Phylogenetic diversity, functional trait diversity and extinction: avoiding tipping points and worst-case losses

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The phylogenetic diversity measure, (PD), measures the relative feature diversity of different subsets of taxa from a phylogeny. At the level of feature diversity, PD supports the broad goal of biodiversity conservation to maintain living variation and option values. PD calculations at the level of lineages and features include those integrating probabilities of extinction, providing estimates of expected PD. This approach has known advantages over the evolutionarily distinct and globally endangered (EDGE) methods. Expected PD methods also have limitations. An alternative notion of expected diversity, expected functional trait diversity, relies on an alternative non-phylogenetic model and allows inferences of diversity at the level of functional traits. Expected PD also faces challenges in helping to address phylogenetic tipping points and worst-case PD losses. Expected PD may not choose conservation options that best avoid worst-case losses of long branches from the tree of life. We can expand the range of useful calculations based on expected PD, including methods for identifying phylogenetic key biodiversity areas.

1. Introduction

The theme of our recent Discussion Meeting at the Royal Society, London, was 'phylogeny, extinction and conservation'. The range of talks at the meeting highlighted well the core idea that these three terms are intimately linked. Phylogeny expands our perspectives on biodiversity to include the ideas of evolutionary heritage and the feature diversity among organisms [1,2]. The potential loss of phylogenetic diversity (PD) extends our concerns about the global biodiversity crisis and its conventional focus on loss of species. Estimates of extinction probabilities, for species or other taxa, may be used to consider also the possible consequent loss of PD. Our discussion meeting covered the recent progress in exploring these linkages and also raised some important problems and challenges. In this section, I will briefly review the basic PD methods in order to introduce the challenges addressed in this paper.

Why should PD be an important aspect of biodiversity conservation? The term 'biodiversity' now is much used and misused, with a range of proposed definitions (for discussion, see [3]). Nevertheless, at its core, the term refers to living variation, at levels of variation from genes to ecosystems. Conservation of biodiversity therefore is fundamentally about the conservation or maintenance of variety. This focus on maintaining living variation complements the conservation of bio-specifics—specific elements that have known benefits to humans. Biodiversity conservation maintains 'option values'—potential unanticipated future benefits, from various specific elements of biodiversity. Thus, even as we enjoy benefits from bio-specifics, we maintain biodiversity in order to ensure an ongoing flow of such benefits for future generations.

PD is a natural way to address this idea of variation and potential future benefits. The 'PD' measure [1,2] was designed to measure the relative feature diversity of different subsets of species (or other taxa) from a phylogeny. This proposal to use phylogenetic pattern among species (or other taxa) to make inferences at a lower level of variation (features) was based on a general framework for biodiversity, outlined in this journal 20 years ago [4]. In this...
framework, a pattern/process model, defined for objects at one level of variation (among sites, species, etc.), allows us to make inferences and calculations, at some lower level of variation (among species, features, etc.). This inference strategy helps to overcome our inability to directly count all lower level units.

The PD measure illustrates this framework well. It uses a phylogenetic/evolutionary process model to link the representation of phylogeny (by subsets of species, populations, crop varieties or other taxa) to the consequent representation of lower level feature diversity. The pattern/process model underlying PD assumes that shared attributes or features among species are explained by their shared ancestry. This feature diversity interpretation underpins the original rationale for conserving PD: preserving the tree of life provides a vast storehouse of possible benefits for both the taxa and for humans and also provides evolutionary potential in the face of environmental change.

The PD of a subset of species is calculated as the minimum total length of all the phylogenetic branches required to connect all those species on the tree. PD measures the representation of evolutionary history:

"representation of "evolutionary history"...encompassing processes of cladogenesis and anagenesis is assumed to provide representation of the feature diversity of organisms. Specifically, the PD measure estimates the relative feature diversity of any nominated set of species by the sum of the lengths of all those phylogenetic branches spanned by the set [5, p. 248]."

PD’s evolutionary process model, where shared ancestry accounts for shared features, means that PD can be interpreted as counting-up the features represented by a given set of species. Thus, PD values indicate option values at the level of features of species (for discussion, see [3,6]).

A family of PD-based calculations extends conventional species-level indices to the features level. A wide range of indices are calculated using the phylogenetic pattern but are interpretable as if they count-up features. For example, the loss of a species from a protected set is interpreted as a loss in the total number of features represented by the set (PD-complementarity). PD complementarity refers to gains and losses relative to any reference set of species; when the reference set is all other species in the clade, PD complementarity is the ‘unique PD’ of that species [7]. A related measure, ‘PD-endemism’, indicates the extent to which evolutionary features are restricted to a given region [7]. An important part of the PD calculus, particularly relevant to our meeting’s theme of extinction and phylogeny, integrates probabilities of extinction, following the work of Witting & Loeschcke [8]. We have:

\[
\text{expected PD} = \sum_i (p(c)PD(c)). \quad (1.1)
\]

Expected PD is a summation over all possible persisting sets of species, where PD(c) is the PD of the set of species, c, and p(c) is the probability that set c occurs (providing a PD version of ‘expected diversity’ [9,10]). This can be calculated as:

\[
\text{expected PD} = \sum_i \left\{ L_i \times \left[ 1 - \prod_{j=1}^{n_i} q_j \right] \right\}, \quad (1.2)
\]

where \( L_i \) is the length of branch \( i \); descendants of branch \( i \) are counted by \( j \), \( n_i \) is the number of descendants for branch \( i \) and \( q_j \) is the probability of loss or absence of species \( j \).

We also can look at expected PD gains and losses, calculating:

\[
\text{change in expected PD} = \sum_i \left\{ L_i \times \left[ 1 - \prod_{j=1}^{n_i} q_j \right] \right\} - \sum_i \left\{ L_i \times \left[ 1 - \prod_{j=1}^{n_i} q_j' \right] \right\}, \quad (1.3)
\]

where the extinction probabilities have changed value from \( q_j \) to \( q_j' \).

This general form of the Witting & Loeschcke [8] approach is appropriate for all applications in which new extinction probabilities can take a range of values and where conservation efforts may alter the extinction probability of more than one species.

One existing priority-setting approach based on phylogeny and extinction probabilities is the evolutionarily distinct and globally endangered (EDGE) program [11]. A given species gains a credit, or partial contribution, from a given ancestral branch equal to \( 1/n \), where \( n \) is the number of descendants of that branch (the evolutionarily distinctiveness or ED score). Thus, ED partitions the total PD, and an EDGE score is based on the total of these credits for the species over all its ancestral branches multiplied by the species’ estimated extinction probability.

The EDGE programme has successfully promoted the practical use of phylogeny in conservation priority setting. However, for some time it has been known that the EDGE method could be improved by incorporating the existing PD-based methods incorporating extinction probabilities (‘expected PD’ see [12] for discussion). Expected PD (formula 1.2) accounts for complementarity among species, and this provides a key advantage over the EDGE calculations. Faith [12] showed how the EDGE-type methods have a weakness arising from the arbitrary partial credit assigned to branches combined with integration of probabilities that does not take phylogenetic complementarity into account. Consequently, the EDGE method will not reliably provide conservation priorities that deliver high expected PD. Put simply, EDGE could give priority to a threatened species descendant from a long branch, even though the species has closely related, secure, relatives. By contrast, expected PD would take the security of the close relatives into account and would give the species a smaller priority (e.g. [12,13]).

The ED distinctiveness index has been used for a variety of other indices. For example, some measures are based on the summation of the ED values for all species in a region. Faith [14] demonstrates that all measures based on ED are poor indicators of amounts of PD, because these methods do not take phylogenetic overlap among taxa into account.

Priorities for both species and areas can be set by directly looking at expected PD gains and losses [12,14]. May-Collado & Aagnarsson [15] and Kuntner et al. [16] similarly concluded that the expected PD methods have advantages over EDGE for phylogeny-based conservation. Jono & Pavoine [17] applied expected PD to phylogenies for the major mammal groups, using transformations of red list categories [18]. They found that larger losses in expected PD were found in those groups with a greater number of different threats.

Given the available phylogenies and estimated extinction probabilities for key taxonomic groups, the EDGE program could be extended to assess marginal expected PD gains or
losses for species, with updates as probabilities change [13]. Faith [12, p. 1467] suggested that:

‘A successful EDGE type program conceivably might use a modified list of individual top-scoring species... Following any conservation action (or the inevitable changes in species status due to other factors), all the scores among the top 100 species could be updated (optionally allowing new species to enter the list). Notably, a species’ score now could change as a result of a change in the probability of extinction of one or more related species, and proposed that species scores might ‘reflect the gain or loss if the species were to change from one red list category [19] to another (e.g. the gain in expected PD if the species were shifted from critically endangered to endangered’.

This may be a very useful index, given the likelihood of many changes in red-list rankings [19] in the near future. For example, Di Marco et al. [20] estimated that 23% of all carnivore and ungulate species moved one or more red-list categories closer to extinction over four decades. To address these needs, Billionnet [21] outlined practical methods for expected PD applications that consider costs and constraints in making decisions about alternative conservation efforts that can reduce probabilities of extinction for one or more species.

This recent progress highlights the emergence of a practical toolbox that integrates PD into decision-making and planning. However, some important challenges remain for applications of PD and expected PD. In this paper, I will address three fundamental challenges. First, we must acknowledge that expected PD may not be the best version of ‘expected diversity’ (sensu Weitzman [9,10]), even when considering inferences about features. Second, potential extreme losses of PD, as represented by phylogenetic tipping points [22] and PD worst-case losses [23] may call for modified decision-making that is more risk averse. Third, while much of priority setting for PD has operated in tree-space, there is a need to prioritize areas, but identifying key priority areas raises unsolved problems. These challenges form the next three major sections of this paper.

2. Challenge 1: expected functional trait diversity
Discussion of phylogeny and extinction risks would not be complete without considering some limitations in interpreting species extinctions as loss of PD. PD sometimes is considered as a measure of functional trait diversity (for review, see [24]). However, PD’s assumption that shared ancestry explains shared features cannot account for all shared functional traits [25]. The original rationale for PD [1,4] clearly emphasized that convergently derived (‘homoplasious’) features will not be reflected in PD calculations; many functional traits may fall into this class.

Another pattern–process model provides an alternative objects-units relationship within the general biodiversity framework [4]. A functional diversity index, EDf, assumes shared habitat as the explanation for shared traits among species [24,25]. The informative pattern for EDf is an ordination space, with dimensions reflecting habitat gradients. EDf assumes that shared habitat explains shared traits among species (species with the same trait tend to be close together along a habitat gradient, supporting what is called a ‘unimodal response’ model of traits to habitat gradients). This model allows inference of the relative trait diversity of different subsets of species (based on the p-median-based environmental diversity or ‘ED’ method, and called the ‘ED’ method when applied to a functional space; see [25]). This ‘counting-up’ of traits is analogous to PD’s counting up of features, and it means that EDf provides analogous calculations supporting conservation planning. Expected diversity in this context (‘expected EDf’) uses estimated species’ extinction probabilities in a way analogous to expected PD.

Figure 1 re-visits an early example, for an ordination representing a functional space for Anseriformes (ducks, geese and swans; see [25]). That early study illustrated basic EDf and I now extend it to explore expected EDf. The original study showed how phylogeny was informative in highlighting many features or traits that showed convergent evolution; such traits might be explained by shared habitat or function [25]. Figure 1a illustrates how a trait arising multiple times on the tree (individual loops) is accounted for by a functional space that unifies those species. Figure 1b extends this early example to highlight those species that are threatened according to recent International Union for the Conservation of Nature (IUCN) red listing [24]. Based on this space and the probabilities of extinction inferred from the red-list categories, we may determine which reductions in extinction probabilities among these species would best increase expected EDf. For example, suppose that threatened species 20 (Merganetta armata) and 32 (Rhodolissa cargophylacea) are alternative options for conservation action. Expected EDf gives priority...
to *M. armata*. This takes into account the threatened status of nearby species in the functional space (by contrast, *R. carophyllus* has a similar species that is secure). Thus, when EDf identifies priority ‘functionally distinctive, globally endangered’ (FUDGE) species, it avoids the failure to address complementarity that is found in EDGE methods.

This example illustrates how EDf provides an alternative to PD and expected PD for assessment of feature or trait diversity, but it also raises an important issue. If all three threatened species around species 20 (*M. armata*) were to be lost, EDf calculations would imply a very large loss in functional trait diversity (reflecting the large gap created in the functional space). On this occasion, prioritizing *M. armata* helps avoid such a ‘worst-case’ loss. However, in general, decisions that simply maximize expected diversity will not always be the decisions that best avoid such worst-case losses. This has implications also for use of expected PD, and this issue is explored in the next sections.

### 3. Challenge 2: phylogenetic tipping points and risk analysis

The scenario of a worst-case loss of functional trait diversity, as a consequence of successive loss of multiple threatened species, illustrates a ‘tipping point’: many functional traits persist over successive losses, until that last species is lost in that part of the space. This parallels ‘phylogenetic tipping points’ [22,23], where an ancestral branch persists while descendant species are successively lost, until finally all of its descendants, and the ancestral branch, are lost. Faith & Richards [23] explored possible phylogenetic tipping points for corals, a taxonomic group severely threatened by climate and land use changes. For example, all red listed coral species within the genera *Catalaphyllia*, *Physogyra* and *Euphyllia* are listed in one of the threatened or near-threatened categories. Each of these clades may represent a phylogenetic tipping point given that each group represents the only descendant taxa of a relatively long phylogenetic branch.

Phylogenetic or PD tipping points [22] capture the more general idea of a biodiversity tipping point [26], where a threshold is crossed, resulting in a relatively large, irreversible, biodiversity loss. Previous proposals for biodiversity tipping points have suggested that there may be local biodiversity tipping points, but gradual change globally [26,27]. Alternatively, the term has simply been used to refer to large global biodiversity losses without any clear threshold [28]. By contrast, a PD tipping point may correspond to small local losses (loss of different members of a clade in different places) that imply a global tipping point when the long ancestral branch of the group is lost. At the same time, over many different clades, the overall losses globally will appear more gradual, perhaps corresponding more to the biodiversity ‘tipping points’ proposed by the Global Biodiversity Outlook [28], which correspond to very large diversity losses (e.g. in species diversity), without any clear thresholds crossed.

Thus, we can distinguish between two kinds of worst-case PD losses. One focuses on the prospective loss of the PD associated with a long ancestral branch, and the other on massive loss in the overall PD of one or more groups (with losses distributed over the phylogenies). In the next subsections, I consider both aspects of worst-case PD losses, and introduce some useful expected PD calculations.

### (a) Expected phylogenetic diversity examples

I will examine expected PD calculations, tipping points and worst-case losses using a New World Anurans phylogeny, provided in the study of Batista et al. [29]. A clarification will be helpful. Their evolutionary history (“EH”) calculations appear to correspond to PD (they make no explicit link to PD calculations), but their implementation only measures incremental PD losses from single branches (referred to above as the unique-PD of a species). This disconnect from broader PD calculations implies an inability to ‘look ahead’ and anticipate worst-case losses. Batista et al. [29, p. 3] set out to calculate ‘the maximum and minimum rate of EH loss that theoretically bounded any possible extinction scenario’, and claimed: ‘the maximum rate of EH loss is achieved when the species with the longest branch length is always the next to be removed from the phylogeny’, which ‘represents the fastest rate of EH loss (worst-case scenario)’. However, basic PD calculations indicate that this will not in general identify the fastest rate of PD loss. For example, we could have a massive loss of evolutionary history, as measured by PD, after the loss of two species that are on short terminal branches but also are the sole descendants of a very long branch. A focus on terminal branches would miss the loss of the ancestral long branch. Here, I examine one of the worst-case losses that would have been missed on the Batista et al. phylogeny, and use this to demonstrate useful PD analyses.

Figure 2 shows a portion of the phylogenetic tree from Batista et al. [29]. It covers several red list threatened frogs in the genus *Lynchius* and provides a good example of a phylogenetic tipping point. Based on the ‘pessimistic’ red list transformations [18], the endangered species, ‘Parkers Andes frog’, *Lynchius parkeri*, has a probability of extinction of 0.9. *Lynchius flavomaculatus* is rated vulnerable, with a probability of extinction of 0.8. *Lynchius nebulanastes*, believed to be restricted to the Huancabamba region, is data deficient, but for this example, also will be given a rating of vulnerable. The probability of loss of the long ancestral branch (marked ‘a’ in figure 2) therefore is the product of these probabilities (assuming independence), or 0.58. The current expected PD loss (formula 1.3) is 0.8b + 0.9c + 0.72d + 0.58a. This expected PD loss in part reflects the probability of losing that ancestral long branch.

If the endangered species *L. parkeri* could be conserved to the level of near-threatened (pessimistic case probability of extinction of 0.4), then the gain in expected PD would be: (0.9–0.2)e + (0.72–0.32)c + (0.58–0.26)a. The large gain reflects the decrease in the probability of loss of the PD associated with long branch a. This result suggests that expected PD calculations not only may provide the early warning of a PD tipping point, but also may inform decisions about the best course of conservation action. I return to this issue below.
The coral and frog studies referred to above provide simple tipping point examples, based on phylogenetic pattern among threatened species. However, the PD tipping point problem importantly extends to other phylogenetic levels—including animal breeds or plant crop varieties. The integration of phylogenetic pattern and extinction probabilities is central to conservation strategies for threatened animal breeds and plant crop varieties. The Global Databank for Animal Genetic Resources [30] reports that about 22% of the approximately 8000 listed breeds are classified as at risk. The loss of a given number of breeds can imply a larger or smaller genetic diversity loss, depending on the degree of similarity among the lost breeds. Variation among breeds may be summarized as a phylogenetic tree (for discussion, see [31,32]). In such cases, PD indicates the amount of genetic diversity represented by a given subset of breeds (see also [9]). Given estimated extinction probabilities, priority setting typically uses variants of Weitzman’s expected diversity framework (here equivalent to expected PD; for review, see [32,33]). Here, I explore this issue by examining an expected PD analysis for several cattle breeds, based on a study by Simianer et al. [31].

Cattle have the highest number of threatened livestock breeds [30], and even this small portion of the phylogenetic tree reveals several breeds with high estimated probabilities of extinction (figure 3). We see that there is a 0.30 (=0.6 \times 0.5) probability of losing the long branch ancestral to two of the threatened breeds, Iringared (3) and Malazebu (4). The expected PD loss includes 10 \times 0.57 = 5.7 units for the green branch and 8 \times 0.6 + 8 \times 0.5 + 12 \times 0.3 = 12.1 units for the orange branches. As found for the frogs study, expected PD here flags potential worst-case losses, and can guide priorities for conservation of breed diversity.

(b) Risk analysis

The frog and the cattle breed examples suggest that expected PD calculations may inform decisions about conservation. However, a hypothetical example suggests difficulties. Suppose that all four species in the hypothetical tree in figure 4a have probabilities of extinction of 0.5. The initial expected PD is 4.0. Suppose that the status of either species a or species b can be improved to a probability of extinction of 0.1. Either choice would improve the expected PD to a value of 4.4. However, it is informative to compare these options in terms of the range of possible PD outcomes. In figure 4b, we see that the starting scenario (black bars) has a small probability of worst-case losses of four or five units. Protecting species a (light grey bars) improves expected PD but does not change the total probability of these worst-case losses. By contrast, conserving species b (dark grey bars) reduces the probability of worst-case losses to near-zero (0.025 compared to the original 0.125).

I now re-examine the expected PD analysis for the cattle breeds phylogeny (figure 3). Suppose that we are to compare the expected PD gains for two alternative conservation efforts: Nuba can have a reduction in probability of extinction of say 0.2 (from 0.57 down to 0.37), or Iringared can have a reduction of 0.1 (from 0.60 down to 0.50). The expected PD gain for the Nuba option is approximately 2 units (0.2 \times 10). The expected PD gain for the Iringared option is only 1.4 ((0.5 \times 8 + 0.25 \times 12) – (0.6 \times 8 + 0.3 \times 12)). Thus, the simple expected PD criterion would give priority to conservation action for Nuba. However, investing in Iringared could more effectively reduce the probability of a worst-case loss of PD among these breeds. The probability of a loss of 28 branch length units (figure 3) initially was 0.3, but the conservation investment in Iringared could reduce that probability of a worst case outcome to 0.25.

I conclude that strategies for setting of conservation priorities using expected PD should be extended to explicitly consider worst-case outcomes. Calculations of expected PD focus on the average outcomes from a distribution of possible outcomes. However, given the irreversibility of extinction, we may want to avoid landing in the bad tail of this distribution [12]. Decisions that maximize expected PD may not be the same ones that minimize worst-case losses. Given the dramatic rate of loss of crop and animal breeds, risk analysis may help to avoid such tipping points in the loss of genetic diversity.

As one strategy, Faith [34] explored variants of expected PD in which the possible outcomes (formula 1.1) are placed in different categories corresponding to their PD values. For example, we might partition formula 1.1 so that ‘c1’ corresponds to all those outcomes yielding designated worst-case PD values. We then can calculate the probability that we fall in this worst-case category and target our decision-making to reduce it. Such a strategy would better distinguish between the species a versus b conservation options in figure 4b.

Characterizing worst case outcomes as some total PD loss provides one strategy for ‘phylogenetic risk analysis’ [34]. This allows for worst case outcomes arising from multiple locations on the phylogeny. Another strategy, more in accord with recognized individual tipping points, is to focus on the probability of losing a specific long branch. For example, for the frogs (figure 2) we had a probability of loss of 0.57 for the designated long branch, and conservation options could be evaluated directly in terms of changes to that probability. For the breeds example, the probability of loss of the tipping point branch, ancestral to Iringared and Malazebu was 0.30 (0.6 \times 0.5) and taking this into account in assessment would have pointed to the advantages of conservation action for Iringared to reduce this probability.

(c) Key species

The examples above suggest that we can identify the species whose reduced probability of extinction would provide the greatest increase in expected PD and/or best-reduce the probability of worst case outcomes. However, we also may learn a lot by examining species’ increased probabilities of extinction. Consider the loss in expected PD if a nominated species was
given a probability of extinction of 1. We assess the new probability of extinction for each branch, yielding the new expected PD (and the expected PD loss).

A species whose loss implies very large loss in expected PD is likely to be a relatively secure species, with long ancestral branches. Also, any other descendants of these long branches are likely to be threatened species. As an example, consider the *Lynchius* phylogeny (figure 2) and suppose that the data-deficient species, *L. nebulanastes*, is ultimately evaluated as Least Concern (pessimistic probability of extinction a low 0.2). The current expected PD loss (formula 1.2) is then $0.8b + 0.2d + 0.9e + 0.18c + 0.14a$. The deep long branch is much more secure, as a consequence of the security of *L. nebulanastes*. If this secure species was lost, then the expected PD loss now would be a much larger $0.8b + 0.9e + 0.9c + 0.72a$. This large expected PD reduction under the hypothetical loss of the secure species, *L. nebulanastes*, suggests that it is worth highlighting such 'loss-significant evolutionarily distinctive globally enduring' (LEDGE) species. These species are the secure, distinctive, species whose loss would mean a big loss in expected PD.

A good example of these PD ‘bright spots’ is the aardvark, a species rated as Least Concern, and uniquely representing nearly 90 Myr of evolutionary heritage (it is the only living species of the order Tubulidentata). If the aardvark were to go extinct, the change in expected PD, corresponding to its LEDGE score, would be about 90 Myr.

A species might be a LEDGE species because all of its close relatives, sharing an ancestral long branch, are extinct or threatened. In such a case, the LEDGE species also is a ‘bulwark’ species—the last secure surviving species at the end of a long branch. Bulwark species, while presently secure, may deserve attention because they may be pointers to possible future phylogenetic tipping points.

A good example is the shrub frog species *Pseudophilautus hoipolloi* (synonym *Philautus hoipolloi*) [35] (figure 5). *Pseudophilautus hoipolloi* is endemic to central and southwestern Sri Lanka. It is regarded as common and adaptable, with no evidence of decline, and is listed as Least Concern [19]. It is a member of a clade of six species representing approximately 15 Myr of shared evolutionary history. The other five species all are endangered. Under the IUCN500 conversion [18], their probability of extinction is close to 1.0, and *P. hoipolloi* therefore has a LEDGE score of approximately 15 Myr of PD.

*Pseudophilautus hoipolloi* is a good exemplar for LEDGE species. ‘Hoi polloi’ means ‘the majority’, and the term is used to refer to the working class, or the commoners, often in a derogatory sense. This resonates with our conventional conservation biases. We focus a lot on threatened species as special, including those that also are evolutionarily distinctive, but *P. hoipolloi* suggests that the common secure species sometimes are under-appreciated. Those secure species whose loss would imply a very large loss in expected PD deserve acknowledgement as key PD species because they safe-guard a large amount of our evolutionary heritage.

4. Challenge 3: priority phylogenetic diversity areas

(a) Phylogenetic diversity loss for Sri Lanka’s freshwater crab species

A powerful illustration of threats to PD is found in the Beenaerts *et al.* study of Sri Lanka’s freshwater crab species.
They note that ‘over 50% of the freshwater crabs in this study are threatened . . . equivalent to about 77 Myr of evolutionary freshwater crab history’. However, this reference to evolutionary history may be misleading; it was calculated as the total PD of those individual species and was not equivalent to the total amount of PD under threat (an ancestral branch of a threatened species may be secure because it has some other secure descendant species). Expected PD loss calculations properly determine which ancestral branches may be lost. The expected PD loss (assuming pessimistic transformation [18]) will include the probable loss of some long branches (figure 6): branch length 1 times 0.99 probability of extinction; length 2 times 0.4; length 3 times 0.9, and length 4 times about 0.63.

The freshwater crabs study also is informative about how best to consider priorities for areas or regions. Threatened species, including *Pastilla ruhuna* and *Perbrinckia cracens*, are found only in the highly threatened lowlands of Sri Lanka. Thus, the probability of worst-case losses may be greater than that indicated by assuming independent probabilities from the red list ratings.

One of the advantages of focusing in on key vulnerable branches is that we can consider dependencies among the probabilities of extinction of the descendant species. For example, in our frog example (figure 2), the three threatened *Lynchius* species are largely restricted to the Huancabamba region in Peru. This area is threatened by land use changes [34]. Consequently, we may estimate probabilities of loss that go beyond the red list information, and we may conclude that the current probability of reaching a phylogenetic tipping point is even greater.

Expected PD calculations may help to identify key areas for conservation of PD. In this context, priority areas based on EDGE and/or ED methods have been proposed; however, the weakness of the ED/EDGE method in not taking complementarity into account extends to these methods focused on areas. Prioritizing a place with many high ED species, or many high EDGE species is not an effective way to set priorities for PD conservation—the actual represented PD will vary depending on how those high-ED/EDGE species are distributed on the tree. Faith [24] describes weaknesses of the Safi et al. [37] and the Gudde et al. [38] criteria, which seek places with lots of high-scoring ED or EDGE species.

As an alternative, expected PD can identify key areas for conservation of PD when integrated into methods of systematic conservation planning. I referred above to methods [21] for selecting areas that collectively maximize expected PD, while taking costs of conservation into account. For a given budget, we can select priority areas to maximize the total gain in expected PD, or identify areas of high PD irreplaceability.

(b) Phylogenetic key biodiversity areas

Key biodiversity areas (KBAs) [39] are an important existing framework that may provide guidelines to identify important areas for the conservation of PD. A recent IUCN workshop [40, p. 12] proposed a methodological framework for KBAs as sites ‘that contribute significantly to the global persistence of biodiversity’. The workshop report also noted that ‘The definition of biodiversity follows the Convention on Biological Diversity’s definition, incorporating genes, species and ecosystems’ (p. 1). However, a phylogenetic KBA framework does not yet exist (but see Brooks et al. this volume for recent progress [41]). KBAs already focus on the preservation of natural heritage [42], so it is natural to extend this approach to also consider evolutionary heritage, as measured using PD.

When species are considered, the sites ‘that contribute significantly to the global persistence of biodiversity’ are any intact sites that have one or more threatened species [40–42]. Thus, for a phylogenetic key biodiversity area (or ‘PD-KBA’), a direct analogue is any site that has one or more threatened branches, for the nominated taxonomic group. Naturally, any site that is a species-level site then is also a PD-KBA; minimally, the branch defining the species’ unique-PD is threatened. Nevertheless, a score for an area reflecting the total amount of threatened PD would allow prioritization among PD-KBAs. A difficulty is that different transformations of IUCN red-list categories [19] into probabilities of extinction [18] create differences in the designations of threatened branches. The following conservative approach provides one useful option. We adopt the ‘pessimistic’ transform [18]. This suggests that any branch that has all endangered and critically endangered descendant species, and not more than, say, 2 or 3 vulnerable (or data-deficient) descendants, is then counted towards the area score. The total score for an area is the total length of all such branches (among all the branches represented in the area by one or more descendant species). This provides one way to calculate the ‘threatened PD’ (TPD) score for the area. This simple approach clearly has advantages over area scores based on counts of total ED among species, given that the ED approaches ignore phylogenetic complementarity among species.

A TPD area score captures the spirit of KBAs as indicating areas that contribute significantly to the global persistence of biodiversity. The current persistence of the species in such a site is counting prospective loss of lots of PD. However, the idea of ‘significantly contributing’ suggests that we also might want to highlight those sites that have threatened branches found in few other places. The phylogenetic endemism (PE) measure [43] scores areas by calculating a modified total PD, where each branch length is inverse-weighted by the proportion of the total range extent of that branch that is represented in that area (thus, the weight is 1 if the area has the entire range). I define threatened PE (‘TPE’) as the PE score calculated only for designated threatened branches. An area with high TPE arguably contributes significantly to the global persistence of PD.
While TPE reflects to some degree an irreplaceable contribution, it does not fully incorporate information about how much the area, if lost, would imply reduced global persistence of PD. Expected PD calculations may indicate how much the persistence of PD suffers if the site were to be ‘lost’ (none of its species persist in that place). A simple way to quantify this reduction in persistence of biodiversity is to ask how much the expected persistence of biodiversity or the expected PD is reduced. A PD-KBA may be indicated in principle by the degree of loss in expected PD if the area were lost. Loss of any area will reduce expected PD to some degree, but ‘significant’ suggests that, among all sites, this site has so much of the PD of the clade that its loss would have a major impact on expected PD.

How does loss of the site translate into a change in expected PD? We can assess the change in probability of extinction for those species that are found in that place. The loss of the site might be translated first into a range loss of each species, and this would imply a consequent increase in their probabilities of extinction. These new values then would indicate the corresponding reduction in expected PD (formula 1.3).

Expected PD again may need to be extended to address worst-case losses. As an example, consider again the hypothetical tree in figure 4a. Suppose that species a and species b have low probabilities of extinction of 0.1 and the others have probabilities of extinction of 0.5. The initial expected PD is 4.8. In figure 7, the dark grey bars show that there is a small probability of worst-case losses (0.025). Suppose we have two candidate KBA areas: one with species a and another with species b. Suppose for each area that its ‘loss’ implies a change in the probability of extinction (for a or for b) from 0.1 to a higher value of 0.5. Either site, if lost, would imply a reduction of 0.4 in expected PD. However, the loss of the site with species b (black bars, figure 7) makes the probability of a worst-case loss a much higher 0.125 (compared with the initial 0.025). By contrast, the loss of the site with species a (light grey bars, figure 7) maintains the probability of a worst-case loss of 0.025. The site with species b arguably contributes most significantly to the global persistence of PD. This is also apparent in the higher probability of loss of that long branch when the species b site is lost.

I conclude that these expanded expected PD assessments can identify PD KBAs, by providing a meaningful measure of the contribution of a site to the persistence of global PD.

5. Discussion

The PD measure provides a phylogenetic basis for setting conservation priorities among species or areas. The framework explored here, focusing on expected PD, tipping points and risk analysis, may increase the adoption of PD in biodiversity assessments. One opportunity is found in the Convention on Biological Diversity’s (CBD) Aichi biodiversity targets under the CBD strategic plan for 2011–2020 (http://www.cbd.int/sp/). Two of the targets would benefit from inputs on PD.

Target 11 states that:

By 2020, at least 17% of terrestrial and inland water, and 10% of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved …

KBAs, including those for PD, may provide a natural way for countries to address this target. There is a good value-adding aspect as well, if phylogenetic KBAs take advantage of existing progress made in red-list assessments in various countries.

Target 11 may well be addressed using conventional phylogenies among species, covering multiple taxonomic groups. However, as this paper has emphasized, PD assessments are also important for phylogenetic patterns among breeds and crop varieties. This suggests that an important contribution may be made to Target 13, which states:

By 2020, the genetic diversity of cultivated plants and farmed and domesticated animals and of wild relatives, including other socio-economically as well as culturally valuable species, is maintained, and strategies have been developed and implemented for minimizing genetic erosion and safeguarding their genetic diversity.

Expected PD provides a contribution to these goals, particularly in addressing worst-case losses that are possible given the large number of breeds and crop varieties that are at risk. Future work may also use expected PD methods to recognize key areas for these threatened varieties, as a focus for conservation efforts.

The species level and breeds level phylogenies equally highlight the issues of worst-case losses and tipping points. These PD tipping points all involve a threshold that is crossed when the last descendant of a long phylogenetic branch is lost, producing a large irreversible biodiversity loss. This ‘tipping points’ description therefore seems apt, but the term itself is currently much debated in the broader literature, with a mixture of ideas about whether biodiversity tipping points even exist.

Tipping points generally are described as points of change in some aspect of the earth system, typically involving thresholds and large, non-reversible, changes, at a global scale. Much of the previous work on possible biodiversity-related boundaries or tipping points sees biodiversity as providing ecological functions that support biophysical subsystems of the Earth (e.g. [26]). In this context, actual tipping
points remain unclear. Rockstrom et al. [26, p. 1] argued that biodiversity is one of the ‘slow variables’ in the Earth System: ‘We never claimed there were ‘planetary tipping points’ for these slow variables, but rather evidence of tipping points at local and regional scales that add up to a global concern if they occur at the same time in multiple places on Earth’. Brook [27, p. 396] has argued that ‘spatial heterogeneity in drivers and responses, and lack of strong continental interconnectivity, probably induce relatively smooth changes at the global scale, without an expectation of marked tipping patterns’.

These arguments suggest that there may be local biodiversity tipping points, but gradual change globally. As noted above, a PD tipping point, by contrast, suggests possibly small local losses (loss of different members of a clade in different places) that imply a global tipping point when the long ancestral branch of the group is lost. Thus, phylogeny provides the ‘interconnectivity’ among localities that Brook finds missing for global biodiversity tipping points.

This is now a key topic for bioGENESIS, a programme focused on the role of evolutionary biology in multi-disciplinary biodiversity science, and the organizer of this Discussion Meeting. bioGENESIS is now part of Future Earth (http://www.futureearth.info/), a new global research programme focused on global environmental change and global sustainability. Among the key goals of Future Earth is ‘observing, explaining, understanding, projecting earth, environmental and societal system trends, drivers and processes and their interactions; anticipating global thresholds and risks’. One focus is on providing early warnings of boundaries and tipping points, and how these impact on human well-being. PD tipping points will be an important aspect of this work, given its links to feature diversity and option values underlying human well-being [22].

References


