

# Biodiversity Realism: Preserving the tree of life

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**Abstract** Biodiversity is a key concept in the biological sciences. While it has its origin in conservation biology, it has become useful across multiple biological disciplines as a means to describe biological variation. It remains, however, unclear what particular biological units the concept refers to. There are currently multiple accounts of which biological features constitute biodiversity and how these are to be measured. In this paper, I draw from the species concept debate to argue for a set of desiderata for the concept of “biodiversity” that is both principled and coheres with the concept’s use. Given these desiderata, this concept should be understood as referring to difference quantified in terms of the phylogenetic structure of lineages, also known as the ‘tree of life’.

**Keywords** Biodiversity · Phylogeny · Conservation science · Taxonomy · Phylogenetic diversity

## Introduction

“Biodiversity” is an indispensable concept for conservation biology. Since conservation biology emerged in the 1980s it has been often described as a ‘crisis discipline’. Often compared to medical practice, it applies biological science to the preservation of biological systems (Soulé 1985). For conservation to be a science, a rigorous concept was needed to describe the features biologists want to preserve. This can be viewed as analogous to establishing medical concepts like ‘health’ or ‘disease’. Previous notions of ‘wilderness’ and vague demarcations between the

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natural world and humanity could not provide clear targets for conservation. In 1985, the same year that the journal *Conservation Biology* started, a key term for the discipline emerged: *biodiversity*. This concept, a truncation of “biological diversity”, characterises the features that conservation biology aims to preserve. These include biological features whose preservation or cultivation does not provide an immediate or obvious financial benefit.

The use of *biodiversity* in conservation biology has become near ubiquitous but there remains little consensus on the biological features it refers to (Maclaurin 2016). Current philosophical attempts to explicate biodiversity have converged on what I refer to as the ‘taxonomic assumption’: biodiversity necessarily measures taxonomy (Lean and Maclaurin 2016; Maclaurin and Sterelny 2008; Rolston 2001; Sarkar 2005). This is a natural assumption because taxonomy describes the basic ingredients that compose the biological and ecological systems that conservation looks to preserve. Given the role that we want biodiversity to play, taxonomy appears to be the best deserver for anchoring an account of biodiversity. Most authors, however, put this in terms of a particular taxonomic rank: species. I shall argue instead that we should refer to the biological features that ground all biological taxonomy: namely, lineage structure. The overall lineage structure of life is discovered through phylogenetic inference. Given this, the best option for a general measure of biodiversity will be a phylogenetic measure of biodiversity.

### Explicating ‘biodiversity’

There is a tension in the concept of biodiversity. It is thought that biodiversity must be both a scientific measure of real features in the world and something of normative worth. This leads to two differing methodologies for identifying biodiversity. One starts from our normative values towards nature and works from there to identify the particular different biological features we desire. The other starts with the biology, attempting to find the best account of biological difference and connecting it to normativity through prudential reasoning. I take this second stance towards biodiversity: that of the biodiversity realist. Realists believe biodiversity is a natural quantity and that there are better and worse ways of identifying the diversity of mind-independent biological features. These features are valuable to rational agents and, therefore, should be preserved.

But how should we measure the natural quantity biodiversity? Most biologists, in trying to measure biodiversity, start with a permissive definition. For example, during the 1992 Rio Earth Summit, the Convention on Biological Diversity (CBD) proposed that biodiversity be defined as “diversity within species, between species, and of ecosystems” (CBD 1992). This definition has the virtue of being easy to assent to due to its broadness. It unfortunately is synonymous with all of biology. Under this definition any measure of biological difference represents some aspect of biodiversity. Due to its lack of discriminatory power it does not provide any clear guidance for making actual conservation decisions.

Permissive accounts of biodiversity have yielded a flourishing literature of different mathematical metrics for biodiversity. These measures, however, presuppose a prior choice of the biological kinds being compared. Mathematical measures

of biodiversity are not aimed at measuring *biodiversity* simpliciter. They aim to describe variation in *units* which are constitutive of biological diversity. Common units that are thought to be constitutive of biodiversity include genes, species, functions, phylogeny, and morphology. Differences between units are identified through measuring character sets, which are the individual biological features of these proposed units.<sup>1</sup> These include individual nucleotides, functions, morphology, populations, species, etc. The mathematical formula which quantifies the difference in character sets also varies. A huge range of formulae have been proposed, often borrowed from different sciences, to analyse the data sets produced by character measurement (Magurran and McGill 2011).

This means the units, character set, and measure can be different between explications of *biodiversity*. As a consequence, scientists propose ever more mathematical formulas as measures of biodiversity every year. As one researcher laments, “in the last decade more than two measures of PD (Phylogenetic Diversity) or FD (Functional Diversity) were proposed, each year!” (Cianciaruso 2011). Attempts at consensus, such as “Essential Biodiversity Variables” in *Nature*, have yielded lists of hundreds of individual measures (Pereira et al. 2013). This proliferation of methods is largely a product of the lack of consensus on what a measure of biodiversity needs to do.

This uncontrolled proliferation has negative consequences for both the biological sciences and conservation (previously outlined in Lean and Maclaurin 2016). Here are a few of the problems with such a permissive stance:

### *Openness to manipulation*

Without any guidelines as to what makes a good account of biodiversity, there is no limit on the measures that are admissible in conservation decision procedures. If the criteria for admission has this extreme pliability, it can be easily ‘gamed’ by individuals so that the area which promotes their interests, regardless of the contents, is selected.

### *Exclusion*

If we cannot discriminate between targets for conservation, we have failed. Too many measures of biodiversity include too much of the natural world. This can result in features being massively overdetermined for inclusion. Further, since the biodiversity measures are not equivalent, they can generate conflicting recommendations about what to do. This is problematic when we have no way of weighing the relative importance of these measures.

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<sup>1</sup> Character set usually refers to biological trait held by organisms. I am using it to refer to features of any biological kind.

### *Comparative weighting*

Conservation decision-making should involve the use of decision-theory to make optimal choices (Colyvan et al. 2011). Variables will need to be weighed against each other in decisions about what to conserve. While the details on how to weigh biodiversity variables will require significant debate, we still must identify which variables are the bearers of normative weight. Some biological variables are desirable in their own right as natural quantities of diversity, others are desirable due to their correlation with or promotion of these natural quantities. We can, therefore, divide variables into those which we prioritize in their own right or as means to others. This is similar to the biodiversity surrogate/biodiversity constituent distinction Sarkar (2012) introduces: biodiversity constituents are the features we want to preserve as they comprise biodiversity, surrogates are only preserved insofar as they represent biodiversity constituents. We can comfortably be pluralists about measures that act as surrogates for biodiversity while aiming to describe what constitutes biodiversity as a natural quantity.

### *Informational priorities*

The information needed for decision-making in conservation is hard to collect. We need to be able to prioritize the collection of information according to which features are more desirable or indispensable. Further, without priorities there is always another measure that could be added to the decision procedure. By describing what information is admissible, we have a guide for when the job is finished. This can be done in part computationally through diminishing returns in complementarity; complementarity is the addition of new desirable features, or units, to a set of desirable features or units (Sarkar 2016).<sup>2</sup>

These considerations provide *prima facie* reasons to at least investigate whether there could be particular variables that are better representatives for biodiversity. This project—the attempt to identify the variables that best represent biodiversity—is described as the “units-and-difference” problem by Maclaurin and Sterelny (2008). This paper furthers the project of identifying the preferable set of features to quantify biological difference.<sup>3</sup> However, it does not argue for a particular mathematical formula. While there is much work to be done in identifying the virtues of individual measures, there first remains the job of determining which of the various proposed biological features is best used to quantify biological

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<sup>2</sup> The features or units are relative to the biodiversity measures we use. For example, assume species richness is what counts as biodiversity. If we preserve a habitat with 12 species, we have 12 units contributing to biodiversity. If we preserve another habitat with the same 12 species we will have added no new units of biodiversity; there is no complementarity between the habitats. Only complementary or new species would contribute to biodiversity.

<sup>3</sup> Faith (2016, p. 70) introduces an important alternative to the units and difference approach to biodiversity defended in Maclaurin and Sterelny, *variety* in which a set of elements are counted up. In this paper, I am not committed to the framework of Maclaurin and Sterelny, indeed, I am not strongly committed to any one measurement procedure over another but I lean towards difference in terms of Sarkar's (2016, p. 46) definition. My focus is on what features of the world we should measure not how to measure them. But I am open to future developments in the bioinformatics literature.

difference. The role of the concept of biodiversity is to provide an ‘objective’ account of the biological features that constitute the diversity of living systems. Thus, we should look to the literature on scientific concepts for guidance.

## **Biodiversity as scientific concept**

While conservation practice is taken as a form of ethical or economic action, *biodiversity* itself is a scientific concept useful across multiple biological disciplines. The attempt to categorize biological difference is central to several longstanding hypotheses in biological science, and research into biodiversity has become a common component of ecological and evolutionary journals. There is a long-standing hypothesis in ecology that ecosystem stability increases with diversity of the system. Previously, the measure used to describe diversity in this hypothesis was some version of species diversity (Justus 2011). Since the postulation of new measures for biodiversity, including functional and phylogenetic measures, there has been an increasing amount of work looking for relationships between these various forms of biodiversity and stability (Cadotte et al. 2012; Naeem and Wright 2003). In evolutionary studies there is research on whether biodiverse systems have more potential for evolutionary change (Forest et al. 2007).

Treating biodiversity as a scientific concept that needs to be explicated naturally leads to the question, what makes ‘good’ explication of a scientific concept? Fortunately, there is a long history of explicated scientific concepts we can refer to. One of, if not the, most thoroughly worked through scientific concepts is the species concept. The species concept debate is directly relevant to the biodiversity concept as they both deal with biological taxonomy, broadly construed. From this debate I take some tools to answer the question of when a measure of biodiversity successfully represents biological difference.

Elliot Sober’s *Philosophy of Biology* presents a quick sketch of how to explicate species concepts, which I think can be developed and utilized. Sober argues that a species concept should be considered for its clarity, theoretical motivation, and its conservatism (Sober 2000, p. 160). A species concept has clarity when it makes clear distinctions between populations and can be applied to newly discovered populations. A concept is theoretically motivated when it identifies features that contribute to scientific research. Species concepts should be conservative as we want a new species concept to capture the usage of the term ‘species’ which has been extremely useful in science and common vernacular for thousands of years.

This simple, intuitive framework is applicable to the biodiversity concept with some minor tweaks. Species definitions are focused on species membership and on boundaries between putative species, whereas biodiversity measures quantities, so I substitute “*tractability*” for Sober’s “clarity”. This I understand as meaning that a biodiversity measure must be able to consistently identify features across multiple biological systems. To do this, the features it measures must not be arbitrary or local to some area of life.

Further, while a measure may describe robust features of a biological system, those features may not be particularly interesting. We want the features that the

measure identifies to be theoretically motivated. As biodiversity plays a role in several sciences, the units it describes should be firmly grounded in general biological theory. If the units measured are selected because they are easy to discover or are only useful to a hypothesis local to a biological sub-discipline, then it cannot provide the information needed for a general biodiversity concept. Biodiversity measures should refer to biological features that are relevant to both evolutionary and ecological theory, so they must be *theoretically fundamental*.

Finally, Sober claims that any attempt to give a definition of species should be conservative. It should be able to represent the phenomena which has historically been associated with the species category. Biodiversity does not have as many historical demands as it has a relatively short history of enquiry; while people have discussed species for thousands of years, the modern literature on biodiversity is only 30 years old. But there is a certain conservatism that should be at play when we assess measures of biodiversity. As I have noted, many biological features have been proposed as the right features to measure for biodiversity and for each feature there are numerous measures. The best individual measure of biodiversity should be able to successfully incorporate, correlate, or represent the variation in units identified by other measures. An explication of biodiversity that ambitiously represents variation across different biological systems is desirable. This desideratum is that a measure of biodiversity should be *representative*.

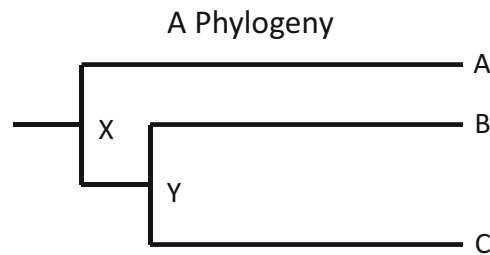
To this list of desiderata I will add a final virtue an explication of biodiversity must fulfil. This desiderata is not admissible to the explication of species concepts but it is important for the biodiversity concept, given its role in conservation. Biodiversity should be desirable for prudentially rational agents. It need not account for all of our normative reasoning towards nature but it should be valuable. Any explication of biodiversity therefore should be *normatively demanding*.

Using this set of criteria—tractable, representative, theoretically fundamental, and normatively demanding—I argue in the next section that biodiversity measures should refer to the overall lineage structure of life.<sup>4</sup> When we assess biodiversity, the more of the ‘tree of life’ we represent the more biodiversity we represent. Under this conception any assessment of biodiversity within a region should include a baseline measure representing the lineage structure within that area. From this baseline of lineages represented any further species preserved would increase biodiversity. Capturing intra-species diversity is also desirable as lineages form within species and a wide representation of intra-species lineages further represents biodiversity. The most direct way to represent lineage structure is through phylogenetics and therefore phylogenetic measures of biodiversity are the best prospect for a general measure of biodiversity.

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<sup>4</sup> My criteria converges with Hull's (1997) criteria for ‘an ideal species concept’, which is generality, applicability, and theoretically motivated.





**Fig. 1** This is a basic phylogeny. This structure represents historical relationships of populations. A, B, and C are individual species. X and Y are at the nodes of the branches. Nodes display speciation events in which one lineage separates from another. Before the lineage split X A, B, and C had a common ancestor so they formed a monophyletic clade. Only B and C share a common ancestor at Y so they form another monophyletic clade. As the split between A was longer ago than the split between B and C we can expect B and C to be more similar to each other than A

## Introducing phylogenetics and biodiversity

To preserve biodiversity is to preserve lineages across the tree of life. We do this by identifying lineages which are representative of unique evolutionary histories. Lineages are real features of the world which can be discovered through multiple streams of evidence, making them tractable. The evolutionary divergence of lineages involves the divergence of biological traits from a common population, making lineages representative of the differences between populations. These differences make the lineages prudentially valuable. Finally, lineages and their historical relationships are indispensable to biological science making them fundamental to biology.

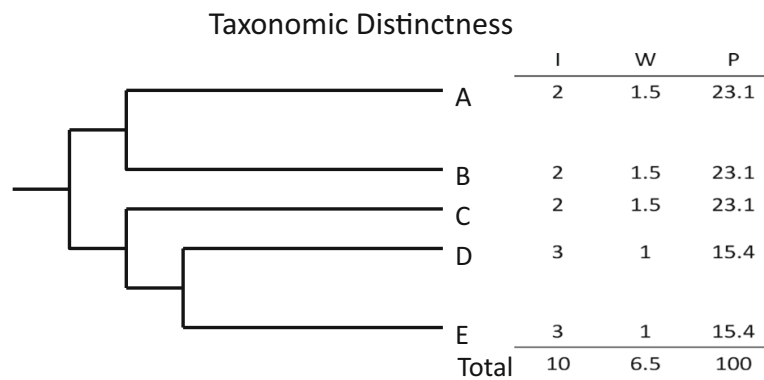
Information about historical relationships between lineages is gained from the science of phylogenetics. Phylogenetics is the study of the evolution of lineages through molecular data. Dendrograms, or the tree-like structures commonly used to represent phylogenetic relations, depict splitting events between branches and branch lengths (Fig. 1.). These branches represent genealogical relationships of lineages and how they separate or hybridize creating new distinct lineages.<sup>5</sup> The nodes of the branching patterns represent speciation ‘events’ in which populations separate, leading to variation that eventually bars the recombination of populations.<sup>6</sup> Branch lengths are used to represent either length of time lineages have been distinct or evolutionary change depending on the measure.

Since the 1990s, there has been a series of methods constructed to prioritize species in terms of phylogenetic distinctness. This is done in two primary ways.<sup>7</sup> The first proposed measure is topology based, which quantifies over the nodes of the phylogenetic tree. The node-based method was first proposed by Vane-Wright et al.

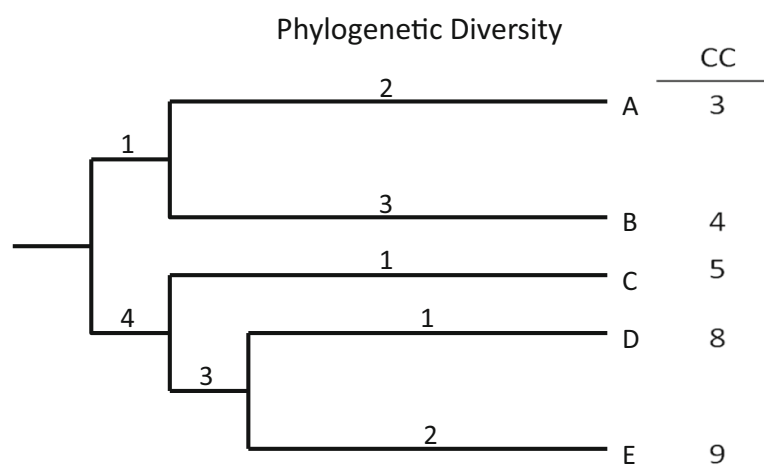
<sup>5</sup> Often just the branch splitting events are depicted.

<sup>6</sup> The ends of the tree will sometimes feature many populations which are only vaguely distinct. They are in a process of speciation but they could possibly recombine or subdivide again. For discussion of how lineages of populations, species, and phylogenies relate see: Velasco (2013).

<sup>7</sup> There are currently numerous variations on these different phylogenetic methods. They include a range of ways of providing relative weights to the branches or adding other variables, such as weighting population abundances.



**Fig. 2** Taxonomic distinctness. This is a node-based measure as it only counts splitting events. Column I counts the amount of clades individual species belong to. W is the standardized weight as given by dividing each I value by the lowest I value. Column P gives the percentage contribution of taxonomic information for the total clade the individual species contributes. This method prioritizes ancient lineages



**Fig. 3** Phylogenetic diversity. This is a distance measure. The numbers next to the branches indicate character changes that occurred along that branch. CC is the total character change in the terminal taxa from the clades shared ancestor. If we were forced to pick just two species we would pick the two which represent the most unique character changes. In this case it would be B and E

(1991) and identifies the relatedness of the populations. In this measure, sister taxa in a clade are evenly ranked (Fig. 2). The second (and more commonly used) method is based on nodes and distance (Faith 1992). Measures derived from this method quantify over both the topological structure of the tree and the length of the branches (Fig. 3). Branch length is gained through quantification of the change in the molecular characters used to identify the phylogeny. This is often done with DNA but can be done with phenotypic characters. I will focus on measures made with molecular data. In the Vane-Wright et al. version, only speciation events count to differentiate populations while, in the Faith version, within-lineage change is what counts.

The target of this paper, however, is the qualitative claim that we should represent the tree structure when considering biodiversity. When we consider an



area for conservation—assuming we are solely aiming to maximize biodiversity—we should pick the area that contains lineages that represent more evolutionary divergence. There are multiple different ways of weighting difference between lineages and it is not uncommon to weight phylogenetic diversity measures with features like the relative abundance of the populations. Some measures also tend to do better at accounting for uncertainty in tree topologies (Vellend et al. 2011).<sup>8</sup> There is an active debate about which of the many different bio-informatic measures best represents lineage diversification. For example, I think that distance measures are preferable to node measures as they represent not only the splitting of lineages, but also the divergence of lineages once they split. While I describe some basic commitments on how to measure biodiversity in the next section, I will generally treat these questions as outside the scope of this paper. What measure better represents lineage structure is debatable, but fortunately there has been considerable convergence on just a few phylogenetic measures in the conservation literature. Further, there is strong redundancy between phylogenetic diversity measures with different measures identifying similar sets of species (Vellend et al. 2011). The aim here is not to advocate for a single mathematical measure but to advocate for a class of measures.

## **Desiderata and biodiversity**

Now that I have broadly described the position I defend—that biodiversity should primarily refer to preserving the diversity of lineages and the history that they represent—I will now consider why this fulfils the desiderata described in “[Biodiversity as scientific concept](#)” section. I argue that representing the difference in lineages is the best way of representing biodiversity. Maclaurin and Sterelny (2008) argue that biodiversity is species richness supplemented with other measures in some contexts, including phylogenetic measures. I believe an area’s biodiversity increases when we add new species but adding more phylogenetically distinct species increases biodiversity more. The justification of this view follows.

## **Tractability**

It seems evident that our measures of diversity need to be tractable, and much of the focus of current bioinformatics is on how to make the mathematics used to measure biodiversity efficient and representative of the biological features they aim to represent (see: Magurran and McGill 2011). This I take as a given; we want to be able to incorporate these measurements into scientific and conservation practice and the mathematics needs to be both efficient and descriptive of the features that they represent. There is a second sense of tractable that I wish to also raise: that the features we wish to represent are robust.

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<sup>8</sup> Note that I will use the term Phylogenetic Diversity (PD) to refer to all measures of phylogenetic distance, the target of the paper. The particular measure of phylogenetic diversity that Faith (1992) proposed, that many studies use, I will refer to as Faith’s PD.

In other words, will slight variation in the initial character set represented result in radically different results in what counts as diversity? Organisms are modular; different parts evolve at different rates. Selecting different modular systems to measure the evolution of population traits will result in different diversity scores, as some systems are evolving faster than others in populations. Further, if the features we measure are not robust, then it is impossible to compare biodiversity measurement across different biological systems or temporal time slices of the 'same' biological system. For example, ecological assemblages may lack distinct identity conditions and be too ephemeral to measure their diversity over time or the diversity between different ecological assemblages (Lean and Sterelny 2016).

Measurement is always on a set of characters. For measurement to be comparable and consistent the characters need to be stable features of the world. They cannot be arbitrary. Some proposed measures of biodiversity struggle to describe biological features in a principled way. For example, morphological measures, which describe physical traits of populations, suffer from problems of arbitrariness if used as a general measure. For any set of characters described from an organism's morphology, there are always more morphological characters that can be added. For birds we can describe aspects of their morphology like their beak curvature, wingspan, and feather colour. But we can keep adding more traits, such as toe length, eye colour, or the number of feathers on its head. For any measure of characters in a population there are more characters we could add. When the difference between characters is quantified the end result will largely be subject to which characters are included or excluded. This results in instability of the output of such a procedure. Ultimately, functional carvings of biodiversity suffer from the fact that there is no single functional description of biological features that a measurement procedure is representing.

Phylogenetic descriptions of biodiversity avoid such arbitrariness problems in two ways. First, the characters used for calculation are very clearly demarcated, as nucleotide bases are distinct. Second, what they aim to represent are robust features of the world on which multiple independent streams of evidence will converge. Phylogenies are constructed primarily using molecular data, in which differences between homologous sequences are analysed.<sup>9</sup> DNA is highly conserved and ubiquitous to everything we conventionally call living. The near universal nature of this data set allows for the comparison of differences between species with very few features seemingly in common. While a giraffe and a sponge share very few identifiable morphological traits they share *Hox* genes that organize their anterior–posterior alignment (Ferrier and Holland 2001).<sup>10</sup> Phylogenetics utilizes a character set that allows for the comparison of all life. This set of characters is resistant to gerrymandering as there is no potential for the arbitrary addition of characters.

To summarize, phylogenetics aims to represent the actual spatio-temporal relationships of populations; this structure is commonly referred to as the tree of life. Populations have a history of physical relationships to each other that the

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<sup>9</sup> Phylogenies can be constructed with other data. Constructing trees from proteins is still common.

<sup>10</sup> *Hox* genes between such distant lineages are unaligned and cannot be used to make comparative phylogenies but can be used to identify homologies between distantly related lineages.

molecular data aims to represent (Felsenstein 1985). This includes genetic data such as nuclear or mitochondrial DNA or protein character phylogenies. Different phylogenies can be built from each set of data and can be used to support hypotheses about the historical relationships between populations. These character sets converge on the actual historical relationships between populations, displaying which populations evolved from a common ancestor. This provides a reliable and consistent procedure for describing diversity.

### **Representative**

Identifying a narrow set of measures for biodiversity is preferable for the reasons described in “[Explicating ‘biodiversity’](#)” section. We must escape the ‘curse of bioinformatics’, the uncoordinated proliferation of biodiversity measures, to have a shared global measure of biodiversity (Faith and Baker 2006). But we should be conciliatory. We want a measure which correlates with the diversity of features measured in other descriptions of biodiversity. Measures of phylogenetic diversity have often been defended primarily due to their representativeness. Regions or species which are described as biodiverse under other measures tend to also appear biodiverse under phylogenetic measures. This idea is at the core of Faith’s defense of phylogenetic diversity (Faith 1992). He argues that we can use the branch lengths of phylogenies to represent the change in biological features and the functional attributes of populations. Branch length is thought to be representative of ‘feature diversity’, which is not just a property of individual organisms, like different gene sequences, but also of whole populations, like evolutionary plasticity. By finding the record of historical change in populations, we can represent the change in biological features of populations. This is the reason commonly given in the biological literature for using phylogenetic measures to represent diversity and has empirical support (Forest et al. 2007; Huang et al. 2012).

The representativeness of phylogenetic diversity is debated within the biodiversity literature. Winter et al. (2013) argue that the relationship between functional features and phylogenetic diversity is variable so we should not use phylogenetic diversity without reservations (also see Devictor et al. 2010). Other researchers have investigated the conditions which cause this relationship to diverge, such as competition driving functional-differentiation in closely related species or slow trait evolution causing a population’s functional differentiation to be limited (Safi et al. 2011). The relationship between phylogenetic diversity and general trait diversity, while contested, is supported but open to the weight of further empirical evidence. But in reply to sceptics of phylogenetic diversity’s representation of function, I will note that they understate the variation in functional diversity measures, given a character set. Varying the characters included in a functional measure will result in different populations being functionally diverse. It is not possible to provide a global set of characters for measuring functional diversity. Without this we cannot anchor our judgements about the relationship of function to phylogenetics on a global scale.

Fortunately for morpho-functional diversity measures, phylogenetic measures can aid in categorizing functional and morphological character sets. Very few traits

are shared throughout life. The evolution of an elephant and an ant involve very different biological mechanisms and traits. These different mechanisms and traits are, however, common to a local clade structure. The evolution of wings and chitin exoskeletons are relevant to the clade that ants (*Formicidae*) belong to but not particularly relevant to elephant evolution. The relevant morphological features can be categorized through homology. These are structures which are modified through selection on variation in developmental processes. By placing traits or mechanisms within their lineage structure we provide a context for analysing these features in reference to their closest relatives. Phylogenetics not only correlates with other categorizations of biological difference but also provides a context that allows for their meaningful differentiation. The clade therefore provides a reference class for the description of morphological traits. This allows for what Maclaurin and Sterelny (2008) call a “local morphospace”, a limited set of morphological features which vary within a clade. These functional measures in many contexts can be used to further supplement phylogenetic measures of diversity.

Equating biodiversity with phylogenetic structure ties biodiversity to biological relations which exist on a global scale. Global phylogenetic diversity can be used to identify key endemic taxa that represent distinct clades with long branches and few extant species. This is already being used by groups such as EDGE (Evolutionary Distinct and Globally Endangered) of Existence program operating out of the Zoological Society of London.<sup>11</sup> From initial global priorities we can move into finer scale, selecting between populations that equally represent clades. Considerations on the finer scale turn on choices of whether to preserve more individual lineages or preserving fewer but more representative lineages. Choices will likely be influenced by features internal to clades including biological features which are not based in phylogenies, which also contribute to biodiversity. These can be biological, such as how plastic or morphologically diverse the clade is, or ecological like the local causal context of the population, particularly what other populations they causally influence.

Identifying a measure which is representative over both global and local scales is critical as it has been discovered that local measures of diversity can appear to contradict global measures. Across the world local species richness has been steadily increasing according to several meta-analyses (Vellend 2017). This is due to invasive species spreading across the globe. This is coupled with species local to these regions becoming extinct, leading to global species diversity being lost. Identifying measures of diversity which can scale relates the local diversity of these systems to the global biodiversity that is being threatened.

### **Normatively demanding**

The connection between norms and biological difference can found a general betting strategy in which we preserve the best range of biological features for the future. The knowledge that the loss of biological features is generally irreversible entails that we account for the risk of losing these options (Arrow and Fisher 1974).

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<sup>11</sup> <http://www.edgeofexistence.org/index.php>.

Diverse biological features, therefore, hold a certain value to agents who prudentially account for risk in the future. These should assign value to these biological features; this value is called *option value*. Option value is distinct from the various immediate instrumental values we have for the environment.

The preservation of as many distinct lineages across the tree of life is normatively demanding as these populations possess this option value. This view is shared by scientists (Faith 1992, 2013), philosophers, and economists (Nehring and Puppe 2004).<sup>12</sup> Lineages, and the individuals that comprise these lineages, possess features which are relevant in evolution and ecology. Preserving lineages, therefore, preserves unique features at multiple levels of the biological hierarchy. Diverse lineages are valued as ‘options’ as: (A) the features they possess may become useful in the future; (B) the features they currently have could lead to the evolution of novel features; (C) they contain information about evolutionary change of possible epistemic use; (D) we may morally value these lineages in unpredictable ways that we currently don’t foresee.

Some philosophers are sceptical of the normative justification of a natural quantity account of biodiversity. They argue there are ‘biological values’ that exist as unique normative ends and that diversity indices do not model these ‘biological values’. Therefore, biodiversity should be eliminated as a useful concept for conservation (Maier 2012; Morar et al. 2015; Santana 2014, 2016). Alternatively, local stakeholders in the environment should decide what biological features count as being the relevant sort of diversity (Sarkar 2005). In agreement with eliminativists and conventionalists, the realist accepts that biodiversity does not represent all the features of nature that people value. Indeed, biodiversity may often clash with the parts of nature that people currently do value; that is to be expected. This is why biodiversity is important: sometimes the parts of nature which are unique are not noticed.

Biodiversity is just one of many things that we are looking to preserve in conservation. Within the Intergovernmental science-policy Platform on Biodiversity and Ecosystem Services (IPBES) option value is one of eighteen different categories of nature’s contribution to people (Pascual et al. 2017). Multi-criteria analyses are used to identify the particular geographical areas we should conserve (Sarkar 2016).<sup>13</sup> These criteria can include multiple measures of biological difference which are significant in the local context causally or instrumentally and ‘wilderness’ areas of beauty or recreational use. There are many reasons to preserve an area including political, aesthetic, or economic reasons but a general measure of biodiversity should be incorporated into any conservation decision-making procedure to identify unique overlooked features.

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<sup>12</sup> Nehring and Puppe have proposed their own measure of phylogenetic diversity (2004) as a development of their project formalizing diversity *simpliciter* (2002).

<sup>13</sup> See Sarkar et al. (2006) for an explanation of multi-criteria analyses and systematic conservation planning. Sarkar et al (2016) is a case where the procedure is used to design and implement conservation areas in West Papua, Indonesia.



## Theoretically fundamental

Biodiversity needs to be in reference to a key feature of life on earth. It should be measurable across life and variations in biodiversity should be explanatory. In “[Tractability](#)” section. I noted the tree of life and DNA are both shared across all life. These features ground modern taxonomy and the belief that biodiversity refers to taxonomic relations is nearly universally shared in the philosophy of biodiversity literature.<sup>14</sup> Sarkar (2005, 2012) introduces it as a stipulation in his account of biodiversity. One of his four constraints for assessing any description of biodiversity is ‘taxonomic spread is important’, and this claim is further clarified in a footnote to refer to not just diversity within a clade but across clades. Maclaurin and Sterelny (2008) centre biodiversity on species richness, supplemented along multiple different gradients. These can but do not necessarily include function, genes, local ecology, and phylogeny. Environmental ethicist Holmes Rolston III identifies species as the right unit for biodiversity as “(s)pecies are a more evident, mid-range, natural kind” (Rolston 2001). Phylogenetic measures take on this taxonomic assumption and base biodiversity in the features that ground all taxonomic inferences, the lineage relations of all populations (De Queiroz 2005).

Species are a sub-set of lineages within the larger structure, and the fact that they have these historical-causal relations is important for option value. Species richness on its own is an inadequate way to represent option value as it assumes that individual species contribute to biodiversity equally. They do not. There are many species which live in a small geographic area and are by any measure unremarkable compared to their close relatives (Sober 1986). Biodiversity is not simply a count of species but must represent the difference between species. This is necessary as the differences between species are not independent. Many features are inherited from a common ancestor. If we treat them as independent variables in a measure, we are committing an explanatory error, often called pseudoreplication, in which we treat dependent variables as independent. Moving to phylogenetic measures stops biodiversity measures from suffering from the ‘phylogenetic pseudoreplication’ that afflicts species richness (Garland Jr 2001). The non-independence of species is what makes phylogenetics explanatorily indispensable to the biological sciences. For example, biogeography aims to explain the distribution of species across the globe. This project requires an explanation of why similar forms, as a defeasible rule, appear near each other. Measuring species relatedness indicates species historical relations, which allows us to construct a picture of their historical distribution and migration.

Phylogenetic measures have recently become prominent even in biological sciences which have traditionally shied away from history like community ecology. Community ecology’s explanatory target is the distribution and abundance of species. Phylogeny can explain current local population interactions and has yielded new avenues of research in community ecology (Cavender-Bares et al. 2009). For example, the hypothesised link between diversity and stability has often been used

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<sup>14</sup> For an extended argument that biodiversity should be taxonomic rather than ecological, see: Lean and Sterelny (2016).



to justify biodiversity conservation. Whereas older experiments tested the relationship using species diversity (usually species richness) newer experiments have used Faith's Phylogenetic Diversity. These have found phylogenetic diversity promotes ecosystem stability (Cadotte et al. 2012; Flynn et al. 2011).

Preserving the lineage structure of life is desirable as a means of preserving heritage. Rosauer and Mooers (2013) argue that "ED (Measures based on phylogeny) need not be a surrogate for other metrics of biodiversity because it is a fundamental measure of biodiversity". Losing branches from the tree of life loses the record of the evolutionary response to Earth's changing environment. The information that can be gained from living populations exceeds what can be gained from palaeontological study. Living populations reveal information which will be lost when they become extinct.

Representing the phylogenetic structure of lineages is indispensable to the biological sciences and epistemically desirable. Referring to it grounds the concept of biodiversity in the most fundamental structure in biology.

### **Biodiversity beyond the species taxa**

Defending phylogenetic diversity measures as an explication of biodiversity raises questions about what I believe the role of species taxa is in conservation. Species are still central to conservation but do not exhaust our interests in biodiversity. Phylogenetic measures situate species within the larger lineage structure that species are nested in. Species are a level of lineage that is historically and genetically isolated from other lineages; in other words, where there is a distinct branching event (De Queiroz 2005). Different causal processes separate and maintain the separation of lineages. These include geographical isolation, isolation due to mate recognition, or environmental differentiation. These different processes provide species with internal cohesion and a *shared fate* that allows species to act as causal units in evolution and ecology. So, when Mishler (2009) declares that "biodiversity is the whole tree of life, not the arbitrary place at which species are named", I agree that biodiversity must correspond to the overall lineage forming structure of life but disagree that species are always arbitrary and unimportant for conservation.

There are, however, many cases in which there are not distinct branching events where lineages create new species. In these cases lineages have begun a process which could lead to speciation or other processes such as Lateral Gene Transfer (LGT) have meant that there is considerable gene transfer between different populations. The evolution of sub-populations within a species is important for conservation under certain contexts. The most obvious is after we have decided we need to preserve a species, we need to identify the intra-species variation necessary for long-term survival. Intra-species lineal variation is preserved for the purposes of saving the species. Intra-lineal phylogenetic diversity is also in itself biodiversity and when deciding between species to allocate resources, it can act as a deciding factor. If we have two species in a clade and one of these species has more intra-specific biodiversity, we should preferentially allocate resources to it. These sub-

species level questions of diversity cannot be addressed within a species richness framework.

Distinct branching events are difficult to identify when genes transfer between lineages. Hybridizing allows for gene flow between quite isolated lineages and Lateral Gene Transfer is common within many sections of life. These processes mean that there is often discordance between gene trees indicating different historical relationships between populations. The discordance between trees has led some to voice a strong scepticism about the existence of a single tree of life that can be identified through phylogenetics (Franklin 2007; O'Malley and Koonin 2011).<sup>15</sup>

Trees constructed with different, or even the same, molecular data can vary but the major question is whether this variation is strong enough to lose our resolution of a single species tree. While there may be reasons to be sceptical of a single species tree—for example polar bears appear to have two different phylogenetic histories (if we count them as a species) (Hailer et al. 2012)—generally, for the more complex organisms which are commonly the targets of ecology and conservation science, we can be confident that they stand in real historical relationships that molecular data can be used to infer. Gene trees may not be identical but if they robustly converge on a single historical relationship we are vindicated in believing in a single species tree. For macrobes this is fortunate as there is a complex relationship between genomes and phenotypes. Phenotypic variation often depends on extra-genetic inheritance and development. The species tree is therefore critical to represent the phenotypic variation in these organisms with their complex scaffolded developments. As phylogenetics identifies the species tree, we capture the phenotypic variation within macrobes by following their evolutionary history.

Distinct lineages become more problematic in single-celled life, particularly prokaryotes, where LGT is common. Within a single microbe genome, we can often find clusters of genes with a different evolutionary history to other parts of the genome. These populations will appear that will have had multiple evolutionary histories rather than one. In practice scientists try to identify species lineages by limiting the genes they build phylogenies from. These genes are thought to be universal and evolutionarily stable and are referred to as 'core genes' (Lan and Reeves 2001; Wertz et al. 2003). The rest of the microbe genome is relegated to the descriptor of 'accessory genes'. Phylogenies of core genes unfortunately only reveal 'trees of the 1%', with the phylogenies being only representative of a small portion of the genome (Dagan and Martin 2006). These phylogenies will not be particularly representative of the evolution of the genome or the functional capacities of this population. The tight pairing of morpho-functional differentiation and evolutionary history supports the use of phylogenetic measures of biodiversity. Taking a phylogeny of such a limited set of genes will be less representative of overall morpho-functional diversity within bacteria.

The problem of core genomes not being representative of the features of a microbe can be addressed in a couple of ways, still within a phylogenetic

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<sup>15</sup> See the Biology and Philosophy Special Issue 'Biology and Philosophy of the Tree of Life' for an in-depth debate about these issues.

biodiversity framework (see: Malaterre 2013; Morgan 2010 for more on microbe biodiversity). The first is to note if LGT is high within a community these accessory genes functionally become public goods; they are shared by all or many of the local populations (see Sørensen et al. 2005 for indication of high LGT in biofilms). Preserving just a few populations within the area will preserve these genes. Microbes do not have complex relationships between genotype and phenotype; if we represent the genes in our measure of biodiversity we have also represented the phenotypes. If LGT is ubiquitous, bacterial biodiversity should be quite easy to represent. This differs to macrobe biodiversity where extra-genetic inheritance is critical.

The shared goods model of LGT derived diversity may be assumed by some microbiologists as it is common for them to use phylogenetic measures of diversity based on 'core genomes' to measure microbial evolution.<sup>16</sup> Scientists find these measures useful as species boundaries are vague or non-existent in microbes (Ereshefsky 2010). Instead, microbiologists categorize diversity in terms of taxonomic rank neutral phylogenetic divergence, settling on a percentage of genetic similarity to distinguish 'Phylotypes'. For example, in an act of navel gazing worthy of philosophy, scientists have studied belly button microbe communities and found six phylotypes—populations of individuals with  $\geq 97\%$  genetic similarity—dominate these communities and appear in over 1/3 of the samples in 80% of humans (Hulcr et al. 2012). They also use these measures to record evolutionary responses in microbial populations to traditional biogeographic environmental factors like temperature and geography (Chu et al. 2010; Lauber et al. 2009). This is indicative that where scepticism about a single tree of life is strongest, the pragmatic use of phylogenetic diversity to represent populations becomes common. This is because phylogenetic differentiation is still representative of the diversity of microbes and computationally tractable despite the LGT between microbe lineages.

While phylogenetic diversity measures in their current iteration are often adequate to represent biodiversity, there are further ways these measures can be developed. Gene transfer between lineages can be represented within a phylogenetic diversity-like measure. Relaxing the bifurcating tree assumption within phylogenetic diversity measures allows for network phylogenies (Huson et al. 2010). Within a network we can still identify the set of populations that have diverged the most. Just as in phylogenetic diversity measures of bifurcating lineages, we will preserve populations with long branches and populations that are representative of the network thicket behind them.

This allows for more genes to be included within the phylogeny but it will still not represent the majority of the accessory genes. These genes will have been passed around too many times to be able to make an alignment. If these genes are not public goods shared amongst the populations then we may need to do further work to represent them in our measures of phylogenetic diversity. Once a phylogeny is established using conserved core genes we could modify branch lengths through a phenetic measure of accessory genes.<sup>17</sup> We would need to construct a presence/

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<sup>16</sup> There are now hundreds of papers using Faith's PD to measure microbial diversity.

<sup>17</sup> Thanks to Rob Lanfear for this point.

absence matrix of accessory genes found within different 'core gene' lineages.<sup>18</sup> The presence of accessory genes can then act as a modifier lengthening the branch of the 'core gene' lineage. These longer branches would be more highly valued within a phylogenetic diversity measure. It is, therefore, possible to incorporate bacterial diversity within a phylogenetic diversity framework even when there is high but non-ubiquitous lateral gene transfer between lineages.

Species often play an oversized role in thought about biodiversity. When we consider diversity above the species level and diversity below the species level, phylogenetics is consistently applicable and useful. Finally, phylogenetics also provides resources for sections of life which do not obviously form species (Ereshefsky 2010). Whereas some may view microbes as posing a problem for a phylogenetic biodiversity I think it displays the virtues of a consistent measure that can scaffold diversity indices.

## Conclusion

This paper has provided a means for assessing the right unit of measure for the biodiversity concept. These criteria can be used to assess the quality of any proposed measure of biodiversity. By treating biodiversity as a scientific concept, we can provide it with criteria that are receptive to new developments. As a concept still under debate, there are many competing interests to be satisfied but a measure of biodiversity needs to be both general enough to capture biological diversity on a global scale but specific enough to be empirically tractable on local scales. Describing biodiversity as referring to lineage structure can do this and thereby provides a firm theoretical basis for the concept. Phylogenetics is the most powerful way of representing biodiversity.

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<sup>18</sup> The description of the same gene across different bacterial lineages is subject to the problems of establishing a 'gene' identity. This is easier in microbes than macrobes but is by no means unproblematic. For discussion of 'genes' and identity see Griffiths and Stotz (2013).

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