

THE QUARTERLY REVIEW *of* BIOLOGY



THE USE OF PHYLOGENETIC DIVERSITY IN CONSERVATION BIOLOGY AND COMMUNITY ECOLOGY: A COMMON BASE BUT DIFFERENT APPROACHES

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The Quarterly Review of Biology, June 2019, Vol. 94, No. 2

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0033-5770/2019/9402-0001\$15.00

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KEYWORDS

phylogenetic diversity, ecosystem services, evolutionary potential, feature variation, option values, spatial planning

ABSTRACT

The use of phylogenetic tools and studies has strongly increased in the last two decades especially in conservation biology and community ecology. Phylogenetic trees are essential to understand the processes of community or network assembly, to identify centers of diversification, and to help protect Earth's evolutionary heritage. Despite two decades of research and syntheses, there are still many discussions on how phylogenetic diversity (PD) methods should be effectively applied to those fields. In particular, conservation approaches based on PD have become similar to those used in community ecology. Thus, the main benefit of using PD calculations in conservation biology may have been ignored or misinterpreted. Our goal is to discuss and provide guidelines to the use of PD in biodiversity conservation so that its benefits are not hidden or lost in the approaches employed. We also aim that benefits and uses are better recognized and more easily understood by researchers or practitioners who would like to include PD in their studies and conservation planning.

INTRODUCTION

THE development of humanity has impacted Earth, causing damage to ecosystems, species extinction, and habitat loss that—among the many potential impacts—may in turn threaten human societies. It has become urgent to establish appropriate actions that could mitigate these environmental challenges affecting humankind. However, conserving representative populations of all species is generally perceived to be unrealistic due to limited resources and, therefore, effective decisions are needed to best protect biodiversity. Conservation strategies based on species richness and abundance (which aim to preserve species and habitats at a broad scale) have been the rule rather than the exception. For example, the influential “hot-spots” of biodiversity have been identified based on endemic and threatened species (Myers et al. 2000). Moreover, these approaches were easier to implement than those based on functions or phylogenies (e.g., no need to collect time-consuming and expensive traits or molecular data nor to estimate

functional/phylogenetic relationships between species). However, approaches that consider all species as equal are limited when conservation priorities have to be defined because they fail to recognize their distinctiveness (Aise 1989; Vane-Wright et al. 1991; Faith 1992). On the contrary, progress in phylogenetic inference has enabled the prioritization of conservation efforts based on the evolutionary history of species (Mace et al. 2003). Similarly, in community ecology and biogeography, considering all species ecologically equal is inherent to neutral hypotheses (Hubbell 2001), whereas other methodologies, such as phylogenetic approaches, consider that species assemblage may be guided by species niches (Webb et al. 2002).

In the 1980s, the International Union for the Conservation of Nature (IUCN) emphasized the interest of taxonomic distinctiveness for conservation by stating that “the greater the gap between the nearest related family (or genus) . . . and therefore the more distinct” and that “taxonomic hierarchy provides the only convenient rule of thumb for

determining the relative size of a potential loss of genetic material" because "different positions in this hierarchy reflect greater or lesser degrees of genetic difference" (IUCN 1980:22; Faith 2016a, 2018a). The significance of the taxonomic distinctiveness concept prompted its use by several state agencies in Australia at the end of the 1980s and through research in systematics and conservation biology (Avisé 1989; Faith 1994, 2018a). Quantitative measures of taxonomic distinctiveness for conservation originated in the 1990s with studies from May (1990) and Vane-Wright et al. (1991). Vane-Wright et al. (1991) introduced a measure of taxonomic distinctness that ranks species according to the number of cladistic groups they belong to, a perspective that was later refined by other authors (e.g., Erwin 1991; Brooks et al. 1992; Crozier 1992; Faith 1992, 1994; Weitzman 1992; Crozier and Kusmierski 1994; Williams and Humphries 1994; Witting and Loeschcke 1995). However, taxonomic distinctiveness did not allow for the ability to measure the diversity of a set of species (Vane-Wright et al. 1991). Faith (1992) proposed to link diversity and distinctiveness by introducing the notion of phylogenetic diversity (PD) as the sum of the branch lengths of the minimum spanning path joining a set of taxa on a tree. Phylogenetic diversity is assumed to represent the relative feature diversity of organisms so that maximizing PD may be a sound strategy for conservation because it would, *on average*, maximize the protection of feature diversity (a "feature" is a particular trait characteristic of a taxa). Due to their high number and because many are unknown, all taxon features cannot usually be accounted for (Faith 1992, 1994, 2016a; Pavoine et al. 2005). This relation was based on an evolutionary model in which shared features are inherited from shared ancestry (Faith 1992), which was later shown to have important implications not only in conservation, but also in community ecology and biogeography (e.g., Webb et al. 2002; Gerhold et al. 2015; Saito et al. 2018). Indeed, this assumption resulted in the use of phylogenetic information to unravel the process at the origin of diversity patterns and community assembly (Webb et al. 2002; Davies and Buckley 2011). For example, it was hypothesized that the occurrence of distantly

related species in a given area might indicate potential competition exclusions of evolutionary close species with similar niches. On the other hand, communities composed of closely related species may indicate possible environmental filtering of species adapted to a similar environment (Webb et al. 2002). From this, the use of phylogenetic information in conservation biology and community ecology became on occasion indistinguishable, whereas the purposes of each domain highly differ in general. This resulted in the absence of consideration of one of the main goals of the use of phylogenetic information in conservation for many studies: the preservation of features' variations that may allow to maintain future options for humanity (Faith 1992).

This review aims to reinforce the rationale for the use of phylogenetic metrics in biodiversity conservation and their direct link with practical strategies while identifying some limitations and areas requiring further development in the existing methods. A parallel will be drawn with the use of phylogenetic information in community ecology to highlight how different assumptions and objectives, which are discussed for both biodiversity conservation and community ecology, may result in different uses of phylogenetic information. Finally, limitations for those uses in both fields are discussed in detail and we highlight how they may be alleviated.

BASIC PRINCIPLES FOR THE USE OF PD IN CONSERVATION BIOLOGY

The reason to use PD in conservation relies heavily on its link with feature diversity (Faith 1992). Here we present the principles at the basis of this relationship and some of the resulting implications for conservation biology. We focus on the main arguments that justify the use of PD, although some others can be found elsewhere (e.g., Maclaurin and Sterelny 2008; Faith 2016b; Tribot et al. 2016). The aim here is to guide readers to understand the value of PD in regard to practical applications such as the ones proposed in the following sections. We also referred to studies that have investigated the mechanisms at stake to explain the relationships between phylogenetic and functional diversity

in macroorganisms, but also in microorganisms (e.g., Goberna and Verdú 2016; Faith 2018a).

PHYLOGENETIC DIVERSITY AND FEATURE DIVERSITY: A RELATIONSHIP BASED ON EVOLUTIONARY PRINCIPLES

Darwin observed that “species of the same genus have usually, though by no means invariably, some similarity in habits and constitution” (Darwin 1859:76). This observation has been one of the main justifications behind the use of phylogenies in conservation biology, but is also a matter of debate (Faith 2018a,b; Mazelet al. 2018). Many phylogenetic metrics used in conservation were assumed to capture the variability or the scarcity of morphological or functional traits (e.g., Faith 1992; Redding and Mooers 2006; Davies et al. 2016; Kondratyeva et al. 2019). This assumption is inherent to Darwin’s theory that introduced the principle of filiation with modification in which shared characters can be explained by shared ancestry. This principle on which PD (among other measures) relies, have several implications: first, closely related species may share more characters than distantly related species; second, species descending from long branches are more likely to capture more ancient characters than species descending from shorter branches; and, third, summing the branch lengths that join species on a tree (a calculus from which the set of PD-based indices originates) captures, on average, their feature variation. Some approaches missed this pattern-process model, which led to some misinterpretations (Kelly et al. 2014). Yet, when this shared-ancestry model is justified by accomplished tests (e.g., Faith and Cranston 1991), this theoretical basis empowers the use of phylogenies in conservation biology, for example, to encompass ecosystem processes that rely on species features (e.g., Srivastava et al. 2012), but also in community ecology (Webb et al. 2002).

CAN EVOLUTIONARY HISTORY REVEAL FUTURE BENEFITS TO SOCIETIES?

Biodiversity provides multiple services to humanity (Gascon et al. 2015) that have been

classified under the notion of ecosystem services. These services include regulation, production, habitat, and information functions (Millennium Ecosystem Assessment 2005). Going further, Faith (1992, 1994) introduced the primary goal of PD for conservation: by measuring feature diversity, PD maintains unanticipated and future benefits of biodiversity to human well-being, i.e., option values. Although ecosystem services are useful at focusing on current rapidly sensible benefits, option values consider long-term human well-being that may depend on overall and more complex biodiversity sets (Faith 2012). The concept of option values dates back to the 1970s: at this time it was already predicted that high rates of species extinction may cause the loss of options to humanity (Iltis 1972; see Faith 2018a for a review). For Bishop, “the loss of any species irreversibly reduces the reservoir of future resources” (Bishop 1978:17) where resources “are not, they become” (Bishop 1978:11), depending on human tastes, preferences, and needs, among others. Bishop (1978) showed that resources are uncertain and may irreversibly be lost with species extinctions. Today, preserving those unexpected future benefits appears crucial in the face of the many threats accelerating species extinctions and population loss such as climate change (Faith and Richards 2012). Indeed, it is almost given that uncertainties linked to the consequences of biodiversity losses will always persist, but the best conservation decisions have to be taken in spite of those uncertainties (Forest et al. 2015; Oliver 2016).

The unanticipated services of biodiversity may be provided by species evolutionary history and potential and, thus, captured by a measure such as PD that may help to maximize a variety of features on which future services depend (Mouillot et al. 2016). Biodiversity conservation strategies based on PD are a “form of risk analysis that involves estimating patterns of variation, and then trying to conserve as much of that estimated variation as possible—as a way to retain ‘options’ (possible values) for the future” (Faith and Baker 2006:121). A well-known example of option values and PD was presented by Forest et al. (2007) who found through ex-

perimentation that maximizing PD is the best way to conserve the medicinal and economic uses of the Cape flora, whereas a strategy based on species richness alone was less efficient. Oka et al. (2019) found that phylogenetic distant tree species in Japan tended to provide different provisioning, regulating, and cultural services and, therefore, it may be expected that PD could capture the variation of these services. In similar logic, Faith (2018a) highlighted the insurance value of PD at the scale of ecosystems. The identification of species allowing for the preservation of ecosystem resilience is uncertain, but PD may help to maintain a variety of features that may permit an ecosystem to respond to the disturbance. Another striking example is the emerging positive contribution of PD to human health. Indeed, maintaining bacterial phylogenetic diversity could have important consequences on the resilience of those bacterial communities and their metabolic potential (Blaut and Clavel 2007; Lozupone et al. 2012; see also Faith 2018a for some other examples). Although most of this review is built from studies on macroorganisms, PD has also huge implications in the field of microbiology, especially because phenotypes of microorganisms are largely unknown, but their variation may be predicted through phylogenetic information (Goberna and Verdú 2016).

The potential surrogacy of PD for option values has encouraged its use for regional and global conservation programs (Millennium Ecosystem Assessment 2005; IPBES 2018). In particular, it may support the definition of a global measure of biodiversity based on a PD metric, which would guide conservation efforts in the long term in the context of uncertainties regarding environmental change (Faith 1992, 2016b; Forest et al. 2015). Indeed, conservation based on PD-based measures should on average provide more goods to societies than those based on other measures of biodiversity (Forest et al. 2007; Lean and Maclaurin 2016). Measures based on phylogenies were also proposed as planetary boundaries in order to maintain a safe operating system in which biodiversity benefits to societies would be preserved (Faith et al. 2010; Mace et al. 2014).

The rationale for using phylogenetic information as a planetary boundary is that it may provide long-term ecological and evolutionary potential (but see below) and, as previously stated, future benefits for societies. Last but not least, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) called to maintain the options provided by nature to humankind facing future needs (Díaz et al. 2015). From this, IPBES drew a framework based on PD to estimate those “option values” and their threats (Faith et al. 2018; IPBES 2018). All of these proposals based on “option values” make PD a powerful approach for conservation goals that aim to maintain human well-being.

Although conserving PD may allow an increase in the probability that features providing unexpected benefits to humankind are maintained, the relationship between PD and option values would be even stronger if phylogenetic trees could reveal the evolutionary potential of species (Mouquet et al. 2012). Indeed, this would help to predict which set of species would best adapt or diversify in the face of ecological changes and would be more likely to provide or preserve future ecosystem functions and services (Sarrazin and Lecomte 2016).

DO PHYLOGENETIC TREES REFLECT OPPORTUNITIES FOR FUTURE EVOLUTION?

Past and current human activities, besides species domestication, have imposed a strong selection on species, their genetic diversity, and on their number (Hendry et al. 2011). Estimating and preserving the possibilities for species to evolve, as a single unit and in communities, appears crucial for the maintenance of biodiversity, especially in the face of impending global environmental changes. Conserving species with high evolutionary potential would contribute to maintain biodiversity in the future and would help to preserve the functions and associated services it provides to humans (Sarrazin and Lecomte 2016).

How can phylogenies help identify the evolutionary potential of species? First, us-

ing PD to maximize feature variation would in principle increase the probability that feature diversity, which is vital for species to be able to adapt to future environmental changes, will be maintained, consequently providing evolutionary potential. This assumption has been introduced by Faith who noted that PD ensures “that one or more members of the subset can adapt to changing conditions” (Faith 1992:2). Later, Forest et al. stated that features useful for the adaptation of species to change are not known such that “maximizing PD will in turn maximize the options for future diversification” (Forest et al. 2007:759). Yet, the relationship between PD and evolutionary potential require further investigation.

Evolutionary history of species influences their phenotype and genotype, which then may impact on the direction and speed of contemporary evolution (Hendry et al. 2011). In the absence of specific selection pressures, species with a long history of evolutionary independence are more likely to harbor unique genetic variation that, in turn, may allow them to adapt to change in different ways from other species. Indeed, due to random mutations they may become either more vulnerable or more resistant than other species (Hendry et al. 2011). In contrast, young lineages may evolve more rapidly and have a greater capacity to diversify or adapt and could serve as the source of long-term evolution (Hendry et al. 2011; Mouquet et al. 2012). However, whether long or short branches best represent the possibilities of future evolution is still poorly understood and further research on this topic is needed to guide conservation practices (Rolland et al. 2012). Some authors suggested that estimating past diversification rates across current lineages might indicate which lineages would be more prone to diversify in the future (Rolland et al. 2012). The potential for future evolution of a species might also be assessed by combining information on rates of trait evolution and diversification (Morlon et al. 2010). However, several researchers do not support the idea of using phylogenies for estimating the future possibilities of evolution in particular because empirical proofs are lacking, which paves the way for new research (Rolland et al. 2012; Winter et al. 2013). Thus, in spite of

some authors arguing that PD is related to evolutionary potential (e.g., Voskamp et al. 2017), there are no stringent proofs, to our knowledge, that it is actually the case.

CAN PHYLOGENETIC INFORMATION REVEAL ECOSYSTEM PROCESSES?

Although the primary goal of using PD for conservation is the maintenance of feature variation and “option values,” some authors have been interested in the relationship between PD and the diversity of some functional traits (e.g., Loreau et al. 2001; Hooper et al. 2005). Given that phylogenetic variation may represent variation in species traits, based on the principle of “filiation with modification,” it has been argued that PD could be a good surrogate of functional diversity (Faith called this the proxy value of PD; Faith 2018a but see the section titled When Phylogenetic and Feature Variation Are Not Congruent: Limitations and Solutions) and capture ecosystem functions (Srivastava et al. 2012; Davies et al. 2016). The main idea follows the community ecology framework (Webb et al. 2002): communities with high mean phylogenetic distance among species (i.e., communities composed of distantly related species) should comprise species with high niche complementarity owing to the evolution of different traits, implying high niche differentiation among distantly related species (Srivastava et al. 2012). Given this higher niche difference, and consequently higher complementarity, the resources in the environment would be more efficiently used, providing higher yields of given processes such as productivity in plants (Srivastava et al. 2012). Moreover, communities composed of distantly related species should have lower levels of exploitative competition due to niche differentiation and, thus, would be more buffered against competitive exclusions (Webb et al. 2002). Second, as phylogenetic difference may relate to feature difference and ecological functions are generally provided by interrelated multiple traits, a community of distantly related species may be functionally highly diverse, and this was shown to increase the ecosystem functions provided (Cadotte 2015; Cadotte and Davies 2016).

Contrary to the rationale for the use of PD to conserve option values, the relationship between PD and ecosystem functions is thus not based on the preservation of biodiversity units but rather on the maintenance of ecological integrity (Faith 2018a). However, the relationship between PD, functional diversity, and ecosystem functions is not always well supported, a topic we discuss further (see the section titled *When Phylogenetic and Feature Variation Are Not Congruent: Limitations and Solutions*).

A conclusion that can be drawn from this section is that the surrogacy between PD and feature diversity is well founded: it relies on basic evolutionary principles that tend to make closely related species more similar in traits than distantly related ones. Many assumptions that use PD in conservation depend on this relationship. The conservation logics presented here comprise the proxy value (PD may reveal ecosystem processes), the option value (PD may capture unexpected future benefits to humanity), and the insurance value (PD may preserve the resilience of an ecosystem; Faith 2018a). The option value argument is certainly the best-supported reason for the use of PD in conservation. Further, we will discuss appropriate conservation practices that correctly consider the relationship between PD and feature diversity, and others that fail to account for this surrogacy, leading to the loss of benefits linked to the use of PD. In particular, we will emphasize approaches based on evolutionary distinctiveness that, although they may not allow to maximize feature variation, have a high practical interest.

PRACTICAL USE OF PHYLOGENETIC INFORMATION IN CONSERVATION

CONSERVING PD AND FEATURE VARIATION

The PD Calculus

As stated above, the main benefits linked to the use of measures based on phylogenies in conservation is to capture feature variation, which is the basis for the adaptation of biodiversity to change and that may be beneficial to society faced with unpredictable change (Faith 1992). Justified by

the rationale that shared features are due to a shared ancestry, optimizing the conservation of feature variation may be achieved by securing the species that capture the highest proportion of a phylogenetic tree. This aim is reached by maximizing the sum of branch lengths of a phylogenetic tree that is protected, i.e., maximizing the PD calculus (the PD of a set of species is equal to the sum of the lengths of all the branches from the corresponding minimum spanning path; Faith 1992), whereas measures that preserve some branch lengths several times do not maximize feature variation (Faith et al. 2004; Faith and Baker 2006). A direct consequence is that in a scenario where only a limited number of species can be rescued, those capturing the most PD should be prioritized. On the contrary, many metrics based on phylogenetic trees may not be suitable to achieve this goal (see, for example, the section titled *The ED Framework*). Going further, and by considering reasonable that phylogenetic variation is a good surrogate of feature variation, PD and PD-based measures (e.g., Faith 1992, 2008; Rosauer et al. 2009; Veron et al. 2017) are likely to be the only existing measures based on phylogenetic trees that may help to maximize feature diversity of conservation interest (Faith et al. 2004; Faith and Baker 2006).

PD Gain

Various measures have been proposed to extend the PD framework (Faith 2008). In particular, we highlight here a method that allows the preservation of feature variation based on PD gain (Faith 1992; Faith et al. 2018a). Phylogenetic diversity gain is defined as the amount of branch length a species adds to the PD already represented by a given set of species, also known as PD complementarity or PD endemism value (Faith 1992; Faith et al. 2004). In a conservation strategy, PD gain is the additional branch length that is secured after the protection of species and/or sites. Consequently, PD gain is of great interest for conservation planning because it helps to unravel how sites complement each other in order to represent the overall diversity of a region. However, several regional studies have

used the total PD of a given site (often a grid cell) as its conservation value and thus did not consider that branches can be shared among sites. This departure from the basic framework of conservation planning based on the complementarity of sites (Margules and Pressey 2000) may originate from the community ecology framework where the total PD of a site is of interest (e.g., Gómez-Ortiz et al. 2017; see the section titled *Why Approaches in Community Ecology and Conservation Biology Should Be Different*). Yet, in conservation biology, the purpose to maximize the protection of a region's diversity is not achieved with this method because sites with the highest total PD will most likely share branches and thus redundant information (Figure 1; Pollock et al. 2017; Faith et al. 2018a). This could lead to the prioritization of sites that add little branch length (i.e., little PD gain) and, consequently, little feature diversity to a set of already protected sites.

Considering phylogenetic complementarity of sites and species is thus more appropriate to capture feature variation. A recent set of works have incorporated PD gain as a strategy to protect biodiversity (e.g., Pollock et al. 2017; Rosauer et al. 2017; Veron et al. 2018). Interestingly, Pollock et al. (2017) showed how PD gain could be used for conservation objectives at both global and local scales. At the global scale, securing one occurrence of a given species results in a gain equivalent to the full length of the branches supporting that species (Figure 1.3). On the other hand, when the aim is to emphasize local assemblages, the PD gained at a local site is measured on a phylogenetic tree where each branch is weighted by the proportion of its protected range (Figure 1.2; Pollock et al. 2017). Thus, a strategy to spatially protect PD would be to prioritize the minimum number of sites that maximize the gain in PD (Figure 1; see also Faith et al. 2018 to define an order of priority among these sites). Whether conservation objectives are local or global may cause the identification of priority sites to differ (Figure 1).

One drawback of this PD gain approach is that it defines an effective *set* of protected sites yet, in practice, protected areas are

rarely implemented as a set. Thus, it remains essential to identify sites that are likely to be important to include over many possible sets even though they do not optimize the overall PD of a region. Those sites could be based on a hotspot approach as proposed by Veron et al. (2018). Moreover, the PD gain approach for macroorganisms has mainly been used at global or regional scales with the view of preserving "option values" (e.g., Mouillot et al. 2016). This approach could be extended at the scale of ecosystems where PD may provide an "insurance value" (Faith 2018a). Species in the ecosystem that may be useful for its resilience are unknown, but maximizing their PD and feature diversity may maximize its chance to resist and/or recover from perturbations.

PD At Risk

Another strategy is to give priority to the threatened diversity of a region. Several PD-based measures have been developed with this specific aim in mind (e.g., Faith 2008; Rosauer et al. 2009). A crucial aspect to consider is that the risk of losing a deep branch depends on the risk of losing all the species it supports (i.e., the phylogenetic complementarity of extinction risks). If this complementarity is not accounted for, the risk of losing deep branches will be incorrectly assessed and, consequently, so is the risk of losing PD (Steel et al. 2007; Faith 2008; Veron et al. 2016, 2017). Extinction risks are generally based on probabilities of extinctions (Faith 2008) or on the restricted range of species (Rosauer et al. 2009). Estimating PD on a phylogenetic tree where branches are weighted by those extinction risks may represent how much feature diversity is threatened. In spatial planning, those measures can be included in a PD gain strategy as described above. One would prioritize the sites that would secure the maximum threatened PD of a region while considering its phylogenetic complementarity (Veron et al. 2018). This may result in very different conservation strategies than when extinction risks are not accounted for. Finally, information about

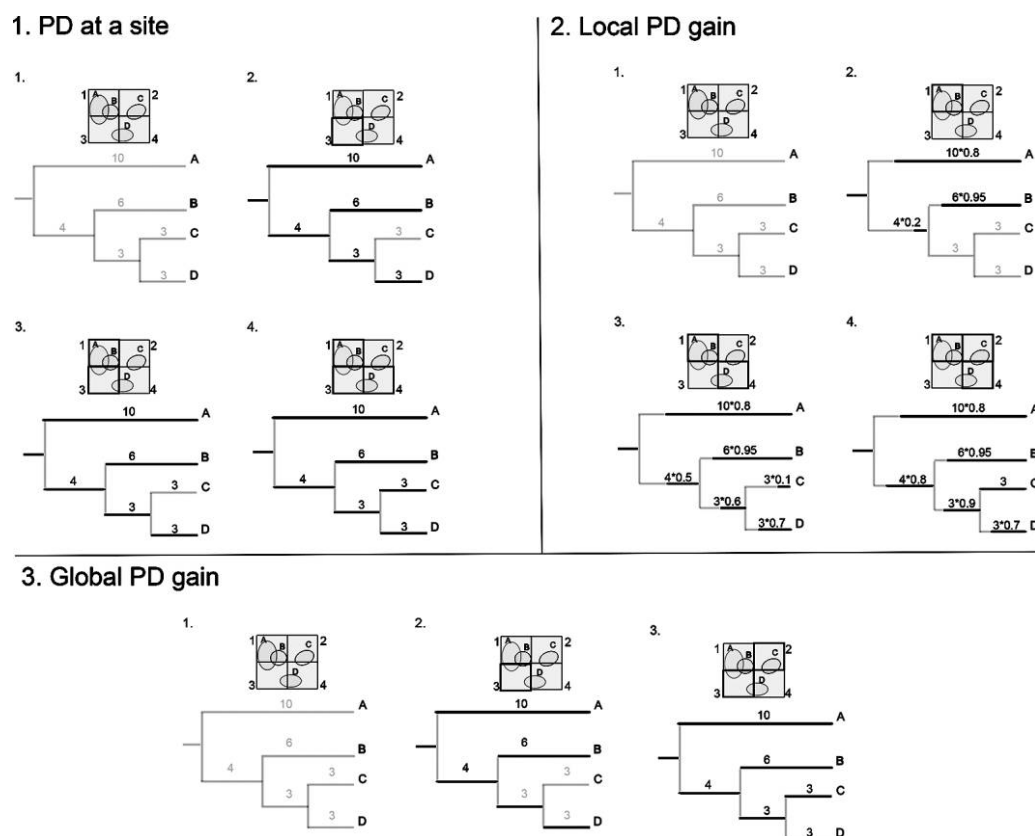


FIGURE 1. THREE PRIORITIZATION STRATEGIES BASED ON PD

PD is measured as the sum of branch lengths on the spanning path joining taxa on a tree to the root. In all scenarios we assume that only three sites out of four can be protected due to limited resources. Protected sites are represented by bold squares and safe branches are shown in black. 1. The conservation value of a site is represented by its total PD. The first site to be chosen includes species A, B, and D (PD = 26 Ma). The second site selected comprises species A and B with PD = 20 Ma, although no additional branch length is protected. Finally, the third site to protect harbors species C and D (PD = 13 Ma). 2. Sites are selected in function of their local PD gain: branch lengths are weighted by the proportion of their range that is safe following the protection of a site. The order of selection of sites is 1, 4, and 2. 3. Sites are prioritized following a global PD gain strategy: the protection of one occurrence of a species conduct to the gain of all branches supporting that species. Only two sites, those numbered 3 and 2, are needed to protect the entire tree. See the online edition for a color version of this figure.

land use, probability of strategy success, or conservation costs could also be used together with a PD gain approach to comply with the requisites for conservation planning assessments (e.g., Billionnet 2013).

In conclusion, the approaches described above are not exhaustive and several strategies may be adopted to conserve PD in spatial planning or in species prioritization strategies (other measures are described by Faith

2008). However, assuming that shared traits are due to shared ancestry, the rationale to preserve feature variation and potential option values should rely on the phylogenetic complementarity of sites and/or species. This may help to clarify the use of PD in conservation (Winter et al. 2013) and to consider the criteria of evolutionary history in the implementation of practical conservation actions.

THE ED FRAMEWORK

Evolutionary Distinctiveness Does Not Allow the Protection of Feature Variation

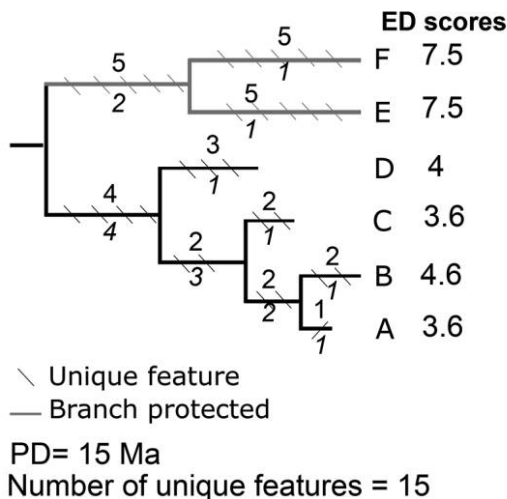
Evolutionary distinctiveness (ED) is another type of measure based on phylogenetic trees that has been widely used in conservation biology (Kondratyeva et al. 2019). It quantifies the number of relatives a species has, how phylogenetically distant they are, and assigns an individual score to each species in the phylogenetic tree. For example, the widely used fair proportion index partitions the branch lengths of a phylogenetic tree (i.e., PD) among all of the species it supports (Isaac et al. 2007). Species are then prioritized according to their ED value. This also implies that the sum of all ED scores measured on a phylogeny is equal to the total PD of all taxa comprised in this tree.

The ED order of prioritization is, however, not as efficient as the PD calculus at capturing the variations of features (Figure 2). This is mainly because ED measures

do not account for the phylogenetic complementarity among species (i.e., by conserving species with the highest ED, some deep branches are likely to be represented several times whereas others may not be represented at all; Figure 2). Feature variation is therefore not properly captured. For example, Isaac et al. (2007) argued that the species with the highest ED scores, and thus the highest priority, would be two closely related species. However, the choice of those two species does not look to be the best strategy to maximize feature variation as it does not represent the highest protected proportion of the tree of life (see the section titled Conserving PD and Feature Variation). In a PD-based strategy, two distantly related species would have been selected to protect most feature variation.

Similarly, some spatial planning research has focused on preserving sites with the highest ED values, especially by summing/averaging ED scores of the species occurring in each site and prioritizing sites with the highest cu-

A. Prioritization based on ED



B. Prioritization based on PD

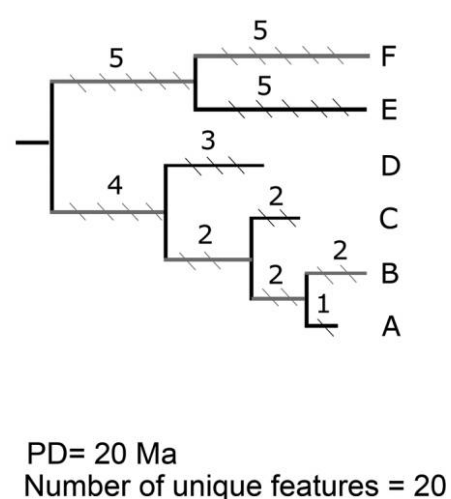


FIGURE 2. COMPARISON OF PD AND ED IN MAXIMIZING FEATURE VARIATION

This figure represents the selection of species based on A. evolutionary distinctiveness (estimated here through the fair proportion index) and B. the PD value. Developing a conservation strategy based on ED does not maximize feature variation. Marks on branches represent the unique features it captures based on the simplified assumption that the number of unique features is proportional to branch length. In A., species E and F are prioritized due to their high ED scores. This represents 15 Ma of branch length and 15 unique features. In B., species B and F (or E), which maximize PD, are selected, and they capture 20 Ma of PD and 20 unique features. See the online edition for a color version of this figure.

mulative ED (e.g., Daru et al. 2013; Safi et al. 2013; Jetz et al. 2014). This method should also not be viewed as a conservation planning strategy that maximizes feature variation because phylogenetic complementarity is not taken into consideration. These arguments related to spatial planning can be applied to all types of ED measures even those that include extinction risks or endemism such as evolutionary distinctiveness and global endangerment (EDGE; Isaac et al. 2007), heightened evolutionary distinctiveness and global endangerment (HEDGE; Steel et al. 2007), biogeographical weighted evolutionary distinctiveness (BED; Cadotte and Davies 2010), loss-significant evolutionary distinctive globally enduring (LEDGE; Faith 2015), or after downlisting expected phylogenetic diversity (ADEPD; Nunes et al. 2015).

Evolutionary Distinctiveness Remains a Useful Measure For Practical Conservation

Although an approach based on preserving species with high ED may not be the best strategy to capture feature variation, this measure is still valuable for conservation biology. First, the rationale of protecting species with high ED values is linked to their isolation from all other species and to the fact that they may represent long branches capturing old features shared by very few species (Magnuson-Ford et al. 2009; Redding et al. 2010; Collen et al. 2011; Stein et al. 2018; but see Grandcolas and Trewick 2016). From this, conservation of species with a high ED generally would be able to capture a lot of PD (although it is not the maximum PD) and would contribute to the maintenance (but not the maximization) of feature variation (Faith et al. 2018).

Other arguments to preserve highly evolutionary distinct species are essentially practical (e.g., Faith 2015; Forest et al. 2018; Stein et al. 2018; Thévenin et al. 2018). Isaac et al. justified the protection of species with the highest ED values, despite the fact that they are closely related, because “the extinction of either would leave a single descendant of the oldest and most unusual lineage in the phylogeny” (Isaac et al. 2007:2). For

Redding and Mooers (2006), real-world conservation practice is based on lists of threatened species, and PD does not offer an order of conservation prioritization, especially because there will be as many possible rankings of species as there are PD maximizing solutions in a set of species. A species list based on PD may be difficult to implement at the management level (Redding and Mooers 2006). Moreover, strategies based on maximizing PD are based on a set of species (or sites). Consequently, the conservation of a species outside this set may lead to the identification of a new and very distinct set to preserve PD, and management actions are rarely implemented on a set of species or sites (e.g., Thévenin et al. 2018). Thus, it remains important to identify species that may capture large amounts of PD independently of a given set. To this aim, because they may be evolutionarily isolated and descending from long branches, species with high ED may capture more branch lengths and more PD than species with low ED as showed by Redding et al. (2008).

Regarding extinctions, Chaudhary et al. (2018) showed that summing the ED scores of extinct species was strongly correlated to PD loss. Going further, and by looking at the calculus of ED and expected loss of PD, Faith et al. (2018) showed that the sum of ED scores of threatened species was approximately the total expected loss of PD, assuming that the probabilities of extinctions of threatened species were close to 1.

To summarize, the ED approach has many advantages, but future research based on this measure should be aware that it does not maximize feature variation and option values. High ED species may, however, capture rare features and have practical interest to capture more PD than expected when the protection of a set of species maximizing PD cannot be set up in real-world conservation actions.

The rationale to preserve feature variation and related conservation benefits may be reached by a PD calculus that maximizes the proportion of the Tree of Life protected. However, some PD approaches were erroneously thought to protect feature variation whereas they may be more informative in

the field of community ecology. In the next section we will underline what these approaches are and how different goals in conservation biology and community ecology require different uses of PD.

WHY APPROACHES IN COMMUNITY ECOLOGY AND CONSERVATION BIOLOGY SHOULD BE DIFFERENT

Some approaches using PD in conservation biology have likely been influenced by those applied in community ecology (or at least they became similar on occasions) resulting in wrong interpretations and practices. Although we previously discussed what phylogenies can tell us about feature variation and its potential for conservation, in this section we go further and discuss what PD can tell us about species interactions influencing community and network assembly. By doing so we will show why and when approaches in conservation biology and community ecology should differ and when they may intersect.

SOME PHYLOGENETIC INFORMATION OF INTEREST IN COMMUNITY ECOLOGY: NICHE CONSERVATISM AND COMMUNITY ASSEMBLY

As previously mentioned, the idea that phylogenetic distance should be related to species interaction can be traced back to Darwin (1859). He hypothesized that, because of their common ancestry, congeners should have many similar characters, increasing the chances of exploiting the environment in a similar fashion—what would be later known as the competition-relatedness hypothesis (Cahill et al. 2008). Gause (1934), inspired by Darwin's ideas and by Lotka (1925) and Volterra (1926), established the foundations for the theory of competitive exclusion. This theory proposes that two species occupying the same ecological niche cannot coexist in a stable manner. It was later complemented by the limiting similarity model—introduced by MacArthur and Levins (1967) and revised by Abrams (1983)—that demonstrates mathematically how species coexistence could be limited by their degree of niche overlap. Works by Felsenstein (1985) and Harvey and Pagel

(1991) introduced the first formal discussions surrounding the concept of niche conservatism. Because a species is expected to not easily adapt to conditions outside its fundamental niche, evolutionary changes are likely to be an inherently conservative process (Holt and Gaines 1992; Wiens and Graham 2005). Thus, closely related species should fundamentally overlap in their niches.

Based on the concepts of niche conservatism and limiting similarity, Webb et al. (2002) proposed the use of phylogenetic relatedness as a surrogate for niche overlap, which allowed for the understanding of community assembly through the analysis of patterns of phylogenetic structure. According to their logic, when closely related species co-occur more often than expected by chance (i.e., phylogenetic clustering), one could infer the predominance of environmental filtering, whereas when closely related species co-occur less than expected by chance (i.e., phylogenetic overdispersion), one could infer the predominance of competitive exclusion due to the limited similarity among closely related species. This concept has been widely used due to the straightforward way that observed patterns can be interpreted and the increasing availability of comprehensive data sets (Cavender-Bares et al. 2004; Vamوسي 2007; Emerson and Gillespie 2008).

PHYLOGENETIC DIVERSITY IN COMMUNITY ECOLOGY—A GENERALIZATION

From the logic described above, several metrics based on phylogenetic trees have been developed in community ecology that are related to divergence, diversity, and evenness (Tucker et al. 2017). We will here focus on the use of PD to show how it differs from its use in conservation biology; reviews on other measures are available elsewhere (e.g., Pavoine and Bonsall 2011; Tucker et al. 2017).

The PD value (Faith 1992) of a set of species found at a given site has been employed as a measure of phylogenetic alpha diversity (e.g., Chai et al. 2016) to assess the coexistence or functional differences among species (Cadotte et al. 2010). One particular approach has been to compare the PD and species richness (SR) at a given site. High PD

compared to SR would relate to the occurrence of distantly related species and indicate potential competitive exclusions, while low PD over SR may reveal communities composed of closely related species and possible environmental filtering (overdispersion versus clustering; see above). For example, Chai et al. (2016) used this approach to reveal the deterministic and stochastic process at the origin of diversity patterns in a long-term study of forest succession. Moreover, relative PD might provide insights into evolutionary processes, including the balance between speciation and extinction that affect community assembly (Pavoine and Bonsall 2011). Davies and Buckley (2011) measured the mammal relative PD in individual sites to disentangle areas where speciation has been rapid and immigration rare (low PD relative to species richness) and areas where diversification has been slow and long-distance immigrations frequent (high PD relative to species richness).

This is, of course, a very general view of the use of PD in community ecology that is often employed in combination with other measures (Cadotte et al. 2010; Pavoine et al. 2013). However, this shows that PD is used for different purposes in community ecology and conservation biology and should not be confused. Although the PD of a given site may be of interest to understand community assembly, it may be less important in conservation biology where, to preserve feature variation, the phylogenetic complementarity of sites and species is considered. There are cases when community ecology and conservation ecology meet, for example, to predict the effect of invasions (Yguel et al. 2011, 2014) or ecosystem functioning, as discussed above. Yet, we prefer to highlight the main differences and avoid sources of confusion in both fields of ecology.

WHEN PHYLOGENETIC AND FEATURE VARIATION ARE NOT CONGRUENT: LIMITATIONS AND SOLUTIONS

A common point in conservation biology and community ecology frameworks is the use of PD under the assumption that large evolutionary distances among species indicate more feature differences among them.

All of the benefits that can result from this relationship make it likely that many studies based on PD will be conducted in the future. Yet, existing limitations and misinterpretations to this assumption have fueled the ongoing debate on the use of phylogenetic information in both conservation biology and community ecology (e.g., Cadotte et al. 2017; Mazel et al. 2018). As stated by Faith and from what is clear in the original PD paper (Faith 1992): "PD should not be expected to magically make inferences about every favorite character or feature" (Faith 2018a:6). This implies that, despite clear benefits, some conclusions from PD investigations should be drawn with care. We present some of the most common sources of limitations in the PD and feature diversity relationship, their consequences, and how they may be alleviated. Some limitations have also been treated in depth by other authors, so the general overview we present here may be complementary to previous work (e.g., Cadotte et al. 2017; Box 1). We focus our attention on how these limitations may (or may not) weaken the conclusions drawn from PD analyses in conservation and community ecology presented in the section above.

A GENERAL OVERVIEW OF EXISTING LIMITATIONS

Phylogenetic Reconstruction

Modern phylogenetic trees originated from cladistics, a set of methods used to reconstruct relationships between organisms established by Hennig (Hennig 1950, 1965). Phylogenetic trees enable the grouping of species/organisms based on the analysis of homologous characters (i.e., characters inherited from a common ancestor). Currently, this method is the preferred principle to classify organisms and numerous statistical and computational tools have been developed (Box 1; e.g., maximum parsimony, maximum likelihood, and Bayesian methods) in the quest to find the most accurate phylogenetic trees (Huelsenbeck et al. 2001; Tamura et al. 2011).

All of the tools available for phylogenetic tree reconstruction have advantages, drawbacks, and limitations that should be carefully

BOX 1

Phylogenetic tree reconstruction methods as source of uncertainties

The construction of phylogenetic trees is a difficult task since there is no methodology that guarantees the recovery of the “true” tree. Methods for inferring phylogenetic trees are classified into two categories according to the type of data used: distance-based and character-based.

DISTANCE-BASED METHODS

Distance matrix methods start by converting molecular data into a pairwise distance matrix, which is then used for inferring a phylogenetic tree. There are mathematical models to calculate distances between each pair of operational taxonomic units (OTUs), based on different models of molecular evolution that result in different genetic or evolutionary distances. Most distance methods use clustering algorithms to construct a single phylogenetic tree. These methods are suitable for the rapid analysis of large datasets as they are not computationally demanding.

UNWEIGHTED PAIR GROUP METHOD WITH ARITHMETIC MEAN (UPGMA)

UPGMA is one of the simplest methods for tree reconstruction. The clustering works by searching for the smallest pairwise distance value between OTUs in the matrix that will form a new cluster. Then a new distance matrix is calculated between the newly formed cluster and the remaining OTUs. The process continues until all OTUs are clustered. The tree is formerly additive and thus all nodes are equally distant from the root. UPGMA assumes that evolutionary rates in all branches are similar, which is generally not the case (Nei 1991).

NEIGHBOR JOINING (NJ)

This method differs from UPGMA in that there is no assumption about the distance between OTUs. The NJ algorithm does not construct clusters, but minimizes the length of all internal branches (Saitou and Nei 1987). The process begins with an estimation of evolutionary distances correcting for multiple substitution events at the same site. In a second step, the minimal distance is used to introduce a new node that groups a pair of OTUs for which evolutionary distance is minimal. Then a new matrix is calculated from the new node to each other's terminal node. The process is repeated until an unrooted tree is constructed. A distantly related taxon (outgroup) can be chosen to root the tree.

A serious weakness for distance methods such as NJ and UPGMA is that the observed differences between sequences are not accurate reflections of the evolutionary distances between them, especially due to non-constant evolutionary rates. In that case, corrections must be applied, but there is no consensus on what correction could be the best. NJ and UPGMA appear as suitable methods when sequences have diverged recently, but could be particularly misleading when estimating old relationships (Holder and Lewis 2003). Other distance-based methods are Fitch-Margoliash, minimum evolution, or least-squares algorithms.

CHARACTER-BASED MODELS

Character-state methods use variation in a set of discrete characters (e.g., sequence data) to construct phylogenetic trees. In contrast to distance-matrix methods, they can be used to reconstruct ancestral character states because they retain the original character status of the taxa.

MAXIMUM PARSIMONY (MP)

Under the maximum parsimony criterion, the best tree is one that requires the minimum number of character changes (e.g., nucleotide substitutions) to produce the data (e.g., a set of homologous sequences). However, there are many plausible scenarios that could have produced a group of sequences and considering a single mutational path, as MP does, may be misleading (Holder and Lewis 2003). MP assumes that common characteristics are inherited from a common ancestor, but when homoplasy (parallelisms, convergences, and reversal events) is present, the most parsimonious method may underestimate the actual evolutionary divergences. The MP algorithm usually finds more than one tree with the same parsimonious length. A consensus approach is then built up to combine all of the most parsimonious trees. The MP method does not consider the fact that the number of character changes may vary on each branch of the tree. Long-branch attraction occurs when rapidly evolving taxa are placed together on a tree because they have many mutations (Rizzo and Rouchka 2007). Yet, parsimony performs relatively well if the amount of convergence is rare compared with the number of mutations that are conveying useful information (Holder and Lewis 2003). There are other different parsimony algorithms such as weighted, transversion, or Dollo parsimony.

MAXIMUM LIKELIHOOD (ML)

This method allows for the correction of multiple mutational events at the same location. Likelihood methods measure the probability of the data given the hypothesis (i.e., it prefers the tree with the highest probability to fit the observed sequences). ML optimizes the likelihood of observing data given a tree topology and a model of nucleotide evolution (Egan and Crandall 2006). ML assumes a model of evolution and the tree returning the highest likelihood is considered the best tree. An advantage of ML is that it accounts for the possibility of unseen events such as back mutations or complex pathways (Holder and Lewis 2003). As for MP, it examines different tree topologies. This method is very robust for reconstructing old relationships and fast evolutionary events, but is one of the most computationally demanding and may be inappropriate for relatively large data sets. To tackle those computer load issues, more recent methods based on ML have been developed, in particular PhyML (Guindon et al. 2010), RAxML (Stamatakis 2006), and IQ-TREE (Nguyen et al. 2014), among others.

All of the methods described above require a form of confidence assessment for the relationships inferred in the tree. The most common tool to establish this confidence is called “bootstrapping,” which consists of creating pseudoreplicate data matrices by randomly resampling the original data set (with replacement) and reconstructing phylogenetic trees for each (Lemey et al. 2009). Bootstrap values provide a measure of support for the monophyly of clades and the relationships among studied taxa.

BAYESIAN METHODS

Bayesian methods simultaneously estimate trees and measures of support for every branch. This approach searches for a set of trees representing the data by using a prior probability for the distribution of each parameter of the model (or equal probabilities if we do not have prior information). The optimal tree is the one that maximizes the posterior probability that is proportional to the likelihood multiplied by the prior probability. The posterior probabilities specify the probability of each tree given a model, a prior, and the data. A technique called Markov chain Monte Carlo (MCMC) is used to explore tree space. An advantage of Bayesian techniques is that they allow the implementation of complex models of sequence evolution. Moreover, contrary to ML, Bayesian approaches may be reliable even when the ratio of data points over the number of parameters is low. Unfortunately, Bayesian methods are very computationally demanding and selecting an uninformative prior may result in serious issues.

considered. In Box 1 we relate sources of uncertainties in some of the most employed methods for phylogenetic reconstruction. This shows that the relationship between phylogenetic variation and feature variation may already be blurred by these reconstruction methods.

Different Rates of Feature Evolution and Convergences Can Blur Phylogenetic Signals

Evolutionary rate variation among features may influence how similar are closely related species in a phylogenetic tree. Fast evolving features may tend to be very different between closely related species and reveal little about evolutionary history (Losos 2011). Phylogenetic signals in features can thus be revealed only when the rates of character evolution are low relative to rates of clade evolution (Losos 2011).

Another reason why phylogenetic similarity may not reflect feature similarity is because of convergent evolution (Faith 1992). This is the process by which evolutionarily unrelated organisms show similar features as a result of natural selection and adaptation. Because of convergences, several features in different clades do not show any phylogenetic signal (Mazel et al. 2017). As stated by Faith (1992), the PD index does not capture convergent features because they depart from the assumption that shared traits are due to a common evolutionary history. Although this principle is inherent

in the evolutionary model on which PD is based, it has been missed in some studies (e.g., Kelly et al. 2014). Therefore, convergent features should be considered through other metrics, such as shared habitats as suggested by Faith and Walker (1996).

Species Descending From Long Branches Do Not Always Retain Old Features

Species descending from deep nodes do not always exhibit features older than species found in shallower nodes (Grandcolas and Trewick 2016). There are two potential reasons for this situation. First, all characters of a species that have been in an evolutionary stasis are not in a primary state. Grandcolas and Trewick (2016) showed that species found on long branches may also have features considered more modern. Second, isolated species on long branches can be remnants from a lineage formerly much more diverse that was decimated by subsequent extinction events. Thus, the species that are remnants from an ancient group previously comprising more species represent a combination of features of this group, but not always the character states present in its ancestor (Grandcolas et al. 2014; Grandcolas and Trewick 2016). The conservation interest of evolutionary distinct species and long branches, capturing large amounts of PD, may not always rely on their unique features and possible related functions in an ecosystem, but also to their level of endangerment

and symbolic value (Isaac et al. 2007; Grandcolas and Trewick 2016; Trewick and Morgan-Richards 2016).

Uncertainties Due to the Model of Feature Evolution

The expectation that greater evolutionary distances indicate that species have accumulated more ecological differences assumes a very particular evolutionary model, i.e., the Brownian motion model. Phylogenies are often built following a Brownian motion model (Diniz-Filho et al. 2013). This model assumes that features continue to diverge linearly over time and that convergence is rare. This supports the rationale to use PD in conservation and community ecology (i.e., that shared features may be explained by shared ancestry; Cadotte et al. 2017). Cadotte et al. (2017) showed that under the Brownian motion model the relationship between ecological and phylogenetic distance was linear only when multiple features (or ecological traits) were considered, whereas this was not true for a single feature. PD may be a good surrogate for variation of multiple features, but this surrogacy may weaken when the number of features decrease (Diniz-Filho et al. 2013; Cadotte et al. 2017; Tucker et al. 2018), as stated in the original paper introducing PD (Faith 1992). Yet, evolutionary, physiological, or ecological constraints tend to make evolution models more complex than a Brownian motion model. Many studies show that only a small proportion of features (or ecological traits) followed a linear model of evolution and a model of bounded evolution was generally favored (Davies 2015). From this, the relationship between phylogenetic distance and ecological distance and between the sum of branch lengths joining species and their feature variation can take many forms (Cadotte et al. 2017; Tucker et al. 2018). For example, if evolution slows down over time, phylogenetic diversity may capture little feature diversity, whereas if evolution occurs in bursts, much feature diversity may be captured (Davies 2015). A useful review of the issues related to the model of evolution can be found in Cadotte et al. (2017), and some

practical solutions have been proposed by Pagel (1999), Diniz-Filho et al. (2012), Davies (2015), Letten and Cornwell (2015), and Mazel et al. (2016).

Yet, despite numerous possible evolutionary models, if “large numbers of species [are examined] and combine multiple traits, which have been subject to different selection regimes, then the pattern of evolution is likely to be indistinguishable from BM [Brownian motion model]” (Cadotte et al. 2017:537–538). When this condition is met, PD may then still be a good predictor of feature (or ecological traits) diversity, independent of the evolutionary model of features (Cadotte et al. 2017).

CONSEQUENCES FOR THE USE OF PHYLOGENETIC INFORMATION IN CONSERVATION BIOLOGY . . .

One main benefit for the preservation of PD highlighted in this review is its relationship with ecosystem processes and option values (Kraft et al. 2007). Up until now, some studies have found that ecosystem processes were related to species richness, with a small fraction of increase due purely to higher phylogenetic diversity (Venail et al. 2015; but see Cadotte 2015). From the discussion above, it is clear that there are many reasons why phylogenetic diversity itself may not be able to forecast functional diversity or the value of ecosystem services (Venail et al. 2015). First, traits that control ecological functions are not phylogenetically conserved, so that maximizing PD may not maximize feature diversity. Moreover, this implies that closely related species do not have similar ecological functions and distantly related species do not complement each other's function. Second, closely related species do not compete more strongly than distantly related ones, given all of the reasons discussed above (see Mayfield and Levine 2010). Thus, communities composed by distantly related species do not have more niche complementarity and better productivity than communities formed by closely related species. Third, closely related species commonly experience facilitative interactions (Cianciaruso

et al. 2009). Thus, communities composed by closely related species can have higher productivity when these species facilitate each other, in comparison with communities of distantly related species that face competitive interactions.

In spite of all of these possible limitations, PD was shown to be a strong predictor of ecosystem functioning (Cadotte 2015). This is likely because by summing the phylogenetic distances of species in a community, PD represents the variation (and not the difference) in species traits (i.e., the total niche space occupied; Cadotte et al. 2017). Moreover, when the additional benefits of using PD over other measures to capture ecosystem processes are not clear, phylogenetic information may still be valuable (Cadotte 2015). For instance, Yguel et al. (2016) argued that, even if PD remained useful for predictions related to ecosystem processes, it may be too simple to depict differences in the phylogenetic structure of communities. These authors then proposed a measure called Evolutionary Legacy of Diversification, which describes branching patterns and may better predict ecosystem processes than other commonly used metrics such as PD. Besides, ecological functions may not always be provided by feature diversity but rather by key innovations (Davies et al. 2016). In that case phylogenetic placement, for example, measured by metrics that describe the connectedness or centrality of nodes and edges within a network, may better represent those functions than PD does (Davies et al. 2016).

In addition, many studies showed that PD was not a good proxy for functional diversity and that spatial patterns were incongruent most of the time (Devictor et al. 2010; Pavoine et al. 2013; Pollock et al. 2017; Cadotte and Tucker 2018; Mazel et al. 2018). Again, these results were expected because only a few traits were considered, convergence may occur or models were not convenient (see discussion in Faith 2018b). Appropriate measures to estimate functional diversity and spatial priorities, which separately consider functional and phylogenetic diversity, are therefore necessary (e.g., Cadotte and Tucker 2018).

Although some limitations and improvements can be found regarding the relation-

ship between PD and ecosystem processes and that some features do not show any phylogenetic signals (Faith 1992), PD remains an important calculus to maintain option and insurance values. PD may *on average* capture feature diversity that may be the best way to maintain unexpected benefits to humanity and for the resilience of ecosystems. As shown above, this relationship does not rely on only a few existing traits, but on the overall features of species with unknown variation and unknown future values. Analyses based on a few traits have sometimes led to the wrong interpretation that PD does not capture option values (Faith 2018b). On the contrary, “option values” is the primary argument for the use of PD calculus in conservation such that “maximizing the retention of phylogenetic diversity (PD) should also maximize option value” (Larsen et al. 2012:7).

In conclusion, despite the fact that niche conservatism provides the foundation for the PD ecosystem services agenda, it has some limitations that should be acknowledged. Although PD has been shown to be a strong predictor of ecosystem functioning, the key to understanding the processes that explain this prediction is to go deeper into the phylogenetic signature of species interactions that may result in the definition of new metrics based on phylogenies. Studies investigating the relationship of PD and ecosystem functions and services will be more fruitful if we acknowledge the underlying premises of phylogenetic signals and niche complementarity, otherwise studies will have strong contingency and with low generalization for conservation purposes.

. . . AND IN COMMUNITY ECOLOGY

From the limitations described above (see the section titled When Phylogenetic and Feature Variation Are Not Congruent: Limitations and Solutions), assuming that niche conservatism indicates the maintenance of the fundamental niche over time a priori and to link it directly to competition between closely related species may sometimes be flawed (Kraft et al. 2007). Although many features are more conserved through evolutionary his-

tory than expected, in cases of convergent or divergent evolution, the interpretation of phylogenetic patterns in the face of assembly processes becomes confused (Losos 2008, 2011). For example, species from distinct lineages where trait evolution is predominantly convergent can be assembled in communities driven by environmental filters and yet their phylogenetic pattern can be overdispersed. In this case, if we assume niche conservatism, phylogenetic patterns, such as the relationship between PD and SR, would be erroneously interpreted as competition between closely related species. Moreover, when species are assembled by asymmetric competition—i.e., species have different competitive abilities—communities can have phylogenetically clustered structures due to the competitive exclusion of distantly related species with inferior competitive abilities (Mayfield and Levine 2010; Gerhold et al. 2015; Saito et al. 2016, 2018). From this, relationships between phylogenetic overdispersion/clustering and competition/environmental filtering is also not uniform across clades (Pearse et al. 2018). Cadotte et al. (2017) provides a review on how to interpret the lack of phylogenetic signals in community assembly. Other points for the weakness and strengths of inferring assembly processes from phylogenetic information, such as understanding how coexistence leads to the macroevolutionary diversification of habitat lineage pools or, on the contrary, how macroevolutionary contingency of habitat lineage pools affects present-day species coexistence (Gerhold et al. 2015) were explored by others (Mayfield and Levine 2010; Mason and Pavoine 2013; Gerhold et al. 2015; de Bello et al. 2017).

The use of PD in conservation biology and community ecology relies on a strong theoretical background. Limitations exist that may blur or nullify the relationship between phylogenetic variation and variation in some traits (e.g., Cadotte and Tucker 2018), potentially influencing the conclusions that can be drawn from PD approaches. In particular, this may influence the predictions of species interactions so that niche complementarity, species assemblage, and ecosystem functioning can sometimes be difficult to interpret through PD. As stated above, this situation

could be improved by a clearer understanding of the phylogenetic signature of species interactions. Finally, the relationship between genotypes and phenotypes and how it affects the use of PD has received, to our knowledge, nearly no attention. Still, the limitations regarding the use of PD in conservation and community ecology are better understood (e.g., Cadotte et al. 2017), corrections have been proposed (Cadotte 2015; Gerhold et al. 2015; Yguel et al. 2016), and we hope this review and other research (e.g., Faith 2016a, 2018a) will help in preventing incorrect interpretations that arise from unfit analyses or inaccurate understanding of the rationale of PD usage (e.g., Kelly et al. 2014; Venail et al. 2015). Although conclusions about the use of PD should sometimes be mitigated, we believe that such improvements and good practices will allow the appropriate use of phylogenetic information as a powerful tool for the future of conservation biology and community ecology.

CONCLUSIONS

1. The use of phylogenetic information in conservation biology and community ecology relies highly on the assumption that shared features are due to a shared evolutionary history.
2. Up until now, confusion between conservation biology and community ecology frameworks may have resulted to a misuse of phylogenetic information in many cases.
3. In conservation biology, the interest is to maintain option values through feature variation. Strategies that do not consider the phylogenetic complementarity of sites and species do not allow maximizing the chances to preserve option values, but some may have a practical interest.
4. In community ecology, phylogenetic information may help to disentangle the process at the origin of diversity patterns and community assembly in a given area, but phylogenetic complementarity among sites is not always essential.
5. Yet, it should be noted that limitations in the relationship between features and evolutionary history may lead to misunderstandings and misinterpretations in both conservation biology and community ecology.

6. Understanding and considering the conditions to use phylogenies for conservation and community ecology purposes is challenging, but recent progress has been made. For example, alternative indices of phylogenetic diversity have been proposed to include factors at the origin of shifts in the relation between evolutionary and trait variation.
7. Improving our knowledge on the relation between evolutionary history and trait variation is more crucial as it has implications in various fields of ecology

such as the understanding of ecological interactions, ecological functions, and the potential future benefits of biodiversity to societies.

ACKNOWLEDGMENTS

This work was supported by a grant from Agence Nationale de la Recherche under the LabEx ANR-10-LABX-0003-BCDiv, in the program "Investissements d'avenir" ANR-11-IDEX-0004-02. We are grateful to the anonymous reviewers for their thoughtful comments.

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Handling Editor: Liliana M. Dávalos

APPENDIX 1

Glossary

Character: All observable characters of an organism, including morphological, anatomical, chemical, and molecular.

Diversification: The process that lead species to diversify; the sum of speciation and extinction events.

Evolutionary history: The history of species evolution that links all species on Earth in a unique natural classification.

Extinction: In its modern definition, a species is considered extinct when there is no reasonable doubt that the last individual has died.

Natural selection: Darwin's natural selection theory stated that the most useful variations of species in their environment (i.e., a new fitness) favored the individuals and thus persisted, and that those advantageous variations were inheritable.

Niche complementarity: This hypothesis states that for coexistence to occur high overlap in one dimension of the niche must be compensated by low overlap in another.

Option value: Biodiversity values that provide benefits and uses, often unanticipated, for future generations.

Operational Taxonomic Unit (OTU): An operational definition used to classify groups of closely related individuals.

Phylogenetic root: The root represents the common ancestor to all taxa on a tree and is their oldest ancestor.

Phylogenetic signal: The tendency for related species to resemble each other more than they resemble species drawn at random from the phylogenetic tree.

Species: Defined for language convention as reproductively isolated populations.

Speciation: Lineage-splitting event that produces two or more separate species.

Trait: The diversity of morphological, biochemical, behavioral, and physiological characters of species.

Tree of Life: Phylogenetic tree depicting the links uniting all of the species on Earth.