to "preserve sufficient diversity of species and of ecosystems" because "we will never reach a point where we shall know which organisms are going to be of value to man and which are not" (Iltis 1972). Myers (1976) argued that loss of what he called "the spectrum of species" "will affect generations into the indefinite future, whose options to utilize species in ways yet undetermined should be kept open." A clear message from these early prehistory papers was that biotic diversity or living variation provides what we can call "option value" or "maintenance of options."

Later, IUCN (1980), in making it clear that conservation "is for people," argued that "preservation of genetic diversity" (their stand-in for the not-yet-defined "biodiversity") "is both a matter of insurance and investment to keep open future options." The investment aspect is "prudent," they argued, because "we cannot predict what species will become useful to us." This nicely echoes the arguments from the previous decade about the option value of biotic diversity. In the next section, I will return to this quote to consider the companion "insurance" aspect.

Option value of biodiversity typically refers to a global benefit for people. Several chapters in this book look at regional/global PD conservation (see Chaps. 4 and 8). Much of this regional/global PD work links to its option value rationale (see also Faith and Richards 2012; Jetz et al. 2014; Thuiller et al. 2011, 2015; Laity et al. 2015; Mouillot et al. 2016; González-Orozco et al. 2016; Pollock et al. 2017). This rationale also extends below the species level. Faith (1992) also proposed within-species geographic priority setting using PD on phylogenetic patterns for within-species genetic variation. Carvalho et al. (2017) developed this further as "the intraspecific phylogeography of multiple species into spatial prioritization."

The PD study of Mouillot et al. (2016) nicely summarized the recognition of PD as indicating global biodiversity option value:

> "Global marine protected areas do not secure the evolutionary history of tropical corals and fishes": "…phylogenetic diversity, represented by the Tree of Life, is becoming an increasingly important component of conservation science since it represents the breadth of

> evolutionary history and supports biodiversity benefits and uses, often unanticipated, for future generations."

Larsen et al. (2012) highlighted the challenge in biodiversity conservation to find a "robust proxy" for global option values, and they concluded that "maximizing the retention of phylogenetic diversity (PD) should also maximize option value."

Forest et al. (2007) carried out a further evaluation of PD as a measure of feature diversity and option value. Using a phylogenetic tree, and a handbook for useful genera found in the Cape hotspot of South Africa, they demonstrated that if we did not know about these medicinal, food, and other uses, then preserving sets of species with high PD would be a good way to preserve these unknown benefits.

Support for PD as a measure of option value is found also in philosophy of science work (e.g., Maclaurin and Sterelny 2008; Faith 2017) and among economists (e.g., Nehring and Puppe 2004). Option value of biodiversity has been promoted well by conservation groups (Gascon et al. 2015) in presenting many examples of surprising benefits from biodiversity. Gascon et al. also noted the "measurement" problem and pointed to "phylogenetic diversity" as a likely good measure of option value.

Chapter 4 of this book describes the important assessment, by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), of PD as a measure of maintenance of options. The Asia-Pacific IPBES assessment (Davies et al. in press) complemented the assessment of PD status with examples of recent unexpected benefits in the region (e.g., noting how the venom of an Australian funnel web spider was found to be the unlikely source for a drug to ward off brain damage caused by strokes; Chassagnon et al. 2017).

PD measures option value, but this does not mean that its conservation utilizes measures only quantifying total PD. The calculus of PD is a calculus of option value. The Laity et al. (2015) study illustrated how the most useful measures for planning and decision-making typically will employ calculations based on PD (endemism, complementarity, etc.; see also Mouillot et al. 2016; Pollock et al. 2017; Veron et al. 2016) rather than total PD. Studies continue to move beyond the local scoring approaches that simply score total PD (e.g., of a grid cell). Scherson et al. (2017) applied some important recent extensions of the PD calculus for spatial analyses, in their study "Spatial Phylogenetics of the Vascular Flora of Chile." PD of individual grid cells, which may not on its own be informative for regional conservation, was complemented by maps showing places with high PD endemism. The calculus has been important in highlighting how PD and species richness calculations for decision-making, such as complementarity, are disconnected (see Forest et al. 2007).

This fundamental point about the PD calculus is still not universally appreciated. For example, Lindegren et al. (2018) used within-area PD for marine conservation priority setting at the global scale, ignoring the marine PD global planning of Mouillot et al. (2016), based on complementarity. Lindegren et al. claimed that lack of correspondence among areas between PD and richness of other aspects of biodiversity or of ecosystem services implies conflicting objectives requiring tradeoffs in designing a protected areas system. In fact, when we consider what matters in designing a protected areas system – complementarity – it is apparent that an efficient system could require no trade-offs, even when richness values lack correspondence.

This section has documented the very early roots of biodiversity option value (even before the term "biodiversity" was invented) and how this is increasingly appreciated as the motivation for PD conservation, particularly at the regional and global scale. The next section examines a closely related biodiversity value that can be associated with PD, providing a possible stronger link to the ecological theme of this chapter.

Insurance Value/Ecological Integrity

In contrast to the previous section, this section will not highlight an early connection to PD. Faith (1992, 1994a,b) did not consider the within-ecosystem community level and did not really consider insurance value (beyond the basic idea that PD is associated with evolutionary potential). Biodiversity insurance value has a range of interpretations but generally relates to resilience in the face of unanticipated environmental changes; viewed anthropocentrically, this maintains ecosystem functions and services. I referred above to the IUCN (1980) arguments that "preservation of genetic diversity is both a matter of insurance and investment." I noted their argument that the investment aspect, related to option value, is "prudent" because "we cannot predict what species will become useful to us." I now consider the other half of their statement, that insurance aspect is prudent as well, because we cannot predict which species will maintain ecosystem services or other benefits in the face of change.

IUCN (1980) nicely combined both of these aspects of biodiversity value, in describing arguments for the conservation of "the range of genetic material found in the world's organisms":

> we may learn that many species that seem dispensable are capable of providing important products, such as pharmaceuticals, or are vital parts of life-support systems on which we depend.

This value dualism as described by IUCN seems to have been a precursor for later summaries of these dual values. For example, Bartkowski (2017) descriptively linked option value/investment to "demand" and insurance value to "supply":

> the two perspectives – insurance and options – are inherently interlinked; however, they depend on different types of uncertainty (supply vs. demand), which makes the differentiation sensible.

Support for these ideas also can be found in the early history of discussions of the "insurance" value of biodiversity, preceding IUCN (1980). This history overlaps with that of option value. Both Roush (1977) and Ehrenfeld (1970), in discussing the value of biotic diversity, distinguish between a within-ecosystem functioning/stability argument and a very different option value argument. Norse and McManus

(1980) similarly discussed both global biodiversity and within-ecosystem diversity for functioning.

Later, Ehrlich and Wilson (1991) echoed these ideas in listing three reasons why we care about biodiversity. One was "moral responsibility," and the second was the future unanticipated benefits (option value). The third was the support for the "recognized ecosystem services provided by natural ecosystems." In the latter case, they made an indirect link to biodiversity in arguing that "diverse species are the key working parts" of such ecosystems. This suggests that this value dualism can be summarized as the value of biodiversity – all the components or units – for unanticipated benefits (option value) or for unanticipated systems support (insurance value).

All this seems straightforward, but insurance value of "biodiversity" cannot be discussed without considering the definition of "biodiversity" and how it relates to ecological "diversity." It is revealing that the Ehrlich and Wilson (1991) insurance argument that "diverse species are the key working parts" echoes the IUCN (1980) insurance phrasing pointing to "vital parts of life-support systems." Both phrases are vague; there are lots of ways that "vital parts of life-support systems" and "diverse species" as "key working parts" might provide insurance that functions and services continue in the face of unanticipated change. Generally, these turn out to be more about ecology than about "biodiversity" in the sense of counting up units.

As an example, Bullock et al. (2017), in discussing insurance value, argued that "resilience is contained in the dynamic and innumerable interactions." Similarly, Pascual et al.'s (2015) statement that the insurance value of soil biodiversity could be inked to "particular soil organisms" also clearly departed from biodiversity as variety. Both of those examples of ecological aspects we might want to measure could fall under the broad banner of "ecological diversity" measures.

One might anticipate that these ecological aspects of insurance (abundance of key species, interactions among species, etc.) logically then would not be characterized as insurance derived from biodiversity as variety. However, this highlights what is perhaps the biggest conundrum in current biodiversity science. On the one hand, "biodiversity" can be interpreted as counting up some nominated units (as advocated by Faith 2017). On the other hand, "biodiversity" might be defined or interpreted as including all those ecological factors, so providing a self-fulfilling prophecy that "biodiversity" is critical to producing and insuring ecosystem services (for discussion, see Faith 2017).

If "biodiversity" is accepted strictly as variety and a counting-up, this has an intuitive link to a natural companion of insurance value – the precautionary principle (basically, the idea that it is prudent to keep all the units, in the absence of knowledge about what the importance of different individual units will be in the face of change). Here, there is a nice parallel with option value and unanticipated benefits. With good knowledge, we may guess the kinds of species or other units likely to deliver unanticipated benefits, but in the absence of such insider knowledge, it is prudent to maintain the biodiversity (all the units), as a kind of investment (to use IUCN wording). Just as we have a *precautionary* principle that addresses insurance, we have a *pre-beneficiary* principle that addresses option value/investment. Biodiversity is valuable because it helps us to be ready for unanticipated "cautions" (changes amounting to disbenefits) and helps us to be ready for unanticipated benefits.

Biodiversity, in the sense of counting up units, therefore has a clear role as insurance, but if we accept that simple perspective, what then happens to all those ecological factors that also may well play a role in insurance of functions and services? One possible reconciliation is that we recognize that these ecological aspects typically are not "biodiversity" but are related to "ecological integrity." Here again, IUCN (1980) has provided early guidance that is reflected in its current definition of "ecological integrity":

> maintaining the diversity and quality of ecosystems and enhancing their capacity to adapt to change and provide for the needs of future generations. (https://www.iucn.org/downloads/en_iucn__glossary_definitions.pdf)

Ecological integrity can include lots of ways in which "vital parts" and "key working parts" contribute – including single keystone species, key interactions among species, and many other aspects of ecology. If we know the system well, measures of integrity and insurance can reflect this ecological knowledge, but in the absence of such knowledge, it is precautionary to maintain biodiversity as insurance.

Thus, one way to view the current biodiversity conundrum is that we have a choice. Either (1) (as above) biodiversity is seen as counting up units, with "ecological integrity" complementing that by capturing the rich ecological story of resilience and insurance value, or (2) alternatively, the ecological factors (often expressed as "diversity" measures) are all taken to be part of "biodiversity."

This conundrum is evident already at the species level, but it has now imposed itself on the phylogenetic level – where every classic species-level ecological diversity measure has a phylogenetic counterpart. Are these measures all measures of "biodiversity" and, indeed, "phylogenetic diversity"? Or are they measures that sometimes might be "biodiversity" but mostly are related to "ecological integrity"?

In the sections below, I will examine the concepts and applications of PD in two sections about ecosystems and community ecology: microbial and "macrobial." Microbial workers have established a coherent framework that uses PD as a primary biodiversity measure while also taking advantage of the PD calculus. Macrobial workers, in contrast, have struggled to find a coherent conceptual framework, with most any phylogenetic index called "phylogenetic diversity" and with no awareness of the recognized utility of the PD model and the PD calculus.

Microbial Community PD

Applications of PD in microbial ecology owe much to the pioneering work of Lozupone and Knight (2005) and Caporaso et al. (2010), who have provided microbial workers with guidelines and tools for applying PD and its calculus (see also Faith et al. 2009).

A review by Lozupone and Knight (2008) refers not only to overall PD but also to "G" (see above) as part of the PD calculus: "PD tells us about the overall diversity of the lineages within a given community, G is a measurement of which communities contain the most previously unseen diversity (i.e. are the most phylogenetically unique)." Thus, early on, microbial workers appreciated the extension of distinctiveness to dynamic, context-dependent, complementarity values.

"G" and complementarity also linked strongly to Lozupone and Knight's "unique fraction" concept of dissimilarity:

> The unique fraction metric, or UniFrac, measures the phylogenetic distance between sets of taxa in a phylogenetic tree as the fraction of the branch length of the tree that leads to descendants from either one environment or the other, but not both … This measure thus captures the total amount of evolution that is unique to each state…

Lozupone and Knight (2008) noted that UniFrac "falls within a broader family of divergence-based β diversity measures related to PD that differ in the details of how the unique and shared branches are combined."

Both PD and UniFrac PD dissimilarities have been used in thousands of microbial studies and contribute to the growing evidence that resilience for microbial communities is linked to a range of aspects of biotic diversity (Shade et al. 2012; Lozupone et al. 2012). In this chapter, I will focus on the human health aspects of microbial ecology and PD. It is now well-known that many so-called "noncommunicable diseases" are associated within reduced microbial diversity in the human microbiome (for review, see Convention on Biological Diversity and World Health Organization 2015; see also Jason Lloyd-Price et al. 2016).

I will focus here also on some examples drawn from studies on the human digestive system. Many of these studies reveal the sensitivity of PD relative to other indices in distinguishing disease factors. These example studies discuss possible interpretations of observed reduced PD as relating to resilience and health. For example, Lindheim et al. (2017) in the study "Gut Microbial Diversity in Women with Polycystic Ovary Syndrome" found affected individuals to have reduced microbial PD of the gut microbiome. This was interpreted as an indicator of reduced health and stability of the microbial community. Lindheim et al. found no significant pattern for an alternative diversity measure (Pielou evenness index), suggesting that PD and phylogeny best captured differences in the microbial communities.

Human Inflammatory Bowel Disease and the Loss of Resilience

Bassett et al. (2015) explored intestinal microbial communities and inflammation, as part of a study of human inflammatory bowel disease (IBD). Bassett et al. noted that IBD "is a chronic intestinal disease where the resident microbiota contributes to disease development, yet the specific mechanisms remain unclear." They examined changes in the caecal microbiota, including changes in PD, associated with colonic inflammation. They concluded that reduced PD implies a greater risk of

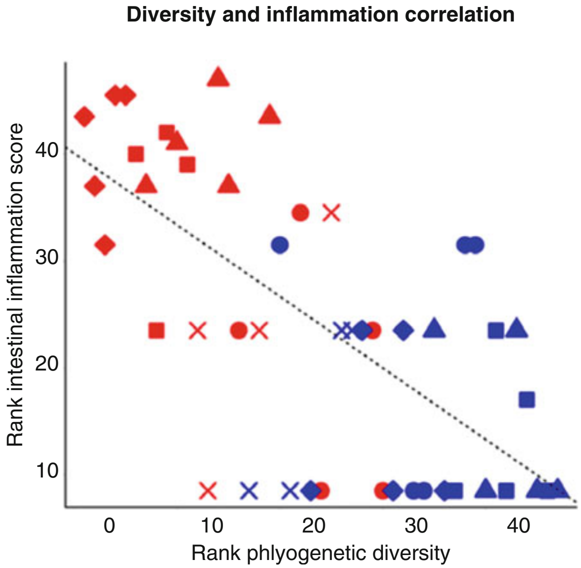

Fig. 1.1 X axis is PD amounts and Y axis is inflammation rating. Blue points indicate less susceptible individuals and red points indicate more susceptible individuals. Shapes of the points indicate treatment groups. Overall, the plot shows that increased inflammation was associated with a decrease in caecal microbial PD. For further information, see Bassett et al. (2015). Figure reproduced from Bassett et al. (2015)

inflammation because the microbial community of the intestine is less able to recover from disruptions to normal "homeostasis" (Fig. 1.1). Thus, PD was associated with a kind of insurance value.

There is support for this interpretation from other PD studies on IBD. Lozupone et al. (2012) similarly concluded "High functional response diversity in human gut-adapted bacteria is likely because phylogenetically disparate microbes often perform similar metabolic functions," and that loss of PD therefore is a loss of resilience. Zhang et al. (2017) noted "it remains unclear whether the observed changes in phylogenetic composition are causative for the development of IBD or simply a consequence of an altered intestinal environment during the progression of IBD" and concluded that "a precautionary approach is advocated by many." Thus, microbial PD studies illustrate a case where our limited current knowledge justifies a precautionary approach, maintaining high PD for insurance and resilience (PD as "bowel-logical" diversity).

The biodiversity (PD) conservation actions also may involve restoration of PD. In a study on gut microbial and inflammatory bowel disease (IBD), Khanna et al. (2016) found fecal microbiota transplantation (FMT) in patients restored microbial phylogenetic diversity (PD) to levels more typical of a healthy person.

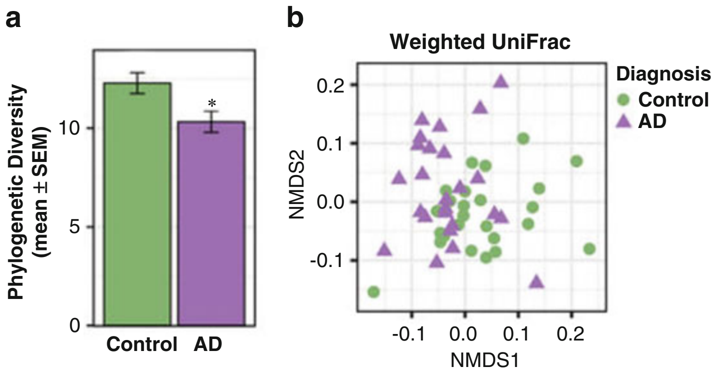

Fig. 1.2 “AD” indicates participants with diagnosis of dementia due to Altzheimers disease. (**a**) PD is decreased in the microbiome of AD participants. *$p < 0.05$. (**b**) Non-metric multidimensional scaling (NMDS) plot of weighted UniFrac analysis of composition. The NMDS analysis reveals differences in composition in AD versus Controls. Figure reproduced from Vogt et al. (2017)

Autism

Similar PD restoration strategies have been explored for autism. Kang et al. (2013) documented lower microbial PD in the intestines of autistic children. Kang et al. (2017) explored restoration or “rebalancing” of human gut microbiota through fecal microbiota transplant (FMT), to treat this autism spectrum disorder (ASD). Their study concurred that, based on PD, gut bacteria were significantly less diverse in children with ASD at baseline. Importantly, at the end of treatment, in contrast, bacterial diversity PD significantly increased in children with ASD.

Alzheimer’s Disease (AD)

A study by Vogt et al. (2017) compared the diversity and composition of the gut microbiome (bacterial 16S rRNA gene sequencing on DNA isolated from fecal samples) in participants with and without a diagnosis of dementia due to Alzheimer’s disease (AD). PD was found to be significantly reduced in the microbiome of the AD participants (Fig. 1.2a). In their study, much of the discussion of possible causes of the links and possible diagnostic strategies focused on compositional changes as summarized using UniFrac (Fig. 1.2b). Vogt et al. concluded that much further work is needed to determine any cause-effect relationship between gut microbiota and AD. The study nevertheless illustrates the complementary information derived from looking at total PD and at PD dissimilarities through UniFrac.

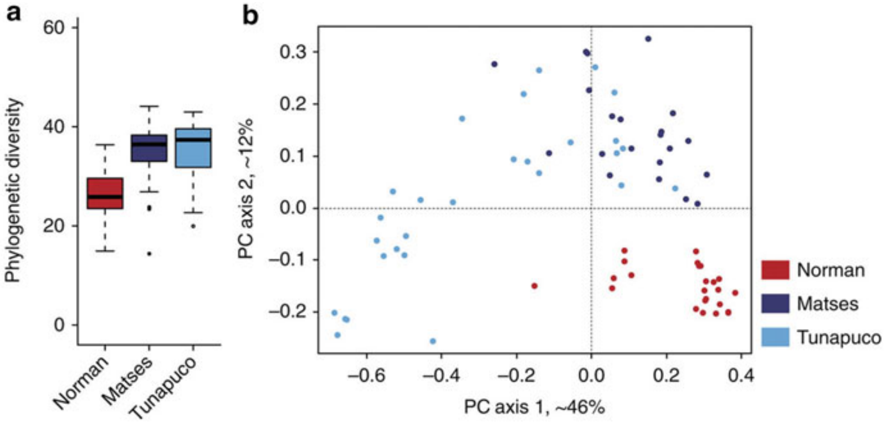

Fig. 1.3 (**a**) Microbial PD comparison of the gut microbiota of traditional hunter-gatherers, traditional agriculturalists, and urban-industrialized peoples. The urban population (Norman) has significantly lower microbial PD compared with the two rural populations. Whiskers in the boxplot represent the range of minimum and maximum PD values within a population, excluding outliers. (**b**) Principal coordinates analysis of UniFrac distances which were weighted by abundance values. The rural and the urban populations (Norman) show clear separation, indicating compositional differences in phylogenetic branches as indicated by UniFrac PD dissimilarities. (**a**) Figure reproduced from Obregon-Tito et al. (2015)

Subsistence Strategies in Traditional Societies Distinguish Gut Microbiomes

Obregon-Tito et al. (2015) applied high-throughput 16S ribosomal RNA (rRNA) gene amplicon sequencing and shotgun metagenomic sequencing to compare the PD of the gut microbiota of traditional hunter-gatherers, traditional agriculturalists, and urban-industrialized peoples. The two rural communities were the Matses, a remote hunter-gatherer population from the Peruvian Amazon, and the Tunapuco, a traditional agricultural community from the Andean highlands. Obregon-Tito et al. hypothesized that dietary differences would correspond to differences in the gut microbiome. They noted that:

> Studies of peoples maintaining traditional subsistence practices are critical for understanding ... how the human microbiome responds to urbanism and Westernization, especially regarding diseases of civilization, such as obesity and chronic inflammatory disorders.

They found that the urban population (Norman, OK, USA) had significantly lower microbial PD compared with the two rural populations (Fig. 1.3a) and also had PD compositional differences (Fig. 1.3b).

Obregon-Tito et al. (2015) found stronger differences for PD, compared to estimated "species" richness, again supporting PD and phylogeny as useful for summarizing microbial community differences. However, this contrast is not a universal pattern. For example, Montassier et al. (2015) found significant reduced

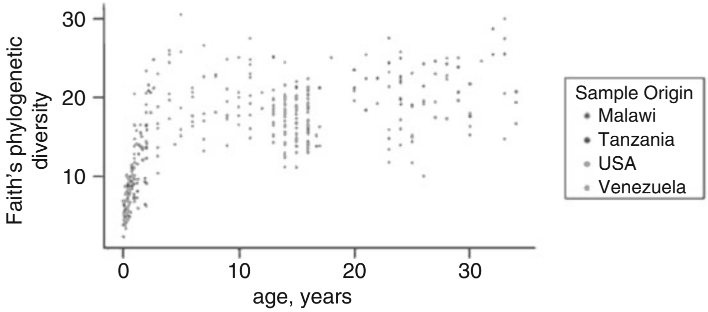

Fig. 1.4 Scatterplot of faecal microbiota of individuals plotted by phylogenetic diversity against age of the Hadza hunter-gatherers from Tanzania ($n = 16$, green), agrarians from Malawi ($n = 81$, red) and Venezuela ($n = 78$, purple) and Americans ($n = 213$, blue). Figure reproduced from Sonnenburg et al. (2016)

intestinal microbial PD following chemotherapy, and this loss of diversity was also clear for estimated number of species.

More on Diet and Microbial PD: Regional Extinctions

The review by Zhang et al. (2017) summarized the normal changes in intestinal PD with age:

> The phylogenetic diversity of the intestinal microbiota increases with growth and development and ultimately leads to a complex and relatively stable community of microorganisms at the age of roughly 2–3 years.

Zhang et al. referred to diet as a well-established factor in microbial PD loss. Sonnenburg et al. (2016) examined this issue by comparing the microbiota of hunter-gatherers in Tanzania, agrarians from Malawi and Venezuela, and "Westerners" from the United States. They found that Western populations have lower PD (see Fig. 1.4) from birth through childbearing years. Sonnenberg et al. argued that such loss can amount to an extinction crisis and concluded that:

> Our data support a model in which consuming a modern diet low in fiber contributes to the loss of taxa over generations and may be responsible for the lower diversity microbiota observed in the industrialized world compared to present-day hunter-gatherers and rural agrarians. The data we present also hint that further deterioration of the Western microbiota is possible.

Sonnenberg et al. also concluded that not only would a low-fiber diet result in a progressive loss of PD but also that reintroduction of a high-fiber diet would not be enough to recover this biodiversity. They concluded that restoring the microbiota to its original state "requires the administration of missing taxa" and predicted that such "microbiota reprogramming" will be important as "more diseases are linked to the Western microbiota and the microbiota is targeted therapeutically." As in the case of the other studies discussed here, a precautionary approach calls for maintaining microbial PD and its resilience/insurance value.

Discussion

A growing number of human diseases are associated with reduced microbial PD. However, it is revealing also to identify the rarer cases where a disease appears associated with *higher* microbial PD. Lappan et al. (2018) studied recurrent ear infection, a common childhood disease. They found that a healthy microbial community in the ear appears protective ("protective commensal bacteria"). Thus, PD again provides insurance and resilience. However, the PD of affected subjects was significantly *higher* because the presence of pathogens meant increased overall PD. Thus, in their study, PD on its own was not informative, and their most informative PD calculations (UniFrac) were those assessing compositional change.

The use of the PD calculus in microbial ecology means that neither overall PD nor PD dissimilarities and compositional change are assumed to have primary analytical importance. With this in mind, future work can further improve the toolbox. One opportunity relates to making better use of robust analyses of PD dissimilarities. Figure 1.3b illustrates a common "horseshoe" distortion that may obscure interpretations. This can be corrected with robust ordination methods (for discussion, see, e.g., Faith et al. 1987, 2009; Faith 2013). The toolbox for microbial PD then may consider also some of the additional analyses enabled by these robust methods (see, e.g., Faith 2015).

Further, other aspects of PD calculations may find use for the first time, including the homogeneity, distinctiveness, and endemism parts of the PD calculus (see Faith 2013). Overall, microbial ecology is well-placed in embracing the PD calculus. This combines appreciation of overall PD of a community, for insurance/resilience, with various compositional PD calculations, for addressing the range of questions related to understanding change. In the next section, I look at the relatively less successful integration of PD and its calculus into macrobial community ecology.

Macrobial Community-Level PD

Pioneering work by Webb (2000; see also Webb et al. 2002) laid foundations for community phylogenetics, or "ecophylogenetics" (for reviews, see Pearse et al. 2014; Cadotte and Davies 2016; Cadotte et al. 2017). However, foundational work also could be regarded as much older, given that phylogenetic community ecology inherited all the decades of development of ecological "diversity" indices. As illustrated in the studies by Chao et al. (2016), some indices created at the species level could be extended to phylogenies. Much of the work in this area following Webb's pioneering work has created more and more phylogenetic "diversity" indices. Following Pavoine and Bonsall (2011), these metrics are often classed into richness, divergence, and regularity categories. In this spirit, PD has been investigated as one of many possible phylogenetic indices, as an analogue to species richness.

In this section, I will try to focus particularly on those macrobial studies about the importance and value of "biodiversity." Here, there have been useful studies using PD, with an interesting transformation from the conventional PD focus on "features" to a focus on ecological "traits." For example, there now is support from multiple studies for the idea that phylogeny and PD can provide a surrogate for general functional trait diversity (Cadotte et al. 2009, 2010; Flynn et al. 2011; Davies and Buckley 2012; Mason and Pavoine 2013; Meynard et al. 2011). Cadotte and Davies (2010) concluded that PD can be expected to capture feature diversity, "including unmeasured, but ecologically important traits." The Cadotte et al. (2017) review concluded that:

> PD has been shown to be a powerful predictor of quantitative measures of ecosystem functioning (Cadotte et al. 2008; Srivastava et al. 2012; Cadotte 2013; Pu et al. 2014)

These findings may support the role for PD as a proxy, but not necessarily the role for PD as providing insurance. Faith (2017) described three values associated with PD and feature diversity – option value, insurance value, and proxy value. The latter covers cases, as in the findings above, where high PD means high functions, high productivity, etc. Here, the current feature diversity represented by PD acts as an effective proxy for a wide variety of current functions/benefits. PD conservation then is not so much a focus on insurance as on the conservation of possibly unknown current functions and benefits.

While these studies noted above represent important findings, there does not appear to be a coherent framework emerging that describes how PD fits into the broader use of phylogenetic measures in macrobial ecology. A coherent conceptual framework could help particularly in linking phylogeny to "biodiversity" and its value in community ecology. I see this limitation of the current research as due to several persisting confusions and misrepresentations. Noting the history of PD development described in the Background section, it is particularly unfortunate that macrobial ecology has ignored this progress. This sad neglect includes ignoring PD fundamentals (see Background), including ignoring:

- The definition as not tied to within-community, but including the global scale
- The shared-ancestry model as the PD link to feature diversity
- The extensive existing support ("tests") for that link to feature diversity
- The fact that PD is not a single index, but is a calculus based on features
- The stated reasons why functional traits often will not be captured by PD
- The alternative method for explaining functional trait diversity

Here, I will present examples of these misrepresentations. I will begin with the basic issue of definitions and use of terms. The false statement is frequently made that Faith (1992) *defined* PD as within community. For example, the Mouquett et al. (2012) review of the emerging field of "ecophylogenetics" defines "Phylogenetic diversity: the amount of evolutionary history represented in the species *of a particular community* (Faith 1992)."

Similarly, Winter et al. (2013) attributed to Faith (1992) this misdefinition: "Phylogenetic diversity (PD). Calculated as the sum of branch lengths between root and tips *for a community*." The unfortunate influence of that confusion is seen, for example, in Gudde and Venditti (2016) where they repeat the false definition, "Phylogenetic diversity represents the total of branch lengths that connect all species found *in an area* (Faith 1992)." (similarly, see Ahrendsen et al. 2016; Davies et al. 2016).

Definition problems extend to the use of "phylogenetic diversity" and even "PD" for other phylo-diversity measures, without explanation. For example, Mouquett et al. (2012) says: "Commonly used measures of phylogenetic diversity are the total branch length of a phylogenetic tree that contains all species present in a community, or the sum of pairwise distances between species weighted by their relative abundances." Winter et al. (2013) interpreted "phylogenetic diversity" as derived from any between-species biodiversity distance, based on phylogeny.

Confusions have been made worse in macrobial community ecology by the popular use of "PD" for lots of other phylogenetic indices. For example, in Pio et al. (2014), "PD" is used to refer to any diversity measure linked in any way to phylogeny. They refer to a variety of published studies on the performance of "PD", but it is not clear if this is Faith's (1992) PD or some other measures. Pio et al. go on to apply the actual PD method in their analyses, but without reference to that as the Faith (1992) method.

It is also unfortunate that the justification for PD in conservation is falsely portrayed as depending on its recovery of functional traits. Winter et al. (2013), in questioning the conservation relevance, refer to the supposed issue that "the generality of the assumption that phylogenetic diversity can indeed be used as a proxy for functional diversity is unclear."

Mazel et al. (2017) similarly also illustrate the misconception that PD's justification for biodiversity conservation depends on functional trait recovery. Mazel et al. (2017) also incorrectly claim that the most prominent argument for PD conservation "is that conserving phylogenetic diversity (PD) will also conserve diversity in traits and features (functional diversity [FD])." This not only ignores the warnings about functional traits, it ignores the actual motivation for PD conservation – option values. Mazel et al. claim to evaluate the rationale for PD, but nowhere refer to option value. Winter et al. (2013) claimed to consider the proposed justifications for conservation of phylogenetic diversity, but also did not even list option value. Davies et al. (2016) similarly ignore option value in arguing that the rationale for PD is countered by a finding that some branches of the same length differ in their functional trait importance.

The Mazel et al. (2017) study also illustrates the common misconception that PD has not been tested and that tests must focus on functional traits. Some workers have suggested that PD has no clear justification and/or that the link to feature diversity is either untested or has failed limited tests (see, e.g., the working group report at https://www.idiv.de/?id=427).

Some evaluations of PD have misrepresented the PD model (of shared ancestry). For example, Kelly et al. (2014) portray the model as distance-based, rather than shared ancestry-based. Misrepresentation of the PD assumptions also has meant that the PD calculus based on features has been ignored. Tucker et al. (2016) had the goal of a unified framework, but ignored the existing PD calculus, which would have unified many measures and helped to clarify the status of a core biodiversity measure as compared to associated calculations for decision-making. In ignoring the calculus, Tucker et al. confused PD with its associated calculations. They assumed that "richness metrics sum up the quantity of phylogenetic differences present in an assemblage" and so lumped together PD and its endemism and distinctiveness calculations as equivalent "richness" dimension measures. Unfortunately, they went on to say: "high redundancy amongst metrics within a dimension can make selection among them somewhat arbitrary" (see also the similar error in Vellend et al. 2010).

The relationship between PD and functional trait diversity has raised many confusions and misrepresentations. Faith (1992; see also Faith 1989) made it clear (along with an example case study (Faith 1989); see also Faith 2015) that conserving phylogenetic diversity sometimes can be a poor strategy for conserving functional diversity. Now, more than 25 years later, ecologists are claiming to have now discovered this (e.g., Mazel et al. 2017), "Conserving phylogenetic diversity can be a poor strategy for conserving functional diversity"), without making any reference to the original insights. These early insights that have been ignored included an effective functional trait diversity approach (Faith 1989, 2015).

Mazel et al. (2017) evaluated PD links to functional traits by adopting a popular convex hull measure of trait diversity. Supposedly PD has justification for conservation if it recovers this trait diversity. However, this convex hull measure of trait diversity is troubling as a conservation target. Suppose, for example, all traits fit the phylogenetic tree perfectly, and one lineage evolved lots of traits for life in one habitat type, while other lineages evolved lots of traits for other habitat types. These traits are reflected in the branch lengths. PD applied to this tree would capture lots of feature/trait diversity, with high contributions from each lineage. However, the trait space based on all those traits, and the convex hull volume, would not reflect that high diversity of traits. Podani (2009) documented the key problem associated with convex hull volume: the presence of lots of correlated traits, as in this example, will not be reflected in a higher volume. It is apparent that convex hull volume is not something that would deserve to be conserved if one is interested in trait diversity, so why should PD try to capture it? We are left to wonder why Mazel et al. ignored the Faith (1992) warning that PD sometimes will not represent functional trait diversity and that another model and method ("ED" discussed earlier) provides a way to quantify and conserve functional trait diversity. Indeed, a review of functional trait diversity measures (Pla et al. 2012) notes that this is perhaps the oldest such measure. We can conclude that progress will be made in PD macrobial ecology applications when the lessons of history, across the different area of study, are better appreciated.

Conclusions

The Faith (1992) proposal of PD built on a rich history of discussions about taxonomy, phylogeny, features, distinctiveness, and also about the core values of biodiversity including option value and insurance value. Some of this appears in IUCN (1980), but in addition earlier papers, some largely ignored, have explored these issues. Faith (1992) in considering primarily regional and global and whole-clade applications emphasizes PD links to option value. In contrast, ecological community-level studies will be more focused on insurance value and resilience. These ideas have perhaps had the most compelling development in microbial ecology. Here, I described just one portion of that discipline, relating to human health. The study of various diseases suggests that insurance value and resilience are linked to microbial PD, but these studies also showed that the PD calculus (e.g., dissimilarities) is an equally important tool.

Insurance value and resilience no doubt will be equally important in macrobial ecology, and PD can be expected to be informative. However, progress in this area has been slow. Part of the problem is that ecology, even at the species level, remains uncertain about its definition of “biodiversity.” A helpful approach may be to separate biodiversity and other important aspects such as ecological integrity. In addition, there is an urgent need clearly to develop meaningful ways to look at functional trait diversity. This may include both phylogenetic and other models as equal status explanations of trait diversity patterns. All these issues make it clear that progress will depend on not only a shared toolbox across areas of study but also shared conceptual frameworks.

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