The Value of Phylogenetic Diversity

Christopher Lean and James Maclaurin

Abstract This chapter explores the idea that phylogenetic diversity plays a unique role in underpinning conservation endeavour. The conservation of biodiversity is suffering from a rapid, unguided proliferation of metrics. Confusion is caused by the wide variety of contexts in which we make use of the idea of biodiversity. Characterisations of biodiversity range from all-variety-at-all-levels down to variety with respect to single variables relevant to very specific conservation contexts. Accepting biodiversity as the sum of a large number of individual measures results in an empirically intractable framework. However, large-scale decisions cannot be based on biodiversity variables inferred from local conservation imperatives because the variables relevant to the many systems being compared would be incommensurate with one another. We therefore need some general conception of biodiversity that would make tractable such large-scale environmental decision-marking. We categorise the large array of strategies for the measurement of biodiversity into four broad groups for consideration as general measures of biodiversity. We compare common moral justifications for the conservation of biodiversity and conclude that some form of instrumental value is the most plausible justification for biodiversity conservation. Although this is often interpreted as a reliance on option value, we opt for a broadly consequentialist characterisation of biodiversity conservation. We conclude that the best justified general measure of biodiversity will be some form of phylogenetic diversity.

Keywords Biodiversity • Measurement • Surrogacy • Consequentialism • Justification

C. Lean (✉)
Philosophy Programme, Australian National University, Canberra, Australia
e-mail: christopher.hunter.lean@gmail.com

J. Maclaurin
Department of Philosophy, University of Otago, Dunedin, New Zealand
e-mail: James.Maclaurin@otago.ac.nz

© The Author(s) 2016

R. Pellens, P. Grandcolas (eds.), *Biodiversity Conservation and Phylogenetic Systematics*, Topics in Biodiversity and Conservation 14,
DOI 10.1007/978-3-319-22461-9_2

Introduction

It is not surprising that there is a bewildering array of tools available to those who would measure biodiversity. There are of course countless respects in which organisms and ecosystems vary. More importantly, there are many types of scientific projects which exploit different aspects of biodiversity. In *What is biodiversity*? (2008) Maclaurin and Sterelny argue that, although it began as an idea primarily of interest to conservation biologists, there are now many areas of the life sciences in which biodiversity plays an ontological, explanatory or predictive role.

Moreover, within conservation biology the role of biodiversity has become complex. When biodiversity was first envisaged in the 1980s it was intended as a new organising principle for conservation. In many respects it was to be a replacement for the old idea that conservation was fundamentally about preserving species and the even older idea that it is essentially about preserving wilderness (Nash 1990). But alongside this idea of biodiversity as an overarching goal of conservation, our new understanding of the effects of diversity on ecology, genetics, and morphology allows us to harness particular aspects of biodiversity to achieve specific conservation goals. So now biodiversity takes its place both as a goal for policymakers and as a tool for conservation biologists. In both contexts, biodiversity is difficult to measure. For this reason, much of the growth in biodiversity metrics has been in the development of new and more effective biodiversity surrogates.

In this complex theoretical and methodological landscape, is phylogenetic diversity just one more tool to be used as and when appropriate? In this chapter, we focus on conservation biology and argue that phylogenetic diversity plays a unique role in underpinning conservation endeavour.

In the first section we argue that the conservation of biodiversity is suffering from a rapid, unguided proliferation of metrics. These various measures will be categorized by what they aim to pick out and preserve. We then scrutinise the justification for various types of measures as fundamental principles underpinning large-scale conservation (we explain why 'large-scale in the next section) and argue that this role is best performed by phylogenetic diversity.

A Maze of Measures

Our current understanding of biodiversity is a mess. It is a fortunate, productive, and useful mess but a mess none the less. This can be traced to the lack of a guiding set of standards from which to assess the value of proposed biodiversity measures. Although measures are tested, the testing has often been piecemeal across conservation biology and related disciplines leading to conflicts over whether a metric has been proved. An example is the debate between Ross Crozier et al. (2005) and Dan Faith and Andrew Baker (2006) over assessing conservation schemes which use phylogenetic diversity for data sets that include systematized taxa without

phylogenies. While Crozier et al. claim that this study is a "proof of concept", what they take to be an examination of phylogenetic diversity's applicability to conservation projects in the field, Faith and Baker claim that such examinations were already conducted a decade ago! The lack of a guiding set of standards has resulted in difficulty compiling and comparing measurement procedures in an environment in which new measures are proliferating. It is noted that "in the last decade more than two measures of Phylogenetic Diversity or Functional Diversity were proposed, each year!" (Cianciaruso 2011). This has resulted in measurement options for biodiversity increasing without a clear way of choosing between them. This proliferation of varied, uncategorized measures is referred to by Faith and Baker as the "curse of biodiversity informatics" or "bio-miss-informatics" (Faith and Baker 2006).

The proposed measures of biodiversity are of course, not limited to phylogenetic diversity. There are measures aimed at describing biodiversity using many different accounts of functions, abundance measures, ecosystem services, and hybrids of all of the above. The description of these measures is inconsistent throughout biology because; "The vocabulary used to classify indices is continuously evolving and differs between evolutionary and ecological studies, leading to potential confusion when a term is employed without a clear definition or reference" (Pavoine and Bonsall 2011). Biodiversity particularly suffers from ambiguity regarding biological features scientists and policymakers are referring to when they say an ecosystem has high biodiversity.

Individuals and groups have tried to build consensus around which features are worthy of measurement. One recent attempt to collect an index of measures that are fundamental to biodiversity notes that; "a key obstacle is the lack of consensus about what to monitor" (Pereira et al. 2013, p. 277). The authors propose a set of "Essential Variables of Biodiversity". These include:

- Genetic composition e.g. allelic diversity
- Species populations e.g. Abundances and distributions
- Species traits e.g. phenology
- Community composition e.g. taxonomic diversity
- Ecosystem structure e.g. habitat structure
- Ecosystem function e.g. nutrient retention

Each of these "variables" can be measured using multiple (sub-) variables. For example ecosystem function in their account includes nutrient retention in a community. This would include the cycling of Nitrogen, Carbon, and Phosphorous through a community, amongst other important nutrients. Biological features such as species traits not only need to be individuated but there are also numerous different mathematical measures for that trait description to decide between. All these variables, their sub-variables, and the different measurement procedures for the sub-variables are understood as actual measures of biodiversity (although for any real ecosystem the majority of these variables will be unanalysed). To what then do we refer when we talk of biodiversity as a conservation goal? According to these authors, we refer to the sum of all these 'essential' aspects of biological diversity.

This permissive and conciliatory view of biodiversity, while at first seeming attractive, is problematic as a guide to conservation. Accepting biodiversity as the sum of a large number of individual measures results in an empirically intractable framework. Large-scale conservation requires prioritisation of effort and resources across disparate ecosystems. The many available biodiversity measures make such decisions difficult. In all ecosystems there will be incompletely analysed variables. So either policymakers and conservationists accept that many assessments of biodiversity are incommensurate with one another or they must subscribe to schemes for weighting the various measures. In practice, the relative weighting of the many variables will often be treated as equal but there is an open question as to whether we *should* treat each variable as equal. Should ecosystem biomass be treated as equally important as plant trait disparity? If not then we will have to agree on a seemingly arbitrary rubric of relative weights for the various features being measured. In short, the retention of such a large swath of essential measures creates problems for the practice of conservation.

We accept that the many measures representing the diversity of biological systems can be relevant to particular contexts in conservation and their accuracy and utility can be assessed through experimentation or modelling (Pereira et al. critically assess measures through their "scalability, temporal sensitivity, feasibility, and relevance", p. 277). But as a whole, the use of biodiversity as a foundational tool in conservation biology suffers from a glut of information that is hard to integrate in a useable way. Those who agree with Michael Soulé's (1985, p. 727) well-worn description of conservation biology as a crisis discipline, are likely to think such confusion can only get in the way of efficient decision-making. Biodiversity should be a useful concept across disciplines and sites.

Local conservation imperatives often point to particular biodiversity variables to which we should pay attention, e.g. focus on genetic diversity is crucial in trying to bring a single species back from the brink of extinction. However, not all conservation is local. Governments and NGOs must prioritise conservation strategies applied to different ecosystems and applied at different scales, e.g. governments must weigh the conservation value of: conserving endangered species, developing national parks, regulating fisheries, and decreasing carbon emissions.[1] Such large-scale decisions cannot be based on biodiversity variables inferred from local conservation imperatives because the variables relevant to the many systems being compared would be incommensurate with one another. For the reasons noted above, it is impractical to interpret biodiversity in such large-scale contexts as the sum of all the biodiversity variables of all the systems being compared. We therefore need some general or fundamental conception of biodiversity that would make tractable such large-scale environmental decision-marking. In what follows, we shall refer to this as a *general measure of biodiversity*.

[1] Of course some of these are not purely conservation decisions, but all rest to some important extent upon judgements about the value of natural systems.

One of Many Biodiversities

In thinking about large-scale differences in biodiversity, we often employ a concept of biodiversity which is very broad. Sarkar et al. claim biodiversity is "diversity at every level of taxonomic, structural, and functional organization of life" (Sarkar et al. 2006). The Convention on Biological Diversity (CBD) proposes that biodiversity is "diversity within species, between species, and of ecosystems" (CBD 1992). According to such definitions, any mathematical measure that categorizes biological difference and preferentially organizes that difference is a measure of biodiversity (including many unimportant and unused metrics e.g. diversity of spottiness as quantified by the number of non-contiguous circular patterns averaged over the members of a species).

This broad characterisation of biodiversity has permitted a range of targets of measurement such as species richness, species diversity, ecosystem function, species function, population relations, ecosystem diversity, biomass, genetic diversity, phylogenetic diversity, and many more. In what follows we collect these measures into broad categories and assess each as the basis for a general measure of biodiversity. We begin by tackling a couple of red herrings.

Measures We Rule Out

A general measure of biodiversity must be capable of guiding large-scale and long-term conservation effort. We think this rules out two types of biodiversity measures: biodiversity surrogates and measures based on ecosystem services. Both are, of course, important tools in conservation, but for the reasons set out below, they cannot underpin a general measure of biodiversity.

Surrogates of Biodiversity

As noted above, most of the growth in biodiversity metrics has been in the development of new surrogates for biodiversity, i.e. measures of features whose presence is correlated with high biodiversity. If biodiversity measurement is to succeed as a large-scale goal of conservation, then we must be able to assess the success of biodiversity surrogates and we can only do that if we understand what it is that these metrics are surrogates for. Sarkar et al. (2006) argue that "general biodiversity is too diffuse a term to be precisely defined". The best we can do is to agree to "some convention or consensus about what constitutes the relevant features of biodiversity in a given context". We think this 'nothing but surrogates' view of biodiversity measurement, in effect, risks giving up on the idea of biodiversity as an overarching goal for conservation. Crucially this convention-based view on how we should

characterise biodiversity appears not to rest on underlying principles for the assessment of the conventions underpinning such a consensus on biodiversity measurement.

On our view, a general measure of biodiversity must be definable (or at least capable of clear characterisation) and it must be a feature of biological systems that we can practically assess across clades and ecosystems. This is essential if such a measure is to assist us in forging large-scale conservation policy. Moreover, it must not itself be a surrogate for some further more basic characteristic of living systems that can also be measured across clades and ecosystems.

Anthropogenic Variables

The idea of ecosystem services as a foundation for a general measure of biodiversity is fraught with difficulty. This is partly because the whole idea of ecosystem services is at best very open ended. The Millennium Ecosystem Assessment report (2005) defines ecosystem services as "benefits people obtain from ecosystems". Despite gallant attempts to assess the global value of ecosystem services in dollar terms (e.g. Costanza et al. 1997), many of the psychological and social benefits are difficult to measure even at small scales and, as a group, the benefits people obtain from ecosystems seem incommensurate with one another (Boyd and Banzhaf 2007). Moreover, while ecosystem services are usually interpreted as inventories of current benefits to humanity, conservation is inherently forward-looking and it is even more difficult to accurately assess the benefits that species and ecosystems will provide to our descendants. Indeed, even if we could agree on a reliable set of measures and agree on a way to aggregate them, many environmental ethicists and many members of the public would balk at the idea that only human interests need be taken into account in conservation decision-making (see for example Stone 1972). So although ecosystem services are an important driver of conservation effort, we think this tool is too limited to form a plausible basis for a general measure of biodiversity.

The idea of biodiversity should capture the diverse features of life not the diverse interests of people. While we grant to Reyes et al. (2012) that there is 'functional overlap' between these two features of biological systems we agree with Faith (2012) that ecosystem services and biodiversity are distinct. It is in the interests of humanity to preserve biodiversity, but this fact does not warrant defining biodiversity in terms of current human needs and interests. Moreover, there is practical utility in keeping these ideas separate. Differentiating between ecosystem services and biodiversity has allowed research into whether these features co-vary and what biodiversity targets yield ecosystem services (Benayas et al. 2009; Mace et al. 2012; Worm et al. 2006). In certain cases we may want to prioritize the maintenance or reinstatement of ecosystem services. Differentiating the services from the diversity serves to distinguish such conservation that focuses squarely on the economic and social needs of human populations.

The Main Candidates

As noted in the previous section, current broad characterisations of biodiversity permit a range of targets of measurement including species richness, species diversity, ecosystem function, species function, population relations, ecosystem diversity, biomass, genetic diversity, phylogenetic diversity, and many more. In this section, for the sake of manageability, we categorise that large array of strategies into four broad groups for consideration as general measures of biodiversity.

Species Diversity and Species Richness

Species diversity is an intuitively simple concept that has yielded numerous mathematical explications combining species richness, the number of species in an area, species evenness, and the relative abundance of species (see Maurer and MacGill 2011). Species richness is extremely common as a measure of biodiversity, partly due to its relative ease of discovery. It is a key variable from which many diversity metrics are constructed influencing the output of species diversity, functional, genetic, and phylogenetic measures. It is, in many contexts, a good indicator of biodiversity. Holmes Rolston goes as far to claim that species richness *is* biodiversity as "(s)pecies are a more evident, mid-range, natural kind" as opposed to other proposed units of biodiversity like genetic diversity or ecosystem diversity (p. 402, Rolston 2001).

Species richness is usually supplemented with other information as just counting the species present gives limited insight into the dynamics of an assemblage. Often species richness is combined with species evenness to create many of the common species diversity measures.[2] This is based on the idea that, given a species richness in an area, species diversity increases when the populations have more even abundances and vice versa. Information theory has provided the most common indices of species diversity, the Shannon evenness and the Simpson evenness indices. Other measures include: Hill's Indices, Hurlbert's "Interspecific encounter Index", Rao's "Quadratic Entropy" Index, and Fager's Indices (See Justus 2011; Maurer and Macgill 2011).

While there is a range of ways that species diversity is calculated there is one feature common to these measures. Measures of species richness and diversity are blind to each individual species' identity. No species is treated as being more valuable to than any other. This assumption is directly rejected by measures that prioritize species by any of their individual features including morphology, genetics, or phylogeny.

[2] For a sceptical take on the success of such measures see Justus (2011).

Function and Morphology

Functional diversity, as it is commonly used, is a subset of trait diversity. Functional traits are commonly morphological traits differentiated by the effects the trait has on an ecosystem (Petchey and Gaston 2006). Some ecologists have rejected the need to associate 'functional' traits to ecosystem effects and treat function diversity as a synonym of morphology. Evan Weiher (2011) in his summary of functional diversity measures states, "Some have suggested the term 'functional diversity' be restricted to measures of trait diversity that affect the functions of ecosystems (Tilman et al. 2001; Petchey and Gaston 2006). We should be wary of unnecessarily restrictive definitions for terms that are conceptual, general, or useful" (pg. 175). He further notes that general morphological trait space can be differentiated without reference to a schematic for differentiating traits. The dizzying range of mathematical measures for dividing morphological space include: distance measures, dendrogram-based measures, variance-based measures including abundances, trait evenness, convex hull mathematics to measure trait volume, and graph theory (See Weiher 2011).

Genetic Diversity

Genetic diversity is considered by many to be the lowest level of a nested hierarchy of diversity comprising of genetic diversity, species diversity, and community diversity (Culver et al. 2011). Culver et al. suggest that genetic variation is "the essence of all biodiversity" (p. 208). Genetic barcoding of populations has become increasingly common due to the efficiency of new sampling techniques and the increase in computational power. Clearly, there will in the future be more genetic information available to researchers that will aid, not just our understanding of genetic difference, but also our assessments of other forms of diversity such as species diversity and phylogenetic diversity. Despite its clear practical importance, it is implausible that genetic diversity should underpin a general measure of biodiversity. This is partly because genes vary greatly in their effects so that the amount of raw genetic difference between two populations tells you relatively little about the extent to which they differ functionally and ecologically. It is also partly due to the undoubted importance of non-genetic factors in both ecology and evolution (Laland et al. 1999; West-Eberhard 2003; Jablonka and Lamb 2005).

Phylogenetics and Phylogenetic Diversity

Phylogenetic inference recreates the branching structure of evolutionary relationships between species via cladistic analysis from molecular and morphological data in the form of discrete character states or distance matrices of pairwise

dissimilarities (Vandamme 2009). The computational models used differ both in methodology and epistemological grounding; prominent methods include Maximum Parsimony, Maximum Likelihood, and Bayesian Methodologies. Phylogenetic distance measures aim to quantify the relatedness of groups of species. As the phylogenetic tree represents the evolutionary relations between species it can also be used to calculate how distinct these species are relative to the tree in which they are nested. Methods differ in the way they characterize distance and uniqueness. Some do it in terms of speciation events and others in terms of change in genomes between species. Following Velland et al. (2011), we distinguish two types of fundamentally different measures of phylogenetic diversity (p. 196):

Node-based trees represent only topology. They are based only on information about speciation events and so we can infer from them only facts about relatedness. Such measures include: Taxonomic Distinctness (Vane-Wright et al. 1991) and Species Originality (Nixon and Wheeler 1992).

Distance-based trees include topological information as well as branch length. Branch length either represents the accumulation of evolutionary change or alternatively the passage of time. Such measures include: PD (Faith 1992, 1994); Originality of Species within a Set (Pavoine et al. 2005); Pendant Edge[3] (Altschul and Lipman 1990) and Species Evolutionary History (Redding and Mooers 2006).

Both groups of methods represent speciation and its creation of distinct evolutionary trajectories and both provide, with varying degrees of success, a means to prioritize the conservation of phylogeny and therefore of species that are particularly distinct in their features and history.

The Roles of Phylogenetic Diversity

Although the role of phylogenetic diversity in conservation biology is open-ended, extant uses can be categorised into three distinct groups.

(i) *Phylogenetic Diversity as a tool for prediction and explanation*

Conservation is only possible when we have a good understanding of the dynamics of communities and ecosystems. Although we often think of this in ecological terms, evolution is an important contributing factor. In such contexts the measurement of phylogenetic diversity can help us distinguish these component forces at work. For example, all else being equal, we expect species that are closely related to be both morphologically similar and similar in the functional roles that they play in the ecosystems in which they are found. So we can use phylogenetic diversity to predict functional similarity. Such studies allow

[3] Note "Pendant Edge" is a recent name (e.g. Redding, and Mooers 2006; Vellend et al. 2011) given to the idea introduced but not named in Altschul and Lipman's original very brief discussion note.

us to detect cases that stand in need of special explanation. These are cases where functional diversity is either higher (over-dispersion) or lower (functional diversity deficit) than expected (see for example Webb et al. 2002). The appropriateness of particular metrics will depend upon the explanatory or predictive target, although we note that common metrics show strong correlation with one another in many circumstances (Vellend et al. 2011, p. 207).

(ii) *Phylogenetic diversity as a surrogate*

Phylogenetic diversity has been employed as a surrogate for a wide variety of valuable features of ecological communities and ecosystems. For example, Srivastava et al. (2012) argue that phylogeny largely determines interactions among species, and so could help predict the cascade of extinctions through ecological networks and hence the way in which those extinctions impact ecosystem function. So, on this account, phylogenetic diversity is at least a surrogate for ecosystem function.

Forest et al. (2007) find a stronger correlation between phylogenetic diversity and feature diversity than between species diversity and feature diversity. So they recommend that we employ phylogenetic diversity, rather than species diversity, as a surrogate for feature diversity. Faith et al. (2010) argue that we should recognise phylogenetic diversity as a surrogate for features of value to human well-being:

> We argue that an evolutionary perspective is essential for developing a better understanding of the links between biodiversity and human well-being. We outline the services provided by evolutionary processes, and propose a new term, 'evosystem services', to refer to these many connections to humans. (Faith D.P. et al. 2010, p. 66)

(iii) *Phylogenetic diversity as a conservation goal*

The third context in which one might employ phylogenetic diversity is as a goal of conservation. There are certainly examples of phylogenetically orientated conservation. The *Edge of Existence Programme* (www.edgeofexistence.org), run by the Zoological Society of London, focuses explicitly on the conservation of species that are endangered and phylogenetically distinct. There are many other conservation programmes that take phylogenetic diversity into account (e.g. WWF's Global 200). That said, phylogenetic diversity is not as widely used in conservation as it might be (Winter et al. 2012, p. 1). This is partly for methodological reasons:

> Phylogenetic diversity has long been incorporated in planning tools, but it has not yet had much impact on conservation planning. Applications face limitations of available data on phylogenetic pattern. (Sarkar et al. 2006)

It is also partly due to scepticism about the correlations claimed above:

> In our opinion, the justification for preserving phylogenetic diversity as a proxy for functional diversity or evolutionary potential has so far largely failed. Our current knowledge of the benefits to the (future) functioning of ecosystems and securing evolutionary potential remains equivocal. (Winter et al. 2012, p. 4)

Clearly there is limited employment of phylogenetic diversity as goal for large-scale conservation decision-making. There is also some skepticism about

our empirical and philosophical justification for such uses. In the final section of this chapter it is this question about justification to which we turn.

Moral Justifications for a General Measure of Biodiversity?

We have argued that large-scale conservation decision-making would benefit from agreement on a general measure of biodiversity, one that is not tied to particular projects or contexts. We have set out a group of broad categories of measurement strategies with the aim of determining whether one of these might furnish an appropriate general measure. In this section, we set out a similarly broad brush taxonomy of philosophical justifications for the conservation of biodiversity with the aim of determining whether any of those available might provide a justification for conservation based on a general measure of biodiversity and hence might provide us with a basis for inference about the nature of such a general measure. We will argue that the best justification is one that respects the plurality of human and non-human interests in biodiversity as well as uncertainty about how best to secure those interests and about future changes both in the environment and in human affairs.

Philosophical justifications for the conservation of biodiversity come in many forms but all such arguments fall into one of four categories.

Intrinsic Value

The idea that biodiversity has intrinsic value is enshrined in the Convention on Biodiversity. It is also a central tenet of deep ecology (Naess 1986). Despite its common currency, intrinsic value is capable of multiple interpretations which causes considerable confusion in moral reasoning (O'Neill 1992 p. 119). At least two interpretations are plausible in the current context.

One is the idea that biodiversity has intrinsic value in the sense that it has value over and above its instrumental value. This interpretation is further dependent on what we count as 'instrumental'. If we tie instrumental value to narrow economic purposes, then there seems to be considerable non-instrumental value in biodiversity. If we tie it to a broader set of psychological benefits (provided by recreation, aesthetic appreciation etc.) then the domain of non-instrumental value seems correspondingly smaller and more difficult to characterise.

A second interpretation is that biodiversity has intrinsic value in the sense that it is valuable independently of the valuations of valuers. It does after all seem that the biosphere would remain a locus of value even if some selective extinction event caused the demise of humanity or even the extirpation of all species capable of reasoning about value. But value in this sense seems almost impossible to quantify precisely because it cannot be tied to evaluative judgements made by economic

actors or by environmental stakeholders. The best we seem to be able to say is that some people, when asked, assent to the existence of such value.

Intrinsic value is controversial as a justification for the conservation of biodiversity for two reasons. Firstly, there is philosophical controversy about whether such forms of value exist (Norton 1984, p. 145). Secondly, as it is independent of human projects and human values, it is unclear how it should be measured and hence, how it should be conserved. There seems no way in principle of choosing between variety of ecosystems, variety of species, variety of form and function or variety in genetic make-up etc. as loci for biodiversity's intrinsic value. On the other hand, if intrinsic value is only a justification for the conservation of biodiversity in the very broad sense (set out at the end of section "Measures we rule out"), that will leave us no further along the path in the project of understanding or employing a practical general measure of biodiversity.

Human Emotional Responses to the Natural World

It is also claimed that biodiversity is valuable because the psychological makeup of human beings causes them to feel an intimate connection with the natural world which might be expressed variously in emotions such as love of, or respect for, nature. The idea that such emotional responses are a result of our evolved psychology was promoted by Wilson (1984) and Kellert and Wilson (1993). We note that the so-called Biophilia Hypothesis has received limited support in the literature (Simaika and Samways 2010 p. 903), but let us assume for the moment that we do share a common innate love of nature.

There are two important problems with grounding conservation in common emotional responses. Firstly, such responses are not always reliable guides to rational action. There is after all some fundamental fact about human beings that also causes them to see cigarettes as valuable. We don't think that this implies that we should 'conserve' cigarettes, because we don't think that this common emotional response is adaptive. Human beings feel positively disposed toward all sorts of things that are not actually good for us. But if we must then judge the adaptiveness of our feelings toward biodiversity, it seems that conservation justified thereby would not be a consequence of our feelings towards biodiversity, but rather of the utility of biodiversity to human populations (to which we turn shortly). Secondly, people clearly differ a great deal in the extent to which they feel positive emotions toward biodiversity (Einarsson 1993). If a general measure of biodiversity is to be inferred from emotional responses to biodiversity, then it seems that we will either have to discount the responses of outliers or average across a relatively large range of responses.

Finally, this style of justification for conservation suffers from the same problems as conservation based on intrinsic value. Even if it were true that almost everyone attached the same equally strong positive emotion to the conservation of the biosphere, it is hard to see how we could turn universal love of nature into a practically applicable general measure of biodiversity. For these reasons, we think it

implausible that common emotional responses to nature will justify general measure of biodiversity.

Instrumental Value

The benefits conferred by biodiversity on humanity (and indeed on other species) are themselves diverse (aesthetic, ecological, economic, epistemic etc.). Moreover, as Elliott Sober (1986) so eloquently points out, species differ a great deal in their apparent instrumental value. The great majority of species have small geographic ranges, do not perform unique ecological functions within their ecosystems and are not currently of important economic or psychological value to human populations. So Sober asks whether these facts justify the 'rational attrition' of species whose instrumental value is very small or unknown. This question about whether we should conserve 'unremarkable species' is closely related to the question of whether we should employ a general measure of biodiversity which would see us conserve species and ecosystems over and above those currently known to be of important instrumental value.

The strongest reason for conservation based on a general measure of biodiversity is that preferences or circumstances are likely to change so as to make valuable some proportion of the species in question. It is true that we have at times been overenthusiastic in our predictions about the possible future value of biodiversity such as the claims about the future value of bioprospecting in the Convention on Biodiversity (for more detail, see Maclaurin and Sterelny 2008, pp. 164–7). It is also true that a great deal of economic value resides in ecosystems that have low diversity, viz farms. That said, there has been huge growth in our appreciation for, and enjoyment of, natural variety through ecotourism, national parks, eco-sanctuaries etc. As noted in section "Measures we rule out", there is also evidence that biodiversity is correlated with a wide range of ecosystem services. Furthermore, we should be careful not to base our predictions about future value on current categories. Just as ecotourism and bioprospecting are relatively recent ideas, we may in future discover new types of endeavour which place the value of extant species in a new light. In short, there is a *prima facie* reason for conservation based on a general measure of biodiversity, namely that we hedge our bets against an uncertain future. This idea was originally proposed by McNeely et al. (1990) as an instance of option value,[4] but the use of option value in this context has been controversial. Option value is an idea imported from economics. It is essentially a willingness-to-pay measure—the additional amount a person would pay for some amenity over and above its current value in consumption to maintain the option of having that amenity available for the future (van Kooten and Bulte 2000, p. 295). Although one of us has previously

[4]This idea has been championed particularly by Dan Faith. For excellent discussions of the option value represented by biodiversity see Faith (1992, 1994, 2013).

expressed enthusiasm for the option value idea (Maclaurin and Sterelny 2008, section 8.4) we now think that the answer lies elsewhere.

The crucial problem with option value is that it ties the value of biodiversity to judgements about value made by ordinary people (consumers in the economist's terms). Clearly actual assessments of such option value will be difficult (Norton 1988). Even if we could assess such judgements, human beings are not good at reasoning about risk and they have limited biological knowledge. So it might be that people's actual assessments about the option value in natural systems would be very poor guides to the likely effects of conservation on future human communities or on future ecosystems. If we hedge our bets to maximise future outcomes then we should do so based on our best information about the probability of such outcomes rather than on the estimates that consumers might make about such outcomes.

In light of these issues, the value of biodiversity is better analysed as an instance of consequentialism, broadly applied. We should conserve biodiversity, not because people want to, but because doing so will on average lead to better outcomes for people and human communities of perhaps more broadly for moral patients (organisms capable of experiencing suffering).[5]

However, even the consequentialist interpretation faces an important objection developed at length in chapter 6 of Maier (2012). It might be objected that our uncertainty about future states of the biosphere and future goals and preferences of people implies that conservation based on a general measure of biodiversity is as likely to produce net harm as it is net benefit (after all, the species we are conserving include many whose effects on human populations are currently unknown).

There are of course instances in which diversity works against us, as when we are threatened by a diversity of pathogens. That said, ours is an extremely successful species with an extremely broad niche. We have become adept at harnessing a great variety of features of the natural world to an astounding variety of ends. The number of species that pose a serious threat to humanity is a vanishingly small proportion of the total species count. Moreover, a great number of weeds and pests are not harmful in their native habitat, but only become harmful when that habitat is radically disturbed or when they are introduced by humans into other ecosystems (Baker 1974).

We therefore think it implausible that conserving unremarkable species will on average produce more harm than benefit. Put another way—were possible, at the press of a button, to destroy all those species and biological communities not known to be of special value to humanity, we think it would be irrational to do so. Humanity (and perhaps other sufficiently sentient species) would almost certainly be worse off. So where we cannot assess the likely payoff for conserving an individual unremarkable species, it is nonetheless rational to assume that that payoff will be positive. This does not of course tell us anything about how large such a payoff will be and we acknowledge that there is an interesting and difficult question about weighing the benefits of such conservation against the opportunity cost of forgoing alter-

[5] Although not explicitly consequentialist and still somewhat confusingly called option value, the approach taken by Faith (2013, p. 72) is similar to the current proposal.

native projects (e.g. if we used conservation funding to fight diseases or conservation land to grow more food for burgeoning populations in poor countries). However, we note that this problem of assessing opportunity costs is a global one, affecting all aspects of public policy and hence too large a topic to treat here. Our purpose is to determine how we should in general rank and assess biological systems as candidates for conservation. We leave it to others to determine how what proportion of total human effort ought to be spent on conservation.

Phylogenetic Diversity as a General Measure of Biodiversity

We have argued that the best general justification for the conservation of biodiversity comes from its instrumental value. We also note that there are many types of such value and that the consequences of conservation focused on instrumental value in general are inherently uncertain. The nature and location of aesthetic, recreational, and other cultural values will inevitably be subject to disagreement. Moreover, we are not in possession of the full facts about the ways in which existing species and ecosystems can benefit (or harm) us and we know even less about the effects that conserved species and ecosystems will have on us and our descendants in the future. Can we harness this uncertainty as a means of developing a general measure of biodiversity?

We have argued that, leaving aside species whose value is currently well understood e.g. charismatic megafauna, economically important crops etc., we are warranted in spending some amount of time and effort in the large-scale conservation of biodiversity via some general measure. So we should conserve at least some of Sober's unremarkable species on the grounds that they might be valuable in some respect, but we cannot predict which respect that will be. This implies that a general measure of biodiversity should not aim at conserving particular features, but rather at conserving a maximal variety of features.

While it is sensible under some circumstances to measure variety of features or of functions, characterisation of overall biological diversity (of the sort attempted by Numerical Taxonomy) fails on philosophical grounds. It is not possible to capture differences in morphology[6] across the whole range of biological form because the idea of the occupation of morphospace makes sense only where we can anchor the dimensions of some particular morphospace to actual biological characteristics of closely related species (Maclaurin and Sterelny 2008, p. 15). The idea of a global morphospace is logically untenable because, as Goodman (1972, p. 437) argues, similarity and difference only make sense if we have some antecedent means of

[6] Note that in treating this problem is essentially about morphology, we are running form and function together. This is because we think that, were we to measure all biological form and all biological function, the two groups of characteristics would intersect at the level of physiological traits. So any attempt to develop an overall measure of functional diversity will face the same problems that must be overcome in the development of an overall measure of morphological diversity.

specifying the properties (or in the case of a morphospace, the dimensions) to be analysed. In taxonomy this almost always results in a focus on homologies. So in most cases the measurement of actual morphological diversity is best achieved by anchoring our analysis to actual differences in groups of related species, because only relatively closely related species differ in ways that make the analysis of morphospace tractable.[7]

So while broad difference in form and function is what the moral argument tells us to conserve, it cannot be measured directly in a way that would benefit large-scale conservation decision-making. Nonetheless, we can develop a general measure of biodiversity by exploiting the evolutionary processes that cause functional and morphological divergence within lineages. Both measures of species diversity and of phylogenetic diversity exploit evolution in just this way. If studies like those of Forest et al. (2007) are right, a general measure of biodiversity should be based on phylogenetic diversity, as that will best maximise feature diversity. We therefore conclude that phylogenetic diversity ought to play a fundamental role in conservation biology as the foundation of a general measure of biodiversity. That said, we noted in section "A maze of measures" that there are many measures of phylogenetic diversity. If conserving phylogeny is justified as a means of hedging our bets against uncertainty, this may help us to wrangle the current diversity in measures of phylogenetic diversity discussed earlier.

Variety in topological measures of phylogenetic diversity reflects the fact that phylogeny is complex. Species do not always bifurcate cleanly. Lineages reticulate and so on (Dagan and Martin 2006). Does this imply that, at large scales, phylogenetic diversity is undefined? We first note that such difficult cases are the exception rather than the rule at least across most of the phylogenetic tree. Secondly there are modifications of standard accounts of phylogenetic diversity designed to account for such phenomena as polytomies (see for example May 1990). Clearly over-dispersion studies (see the above discussion of Webb et al. 2002) are at least based on the assumption that it is possible to make large scale phylogenetic comparisons between very different systems. We cannot, in principle, construct a theoretical morphospace that contains humans and fungi and tardigrades, but we can compare their phylogeny. However, there is an important caveat. Large-scale phylogenetic diversity is tractable using topological measures of phylogenetic diversity and time-based distance measures, but it less obviously so for trait-based distance measures of phylogenetic diversity.

The more we incorporate form and function into a measure of phylogenetic diversity, the less plausible it is to think that you can compare phylogenetic diversity in this very rich sense between distantly related clades. Use of distance-based trees incorporating information about character evolution for such purposes requires the further assumptions (1) that there is a fact of the matter as to what we should count

[7] See for example the very wide variety of morphospaces discussed in McGee (1999, 2007). Indeed, it is notable that discussion of "convergent evolution in theoretical morphospace" (2007, pp. 90–2) actually focusses on a theoretical morphospace that models diversity in a single clade, namely the bryozoans (McKinney and Raup 1982).

as a character and (2) that all characters across all clades are of equal significance or contribute equally to biodiversity. To make this more concrete, we would have to assume that there is a fact of the matter as to how many characters contribute to the evolution of human cognition and that the biodiversity represented by the evolution of human cognition is of the same magnitude as the evolution of an equivalent number of characters in some other clade(s) for some other purpose(s).

Conclusion

We have argued that uncertainty about the application of the current maze of measures of biodiversity results, in part, from uncertainty about our reasons for conserving biodiversity in general. This is problematic for decisions about large-scale conservation, particularly where such conservation includes species and ecosystems whose instrumental value is currently unknown. We have argued that, in such cases, use of a general measure of biodiversity is justified on the grounds that it will best hedge our bets against current and future uncertainty about the location of instrumental value and the needs and preferences of human populations. If we are right, a general measure of biodiversity should aim at the maximisation of feature diversity. The most effective and tractable such measure will be one based on phylogenetic diversity.

Acknowledgements Thanks to Daniel Faith, Philippe Grandcolas, James Justus, Arne Mooers, Roseli Pellens, Kim Sterelny, Ted Toadvine and the many others who provided helpful suggestions.

Open Access This chapter is distributed under the terms of the Creative Commons Attribution Noncommercial License, which permits any noncommercial use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

References

Altschul S, Lipman D (1990) Equal animals. Nature 348:493–494

Baker H (1974) The evolution of weeds. Annu Rev Ecol Syst 5:1–24

Benayas JMR et al (2009) Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science 325(5944):1121–1124

Boyd J, Banzhaf S (2007) What are ecosystem services? The need for standardized environmental accounting units. Ecol Econ 63:616–626

Cianciaruso MV (2011) Beyond taxonomical space: large-scale ecology meets functional and phylogenetic diversity. Front Biogeogr 3(3):87–90

Costanza R et al (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260

Crozier RH, Dunnett LJ, Agapow PM (2005) Phylogenetic biodiversity assessment based on systematic nomenclature. Evol Bioinforma 1:11–36

Culver M, Fitak R, Herrmann H (2011) Genetic methods for biodiversity assessment. In: Magurran AE, McGill BJ (eds) Biological diversity: frontiers in measurement and assessment. Oxford University Press, Oxford, pp 175–193

Dagan T, Martin W (2006) The tree of one percent. Genome 7:118

Einarsson N (1993) All animals are equal but some are cetaceans: conservation and culture conflict. In: Milton K (ed) Environmentalism: the view from anthropology. Routledge, London, pp 71–82

Faith DP (1992) Conservation evaluation and phylogenetic diversity. Biol Conserv 61:1–10

Faith DP (1994) Phylogenetic pattern and the quantification of organismal biodiversity. Philos Trans R Soc Lond B 345:45–58

Faith DP (2012) Biodiversity and ecosystem services: similar but different. Bioscience 62(9):785–785

Faith DP (2013) Biodiversity and evolutionary history: useful extensions of the PD phylogenetic diversity assessment framework. Ann N Y Acad Sci 1289:69–89

Faith DP, Baker AM (2006) Phylogenetic diversity (PD) and biodiversity conservation: some bioinformatics challenges. Evol Bioinforma 2:121–128

Faith DP et al (2010) Evosystem services: an evolutionary perspective on the links between biodiversity and human well-being. Curr Opin Environ Sustain 2:66–74

Forest F et al (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. Nature 445:757–760

Goodman N (1972) Seven strictures on similarity. In: Goodman N (ed) Problems and projects. Bobbs Merrill, Indianapolis, pp 437–447

Jablonka E, Lamb MJ (2005) Evolution in four dimensions: genetic, epigenetic, behavioural, and symbolic variation in the history of life. MIT Press, Cambridge, MA

Justus J (2011) A case study in concept determination: ecological diversity. In: Brown B, de Laplante K, Peacock K (eds) Handbook of the philosophy of ecology. Elsevier, New York, pp 147–168

Kellert SR, Wilson EO (1993) The biophilia hypothesis. Island Press, Washington, DC

Laland KN, Odling-Smee FJ, Feldman MW (1999) Evolutionary consequences of niche construction and their implications for ecology. Proc Natl Acad Sci U S A 96:10242–10247

Mace GM, Norris K, Fitter AH (2012) Biodiversity and ecosystem services: a multilayered relationship. Trends Ecol Evol 27(1):19–26

Maclaurin J, Sterelny K (2008) What is biodiversity? The University of Chicago Press, Chicago

Maier DS (2012) What's so good about biodiversity? Springer, Dordrecht

Maurer BA, McGill BJ (2011) Measurement of species diversity. In: Magurran AE, McGill BJ (eds) Biological diversity: frontiers in measurement and assessment. Oxford University Press, Oxford, pp 55–65

May R (1990) Taxonomy as destiny. Nature 347:129–130

McGhee G (1999) Theoretical morphospace: the concept and its applications. Columbia University Press, New York

McGhee G (2007) The geometry of evolution: adaptive landscapes and theoretical morphospaces. Cambridge University Press, Cambridge

McKinney FK, Raup DM (1982) A turn in the right direction: simulation of erect spiral growth in the bryozoans *Arquimedes* and *Bugula*. Paleobiology 8:101–112

McNeely JA, Miller KR, Reid WV, Mittermeier RA, and Werner TB (1990) Conserving the world's biological diversity. International Union for conservation of nature and natural resources.

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington, DC

Naess A (1986) The deep ecology movement: some philosophical aspects. Philos Inq 8:10–31

Nash R (1990) The rights of nature: a history of environ ethics. Primavera Press, Leichhardt

Nixon KC, Wheeler Q (1992) Measures of phylogenetic diversity. In: Novacek MJ, Nixon KC (eds) Extinction and phylogeny. Colombia University Press, New York, pp 216–234

Norton BG (1984) Environmental ethics and weak anthropocentrism. Environ Ethics 6:131–148

Norton BG (1988) Commodity, amenity, and morality: the limits of quantification in valuing biodiversity. In: Wilson EO (ed) Biodiversity. National Academy Press, Washington, DC, pp 200–205

O'Neill J (1992) The varieties of intrinsic value. Monist 75:119–137

Pavoine S, Bonsall MB (2011) Measuring biodiversity to explain community assembly: a unified approach. Biol Rev 86:792–812

Pavoine S, Ollier S, Dufour AB (2005) Is the originality of a species measurable? Ecol Lett 8:579–586

Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol Lett 9(6):741–758.

Pereira HM et al (2013) Essential biodiversity variables. Science 339(6117):277–278

Redding DW, Mooers AO (2006) Incorporating evolutionary measures into conservation prioritisation. Conserv Biol 20:1670–1978

Reyers B et al (2012) Finding common ground for biodiversity and ecosystem services. BioScience 62(5):503–507

Rolston H (2001) Biodiversity and endangered species. In: Jamieson D (ed) A companion to environmental philosophy. Blackwell, Oxford, pp 403–415

Sarkar S et al (2006) Biodiversity conservation planning tools: present status and challenges for the future. Annu Rev Environ Resour 31:123–159

Simaika J, Samways M (2010) Biophilia as a universal ethic for conserving biodiversity. Conserv Biol 24(3):903–906

Sober E (1986) Philosophical problems for environmentalism. In: Norton B (ed) The preservation of species. Princeton University Press, Princeton, pp 173–194

Soulé ME (1985) What is conservation biology? BioScience 35:727–734

Srivastava DS et al (2012) Phylogenetic diversity and the functioning of ecosystems. Ecol Lett 15:637–648

Stone C (1972) Should trees have standing? William Kaufmann, Los Altos

Tilman D et al (2001) Diversity and productivity in a long-term grassland experiment. Science 294:843–845

United Nations Convention on Biological Diversity (1992)

van Kooten GC, Bulte EH (2000) The economics of nature: managing biological assets. Blackwell, Oxford

Vandamme AM (2009) Basic concepts of molecular evolution. In: Salemi M, Vandamme AM, Lemey P (eds) The phylogenetic handbook: a practical approach to phylogenetic analysis and hypothesis testing. Cambridge University Press, Cambridge, pp 3–30

Vane-Wright RI, Humpheries CJ, Williams PH (1991) What to protect – systematics and the agony of choice. Biol Conserv 55:235–254

Vellend M et al (2011) Measuring phylogenetic biodiversity. In: Magurran AE, McGill BJ (eds) Biological diversity: frontiers in measurement and assessment. Oxford University Press, Oxford, pp 193–206

Webb CO et al (2002) Phylogenies and community ecology. Annu Rev Ecol Syst 33:475–505

Weiher E (2011) A primer of trait and functional diversity. In: Magurran AE, McGill BJ (eds) Biological diversity: frontiers in measurement and assessment. Oxford University Press, Oxford, pp 175–193

West-Eberhard MJ (2003) Developmental plasticity and evolution. Oxford University Press, Oxford

Wilson EO (1984) Biophilia. Harvard University Press, Cambridge, MA

Winter M, Devictor V, Schweiger O (2012) Phylogenetic diversity and the nature of conservation: where are we? Trends Ecol Evol 28:199–204

Worm B et al (2006) Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–790