Predicting loss of evolutionary history: Where are we?

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ABSTRACT

The Earth's evolutionary history is threatened by species loss in the current sixth mass extinction event in Earth's history. Such extinction events not only eliminate species but also their unique evolutionary histories. Here we review the expected loss of Earth's evolutionary history quantified by phylogenetic diversity (PD) and evolutionary distinctiveness (ED) at risk. Due to the general paucity of data, global evolutionary history losses have been predicted for only a few groups, such as mammals, birds, amphibians, plants, corals and fishes. Among these groups, there is now empirical support that extinction threats are clustered on the phylogeny; however this is not always a sufficient condition to cause higher loss of phylogenetic diversity in comparison to a scenario of random extinctions. Extinctions of the most evolutionarily distinct species and the shape of phylogenetic trees are additional factors that can elevate losses of evolutionary history. Consequently, impacts of species extinctions differ among groups and regions, and even if global losses are low within large groups, losses can be high among subgroups or within some regions. Further, we show that PD and ED are poorly protected by current conservation practices. While evolutionary history can be indirectly protected by current conservation schemes, optimizing its preservation requires integrating phylogenetic indices with those that capture rarity and extinction risk. Measures based on PD and ED could bring solutions to conservation issues, however they are still rarely used in practice, probably because the reasons to protect evolutionary history are not clear for practitioners or due to a lack of data. However, important advances have been made in the availability of phylogenetic trees and methods for their construction, as well as assessments of extinction risk. Some challenges remain, and looking forward, research should prioritize the assessment of expected PD and ED loss for more taxonomic groups and test the assumption that preserving ED and PD also protects rare species and ecosystem services. Such research will be useful to inform and guide the conservation of Earth's biodiversity and the services it provides.

Key words: biodiversity, conservation, evolutionary distinctiveness, phylogenetic diversity, predictions, species extinctions.

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I. INTRODUCTION

Species extinctions are natural phenomena which, along with the process of speciation, have shaped Earth's biodiversity and its 'tree of life' (Barraclough & Nee, 2001). However, Earth's history also includes catastrophic events which caused mass extinctions, defined as the loss of more than three-quarters of Earth's species in a short geological time (Barnosky *et al.*, 2011). The five most significant extinction events occurred, respectively, at the end of the Ordovician, Devonian, Permian, Triassic and Cretaceous (Raup & Sepkoski, 1982; Jablonski & Chaloner, 1994). Scientists now estimate that a sixth extinction crisis has started in the Anthropocene (Dirzo & Raven, 2003; Pereira *et al.*, 2010; Barnosky *et al.*, 2011). It is estimated that one-fifth of vertebrate species are now threatened with extinction (Hoffmann *et al.*, 2010). Among the best-studied groups current estimates suggest that 32% of the world's amphibians, 31% of sharks and rays, 25% of mammals and 13% of birds are threatened with extinction (IUCN, 2014). Further, the number of extinctions is predicted to increase such that

75% of current vertebrate species could be lost in the following centuries (Barnosky *et al.*, 2011). Extinction risks are less well known for other groups, such as invertebrates, yet evidence of declining populations suggests that some invertebrate taxa may also be highly threatened (Collen *et al.*, 2012). While human-caused species extinctions are for some a great moral wrong and a tragedy (Cafaro & Primack, 2014; Marvier & Kareiva, 2014), they also impact the health of ecosystems. For example, mass species extinctions can result in the loss of ecosystem engineers, and a reduction in functional diversity, behavioural and social complexity, and developmental strategies (Erwin, 2008).

Since the 1990s, scientists have been particularly interested in quantifying the loss not only of species but also of evolutionary history because it has been argued to capture the diversity of life better than simple measures of taxonomic richness (Faith, 1992; Purvis *et al.*, 2000a; Purvis, 2008; Winter, Devictor & Schweiger, 2013). It has been suggested that the rate of loss of phylogenetic diversity in the future could be much higher than the rate of species loss because threatened species are not randomly distributed in the

phylogeny. Biologists have thus looked for solutions to preserve a maximum coverage of the Earth's tree of life (Faith, 2008; Mooers, Faith & Maddison, 2008; Thuiller *et al.,* 2011; Billionnet, 2012; Jetz *et al.,* 2014). The Earth's evolutionary history may be considered to have intrinsic value, and by protecting the maximum coverage of the tree of life we also protect rare and unique species with few relatives (Faith, 1992; Winter, Devictor & Schweiger, 2012). Moreover, protecting evolutionary history may help to preserve a diversity of features (see Section II.5) and biodiversity option values, i.e. biodiversity values that provide benefits and uses, often unanticipated, for future generations (Forest *et al.,* 2007; Faith, 2008; Faith *et al.,* 2010; Faith & Pollock, 2014). Recent methodological developments and new sources of data could allow a better understanding of the potential future loss of evolutionary history (Mace, Gittleman & Purvis, 2003; Roquet, Thuiller & Lavergne, 2013). However, global assessments of loss of evolutionary history are still limited to a few branches on the tree of life (Diniz-Filho, 2004; Davies *et al.,* 2008; Isaac *et al.,* 2012). Here we review existing studies to assess the state of current knowledge of the loss of evolutionary history due to the ongoing mass extinction event. We address four objectives: (*i*) to summarize common indices quantifying evolutionary history and its loss; (*ii*) to assess current knowledge on the evolutionary history that is at risk from human impacts; (*iii*) to assess how well evolutionary history is protected by current conservation practices; (*iv*) to highlight new methods and frameworks that could improve the assessment and preservation of evolutionary history on Earth.

II. A THEORETICAL FRAMEWORK FOR EVALUATING THE LOSS OF EVOLUTIONARY HISTORY

(1) Multiple ways to quantify evolutionary history

There are a myriad of biodiversity indices in the scientific literature and several have been dedicated to evolutionary history. Vellend *et al.* (2011) reviewed existing indices of evolutionary history, and suggested that they could be categorized into two types. Type I indices are focused on the quantification of an evolutionary distinctiveness (ED) score for each taxon on a phylogenetic tree. They have mostly been used in conservation biology, although Cadotte *et al.* (2010) developed these for analysing communities. Examples of this type of index include fair-proportion (Redding, 2003), equal-splits (Redding & Mooers, 2006), and originality (Pavoine, Ollier & Dufour, 2005). Type II indices are calculated from a subset of species and the corresponding phylogenetic tree. Type II indices have been used in community ecology, macroecology and macroevolution as well as in conservation biology. Examples of type II indices include phylogenetic diversity (PD) (Faith, 1992), mean phylogenetic distance (e.g. Webb, 2000) or phylogenetic species variability (Helmus *et al.,* 2007). In community ecology, various indices have been used to study phylogenetic

patterns and to make inferences about the biotic and abiotic factors structuring communities (Helmus *et al.,* 2007), assuming that phylogenetic proximities reflect similarities in traits or niches of species. Related phylogenetic indices have been used to depict the history of community formation, for instance, by highlighting dispersal and speciation events during community assembly (Pavoine & Bonsall, 2011).

Type I indices are used in conservation biology to focus conservation priorities on those species that are both threatened with extinction and evolutionarily distinct. Out of these indices, Vellend *et al.* (2011) recommended the use of the fair-proportion index (Redding, 2003) because of its simplicity and because it may have greater information content than some alternative indices. For example, for a given species, the fair-proportion index captures not only information on the unique terminal branch that connects the species to the tree but also the length and the number of branches the focal species shares with other species. Of the type II indices, Faith's PD dominates in conservation biology, and is seen as quantifying the total amount of independent evolutionary history of a subset of taxa and thus capturing their functional diversity (Nee & May, 1997; see also Section II.6). The dominance of this index is in part due to its simplicity, but also to its tight connection with species richness: PD never decreases when a species is added to a set, a key property for establishing conservation priorities. However, phylogenetic diversity is multifaceted, and as a multidimensional concept it requires a variety of indices for all its facets to be represented (Forest *et al.,* 2015). For example, among the indices of phylogenetic diversity, Faith's (1992) PD is partly linked to species richness, whereas the average phylogenetic distance among species (e.g. Webb, 2000; Pavoine *et al.,* 2013) is not. Further, although both these two indices reflect diversity they do not directly measure how imbalanced a tree is, a property which might reflect diversification and/or colonization patterns (Pavoine & Bonsall, 2011). Among the ED indices, the fair-proportion (Redding, 2003) and the equal-splits (Redding & Mooers, 2006) metrics may be more influenced by the length of the terminal pendant branch that connects the species to the rest of the tree (the 'age' of the species) than the originality index of Pavoine *et al.* (2005), which instead is more influenced by tree topology [the relative amount and evenness of diversification (speciation events) in all clades]. Although many indices have been defined, they are only rarely applied, we thus argue for the use of a greater variety of phylogenetic indices in conservation biology (see also Section IV.1).

In the conservation biology literature, both type I and type II indices have been weighted by data on threats and extinction risks to predict species evolutionary history at risk (Isaac *et al.,* 2007; Steel, Mimoto & Mooers, 2007; Faith, 2008). We here mainly review applications of Faith's (1992) PD (as the most-used type II index), Redding's (2003) fair-proportion (as the most-used type I index), and their most widely used weighted versions: expected phylogenetic diversity (Expected PD) (Faith, 2008), evolutionary distinct and globally endangered (EDGE) (Isaac

et al., 2007), and heightened evolutionarily distinct globally endangered (HEDGE) (Steel *et al.,* 2007). In contrast to many other phylogenetic indices, these weighted indices have been more widely applied to phylogenies at a global scale, and thus provide us with ability to assess potential losses of evolutionary history across several taxa (see Section III).

Some additional weighted indices have been proposed, and these bring important extra information to help predict, understand and avoid loss of evolutionary history. Although we do not focus on those indices here as they have yet to be widely employed, we expect their use to increase in the future. Examples include weighting by species range size or abundance, such as the indices of phylogenetic endemism (Rosauer *et al.,* 2009) and biogeographically weighted evolutionary distinctiveness (Cadotte & Davies, 2010), which allow us to identify places where phylogenetic diversity may be highly concentrated. These indices have mostly been used for regional analysis (Gudde, Joy & Mooers, 2013), for example, to identify Australian diversity hotspots of endemic plants and frogs (Rosauer *et al.,* 2009) and Chinese hotspots of endemic woody seed plant species (Huang *et al.,* 2012*a*), but they are also promising at a global scale (Rosauer & Jetz, 2015).

(2) Phylogenetic diversity

The most common measure used to quantify evolutionary history is Faith's (1992) phylogenetic diversity (PD). The PD of a subset of taxa on a phylogenetic tree is calculated as the minimum total length of all the phylogenetic branches, from the root to the tips, which are required to connect the taxa on the tree (Faith, 1992):

$$\text{PD}\,(\textit{tree}) = \sum_j L_j \qquad (1)$$

where *j* designates a branch on the phylogenetic tree, and L_j is the length of this branch. For a given phylogenetic tree with species as tips, when a subset of species $\{x\}$ becomes extinct the corresponding loss of PD (PD*loss*) can be simply calculated as follows (Faith, 2013):

$$\text{PD}\textit{loss}\,(\{x\}) = \text{PD}\,(\textit{tree}) - \text{PD}\,(\textit{tree} - \{x\}) \qquad (2)$$

where $\textit{tree} - \{x\}$ is a subtree obtained by removing all tips in $\{x\}$ and all branches for which all their descendants are in $\{x\}$. A phylogenetic branch is lost if all the species supported by the branch go extinct. PD*loss* depicts a very pessimistic scenario if we assume that all currently threatened species go extinct.

A more refined measure can be obtained by accounting for species' probabilities of extinctions. Faith (2008) defined the expected amount of PD that may remain after a given period of time as,

$$\text{Expected PD}\,(\textit{tree},\ \textit{proba}) = \sum_j L_j \left(1 - \prod_{dj} p_{dj}\right) \qquad (3)$$

where *dj* designates the *d*th descendant of branch *j*, p_{dj} is the probability of extinction of the *d*th descendant of branch *j* within the defined period of time, and *proba* is the vector of species' probabilities of extinction (Mooers *et al.,* 2008). This index assumes that the extinction of a species is independent of the extinctions of the other species. The expected loss of PD can be estimated simply as,

$$\text{Expected PD}\textit{loss}\,(\textit{tree},\ \textit{proba})$$
$$= \text{PD}\,(\textit{tree}) - \text{Expected PD}\,(\textit{tree},\ \textit{proba}) \qquad (4)$$

Despite its potential, this probabilistic approach is still little used (but see e.g. Faith & Richards, 2012; Jono & Pavoine, 2012; Davies & Yessoufou, 2013). An example of calculation of all indices is presented in Fig. 1. It shows how a probabilistic framework enables refinement of assessments of evolutionary history losses and how it may change conservation prioritization.

(3) How to interpret PD*loss* and expected PD*loss*?

Simulations and empirical studies have revealed factors that can drive high values of PD*loss* and Expected PD*loss*, including the combined effects of extinctions that are phylogenetically clustered (Fritz & Purvis, 2010*b*; Huang, Davies & Gittleman, 2011), the loss of species with few relatives and of clades that contain only a few species (Vamosi & Wilson, 2008), and the shape (imbalance and 'tippiness') of the phylogenetic tree (Heard & Mooers, 2000). For example, tree imbalance may lead to higher loss of PD if extinctions are biased towards old clades supported by few species (Heard & Mooers, 2000; Parhar & Mooers, 2011). As an indicator of tree imbalance, the shape of the species richness–PD curve may characterize the potential loss of PD with extinctions. In particular, a power curve relationship (Faith, 2008), in contrast to the often assumed logarithmic curve (Nee & May, 1997), results in higher loss of PD with species extinctions on an imbalanced tree, even if extinctions are random (Fig. 2). A power-law curve was found to characterize the Mediterranean flora well, and it is expected to be common for taxonomic groups characterized by phylogenetic trees with long terminal branches (Pybus & Harvey, 2000; Morlon *et al.,* 2011). The clustering of extinctions in old species-poor clades on an imbalanced phylogenetic tree could thus be a key indicator of potential large PD losses.

(4) Evolutionary distinctiveness

Tree imbalance may result in some species descending from long branches with few close relatives; such species have been termed evolutionarily distinct (also referred to as phylogenetically distinct or original; Pavoine *et al.,* 2005). An index of evolutionary distinctiveness (ED) thus quantifies how few relatives a species has and how phylogenetically distant they are. The first ED indices were based only on tree topology (May, 1990; Vane-Wright, Humphries & Williams, 1991; Nixon & Wheeler, 1992) and then, as phylogenetic
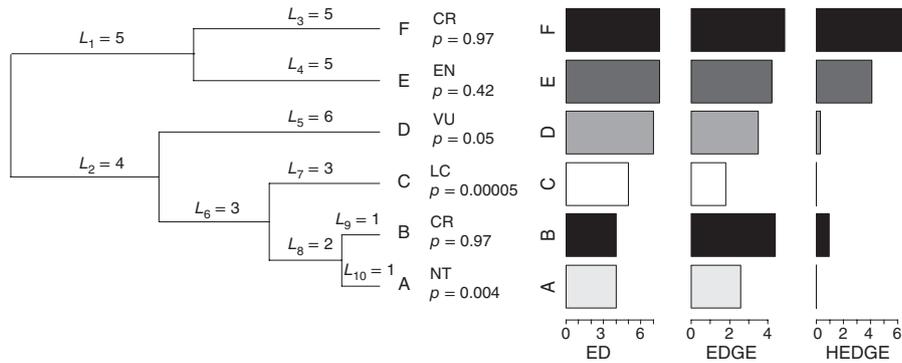
Fig. 1. Practical example for the calculation of phylogenetic indices. A phylogenetic tree composed of six tips (species) is given with branch length (in million years, My) above each branch. A threat status and a corresponding probability of extinction are assigned to each species. The classification is as follows, from most to least threatened: critically endangered (CR), endangered (EN), vulnerable (VU), near-threatened (NT), least concern (LC). This data set can be used to illustrate how phylogenetic diversity and its loss can be calculated. **PD and PD*loss*** [see Equations 1 and 2]: for the whole tree $PD = \sum_j L_j = 5 + 5 + 5 + 4 + 6 + 3 + 3 + 2 + 1 + 1 = 35$ My; if all threatened species classified as CR, EN and VU become extinct PD*loss* would be of $PD - (L_2 + L_6 + L_7 + L_8 + L_{10}) = 35 - (4 + 3 + 3 + 2 + 1) = 22$ My. **Expected PD and Expected PD*loss*** [see Equations 3 and 4]: Expected PD(*tree, proba*) $= \sum_j L_j (1 - \Pi_{dj} p_{dj}) = L_3*(1 - p_F) + L_4*(1 - p_E) + L_1*(1 - p_E*p_F) + L_5*(1 - p_D) + L_7*(1 - p_C) + L_9*(1 - p_B) + L_{10}*(1 - p_A) + L_8*(1 - p_A*p_B) + L_6*(1 - p_C*p_B*p_A) + L_2*(1 - p_C*p_B*p_A*p_D) = 5*(1 - 0.97) + 5*(1 - 0.42) + 5*(1 - 0.42*0.97) + 6*(1 - 0.05) + 3*(1 - 0.00005) + 1*(1 - 0.97) + 1*(1 - 0.004) + 2*(1 - 0.004*0.97) + 3*(1 - 0.00005*0.97*0.004) + 4*(1 - 0.00005*0.97*0.004*0.05) = 24.73$ My. Expected PD*loss* = PD − Expected PD = 35 − 24.73 = 10.27 My. The diagrams on the right-hand side of the figure represent scores taken by three phylogenetic indices for each species. We provide examples of calculations below for species A. **ED and EDGE** [see Equations 5 and 6]: ED(A) can be calculated as follows: $L_2/n_4 + L_6/n_6 + L_8/n_8 + L_{10}/n_{10} = 4/4 + 3/3 + 2/2 + 1/1 = 4$. EDGE scores are calculated with the formula: $EDGE = \ln(1 + ED) + GE*\ln(2)$. GE is a value of global endangerment defined using IUCN threat status, ranging from 0 (least concern) to 4 [critically endangered (see glossary in Appendix)]. Assuming that the GE score of a near-threatened species is 1, then $EDGE(A) = \ln(1 + 4) + 1*\ln(2) = 2.3$. On this tree species F ranks first as it has few close relatives and is highly threatened, species B which is also critically endangered ranks second. **HEDGE** [see Equation 7]: the HEDGE score of species A can be calculated as follows: $HEDGE(A) = p_A*(L_{10} + L_8*p_B + L_6*p_C*p_B + L_2*p_B*p_C*p_D) = 0.004*(1 + 2*0.97 + 3*0.00005*0.97 + 4*0.05*0.00005*0.97) = 0.012$. Again with the HEDGE measure species F ranks first but species B now ranks third and not second.

tree construction improved, branch length information was incorporated into new indices (Pavoine *et al.,* 2005; Redding & Mooers, 2006; Isaac *et al.,* 2007; Steel *et al.,* 2007). We focus on the most commonly used index: fair-proportion (Redding, 2003). This index is the sum, from a tip (species) to the root of a tree, of branch lengths divided by the number of tips the branch sustains. The ED of any species *i* according to the fair-proportion index is

$$ED_i = \sum_{j \in P(i, Root)} L_j/n_j \qquad (5)$$

where *P(i, Root)* is the set of branches on the shortest path from species *i* to the root of the tree, and n_j is the number of species descending from branch *j* (see Fig. 1 for an example).

The fair-proportion index was subsequently extended to identify species which are not only evolutionarily distinct but which also need conservation efforts using their IUCN threat status (Isaac *et al.,* 2007), low abundance (Cadotte & Davies, 2010), endemicity (Rosauer *et al.,* 2009) or small geographic range (Cadotte & Davies, 2010; Jetz *et al.,* 2014). These indices are still underutilized compared to the insights that each could bring to conservation biology. The most widely used extended ED measure is the EDGE index (Isaac *et al.,*

2007) which combines the ED_i (as defined above) of a species *i* with its IUCN threat status as follows:

$$EDGE_i = \ln(1 + ED_i) + \ln(2) * GE_i \qquad (6)$$

where GE_i is a value of global endangerment for species *i* defined using IUCN threat status, ranging from 0 (least concern) to 4 (critically endangered) (see glossary in Appendix, and Fig. 1 for an example). The EDGE index is the basis of a conservation program launched by the Zoological Society of London (ZSL), and can be calculated using easy-to-use software (Mesquite package tuatara, Maddison & Maddison, 2007). To date, mammals, amphibians, birds and reef coral species have been assessed through this method (Isaac *et al.,* 2007, 2012; Collen *et al.,* 2011; Huang, 2012; Jetz *et al.,* 2014). A shark EDGE assessment is nearing completion (EDGE, 2015).

However, the EDGE index has been criticized because, by treating each species as independent, it fails to take into account the true risk of extinction of internal branches in the phylogenetic tree. The extinction of a descendant of a branch may have no effect on this branch if related species ensure its persistence (the complementarity principle; Faith, 2008; Faith & Richards, 2012). Faith (2008) thus advised the use of
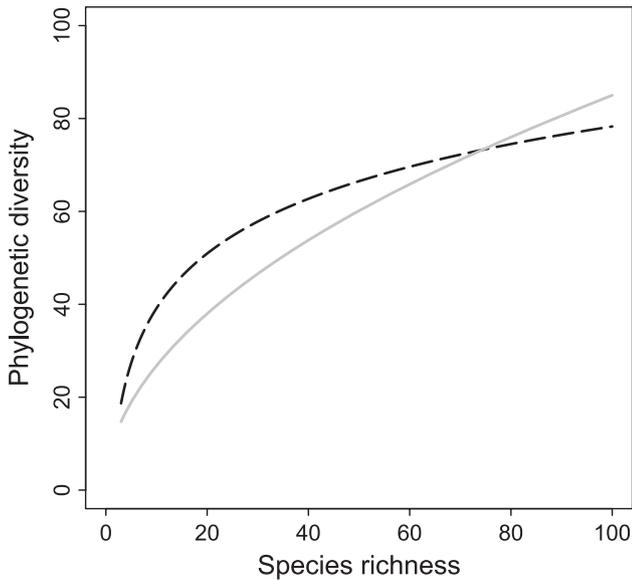
Fig. 2. Illustration of how the curve of the SR–PD relationship influences loss of evolutionary history, where SR stands for species richness and PD for Faith's (1992) phylogenetic diversity index. Two curves are proposed: the logarithmic curve is represented in black and long dash, the power law curve in grey. When species richness decreases the power law curve decreases faster than the logarithmic curve such that species extinctions translate to higher PD loss in the former.

a probabilistic framework for assessing evolutionarily distinct and imperiled species, which was subsequently developed by Steel *et al.* (2007), and termed 'heightened evolutionarily distinct globally endangered' (HEDGE). Although they presented two versions of HEDGE, we consider here only the version that is relevant for species extinctions. For any species i,

$$\text{HEDGE}_i = \sum_{j \in P(i, Root)} L_j \prod_{s \in C(j)} p_s \qquad (7)$$

where p_s accounts for the probability of extinction of species s; $C(j)$ denotes the set of species (including species i) that descend from a branch j; $\prod_{s \in C(j)} p_s$ is thus the probability that all species descending from node j become extinct; L_j, as defined above, is the length of branch j, and $P(i, Root)$ is the set of branches on the shortest path from species i to the root of the tree (see Fig. 1 for an example).

Although HEDGE considers the status of close relatives in addition to the focal species, HEDGE and EDGE may be strongly correlated (Steel *et al.*, 2007; Kuntner, May-Collado & Agnarsson, 2011), and therefore the choice of indices might have little impact in practice. This redundancy may be especially true for globally rare, high-priority species. For instance, little difference was found between the top 30 EDGE and HEDGE species among Carnivora and Cetartiodactyla (May-Collado & Agnarsson, 2011). Nevertheless, lower ranked species can differ greatly as patterns of shared risk among relatives become more important, and the indices differ in their robustness to

uncertainties (May-Collado & Agnarsson, 2011). Although the EDGE metric has been used more widely, we suggest that because of the differences between measures (Mooers *et al.*, 2008; May-Collado & Agnarsson, 2011; Martyn *et al.*, 2012) and the relevance of the complementarity principle to conservation, the use of HEDGE should be encouraged (Agnarsson, Kuntner & May-Collado, 2010; Kuntner *et al.*, 2011; Vélez-Zuazo & Agnarsson, 2011).

(5) When to use PD *versus* ED

PD is a property of groups of species whereas ED is the property of individual species. Several studies have shown that PD measured in an area is a useful proxy for a diversity of features important for maintaining ecological processes and for providing benefits to human societies (Forest *et al.*, 2007; Faith *et al.*, 2010; Srivastava *et al.*, 2012). ED may capture the amount of rare features that a single species possesses, and hence may point out biologically important species for conservation (Avise, 2005; Pavoine *et al.*, 2005; Redding, Dewolff & Mooers, 2010) or species performing distinct ecosystem functions (Redding *et al.*, 2010). PD, PD*loss* or Expected PD*loss* could thus first be used to prioritize the conservation of geographic areas, and then ED, EDGE or HEDGE indices could be used to target individual species, by identifying those which are the most vulnerable and phylogenetically distinct. The two sets of indices should be redundant if species with high EDGE and HEDGE scores were always in areas selected on the basis of their PD*loss* or Expected PD*loss* and conservation of areas was sufficient to protect all species within protected areas. However, those indices are more likely to complement each other because part of high EDGE and HEDGE species may be located in areas with low or moderate PD*loss* or Expected PD*loss*, for example, as was found for mammals and amphibians (Safi *et al.*, 2013).

Even though ED, EDGE, and HEDGE are calculated per species, it is possible to calculate the number of top-ED, top-EDGE, or top-HEDGE species that are located in an area as a criterion for their conservation. For example, Safi *et al.* (2013) prioritized conservation areas according to the top 5% EDGE mammal and amphibian species, while Jetz *et al.* (2014) ranked countries on the basis of the top 10% ED bird species they harbour. Rankings using this approach are partly influenced by species richness and partly by species' relative evolutionary distinctiveness and threats. A complementary approach is to sum the ED, EDGE, or HEDGE scores of all the species located in an area and compare these values to those estimated under a random spatial distribution of species (Vellend *et al.*, 2011; Safi *et al.*, 2013; Rosauer & Jetz, 2015). This latter approach allows consideration of all species in an area and removes the influence of species richness. Both approaches provide different scenarios for conservation priorities than those using PD, PD*loss* and Expected PD*loss*, and the predicted geographic patterns of ED and PD loss over the next decades differ importantly at global scales (Fritz & Purvis, 2010*a*; Huang *et al.*, 2011; Safi *et al.*, 2013).

Globally, PD*loss* and Expected PD*loss* quantify the loss of PD across all species in a clade. As ED species have few relatives, their loss is likely to result in large PD loss (Redding & Mooers, 2006; Vamosi & Wilson, 2008; Huang, 2012; Arregoitia, Blomberg & Fisher, 2013; Jetz *et al.*, 2014). However, large PD loss does not always result from extinction of high ED species as PD loss also depends on other factors such as threat clustering among related species and tree imbalance, as discussed above. Nee & May (1997) showed that under random extinctions on a coalescent tree a large portion of PD is maintained even when a large fraction of species is lost; species loss is thus far more rapid than PD loss. If species are lost in decreasing order of their ED scores, then the loss of PD would be more rapid, but only slightly. However, Redding *et al.* (2008) showed that species selection based on ED indices performs well in capturing PD, better than random species selection. Therefore, on average, the extinction of the most evolutionarily distinct species would result in higher loss of PD than if extinctions were random, in particular, this result was predicted for birds, corals, mammals and plants (Redding & Mooers, 2006; Vamosi & Wilson, 2008; Huang, 2012; Arregoitia *et al.*, 2013; Jetz *et al.*, 2014). PD scores (together with PD*loss*, Expected PD*loss*) and ED scores (together with EDGE, and HEDGE) thus complement each other, and should be used jointly to establish conservation priorities.

(6) Phylogenetic diversity and evolutionary distinctiveness as measures of functional diversity and distinctiveness

We previously alluded to the link between PD and functional diversity. Functional diversity represents the range of physiological, morphological and ecological species traits (see Cadotte, Carscadden & Mirotchnick, 2011, for a review of functional diversity measures). The shared evolutionary history between species can capture their functional similarity and, contrary to most direct indices of functional diversity, PD may capture the aggregate expectations from multiple traits (Faith, 2013). Consequently, PD has been used widely as a proxy of functional diversity, and because it theoretically encompasses a large number of traits it has been argued to reflect the potential to support ecosystem services better than species richness, functional richness or functional diversity (Cadotte, Cardinale & Oakley, 2008; Huang, Stephens & Gittleman, 2012*b*; Srivastava *et al.*, 2012). Conserving phylogenetic diversity may thus result in the protection of ecosystem services (but see Winter *et al.*, 2012; Kelly, Grenyer & Scotland, 2014). Forest *et al.* (2007) showed that in the Cape region of South Africa, designing protected areas to maximize floristic PD would also preserve the economic and medicinal services those species provide. Cadotte *et al.* (2008) found that PD was a significant predictor of biomass production in plant communities and that it enhanced ecosystem stability (Cadotte, Dinnage & Tilman, 2012). Furthermore, Faith *et al.* (2010) argued that PD additionally represented potential evolutionary processes that may provide additional services to ecosystem services, and the possibility of new and useful products, which they called evosystem services. Phylogenetic diversity loss may thus reflect the loss of feature diversity and of services which benefit human populations (Faith *et al.*, 2010). PD is therefore a useful index for practitioners when designing strategies to protect biodiversity and the benefits it provides (Faith, 2013). Similarly, ED species may have rare and unique physiological, morphological or ecological traits (Pavoine *et al.*, 2005) as it has been shown in mammals and primates (Redding *et al.*, 2010; Collen *et al.*, 2011). Consequently, preserving ED species preserves these unique features, and these may be important in the functioning of ecosystems. Yet, the correlation between phylogenetic distance and feature diversity is strongly debated (e.g. Winter *et al.*, 2012, 2013). Kelly *et al.* (2014) stated that, once a given threshold of evolutionary dissimilarity is exceeded, an increasing distance between two species in a phylogenetic tree does not result in an increasing dissimilarity in features. However, this latter example is based on a very specific model of trait evolution. More broadly, the expectation of a relationship between PD and functional diversity would be greatly advanced by evaluating a suite of evolutionary models.

In this section, we have focused on the most commonly used indices to measure and predict loss of evolutionary history, how they relate to each other and to other similar indices, and how they can be interpreted. In the next section, we review empirical studies to evaluate current knowledge of expected losses of evolutionary history, and compare differences among taxonomic groups.

III. CURRENT KNOWLEDGE ON THE LOSS OF EVOLUTIONARY HISTORY: A MULTI-TAXON PERSPECTIVE

At a global scale, assessments of PD and ED loss have focused on the few large phylogenies that are available for major vertebrate groups, such as mammals, birds, amphibians and a few infra-class groups such as corals and some plant clades. Here, we compare across taxa to examine which clades may be at risk of high PD loss and, which may be relatively robust.

(1) Mammals

(*a*) How much mammal PD could be lost at global and regional scales?

Mammals are probably the best-studied group in terms of phylogeny (Bininda-Emonds, Gittleman & Purvis, 1999; Bininda-Emonds *et al.*, 2007; Fritz, Bininda-Emonds & Purvis, 2009; Kuhn, Mooers & Thomas, 2011), threat status (Baillie *et al.*, 1996; Baillie, Hilton-Taylor & Stuart, 2004; Vié, Hilton-Taylor & Stuart, 2008), and taxonomy (Wilson & Reeder, 1993, 2005). As far as we are aware, Mammalia is the highest taxonomic group (class level) for which global spatial PD loss has been assessed. Mammal EDGE scores were also the first to be evaluated in the framework of the EDGE of existence program (Isaac *et al.*, 2007).

Most published studies considered PD loss in a scenario where threatened species [IUCN status Vulnerable (VU), Endangered (EN) and Critically Endangered (CR)] are driven extinct. In an early study under this scenario Purvis *et al.* (2000*a*), using taxonomy, found that more mammal genera are likely to be lost than predicted by a model of random extinction. Among the 1100 genera of mammals recognized in the *IUCN Red List* (Baillie *et al.*, 1996) an extra 85 genera would be lost in comparison to a model of random extinctions. Averaging the loss of genus to a 10 million year (My) loss of evolutionary history, the additional loss of PD would be approximately 850 My. More recently, Huang *et al.* (2011), using an updated mammal phylogeny from Fritz *et al.* (2009), showed that 14% of mammal PD could be lost if currently threatened species were driven extinct, but that this loss was not greater than if extinctions were random. Global mammal PD loss is thus probably less extreme than early studies suggested (Purvis *et al.*, 2000*a*). However, extinction risks differ among mammal clades and this has consequences on how PD may be lost in the future. For example, if all currently threatened species were driven extinct, PD loss would not be greater for carnivores than if extinctions were random in the phylogeny whereas it would be greater than random for primates (Purvis *et al.*, 2000*a*). At the family level, Diniz-Filho (2004) estimated that even the 78.4 My of PD lost in Felidae (34.5% of total Felidae PD) would not be greater than if extinctions were random. Jono & Pavoine (2012) used the probabilistic framework (Expected PD*loss*) to calculate the amount of PD expected to be lost for mammals, using probabilities of extinctions at 50 years (see Mooers *et al.*, 2008), and revealed that approximately 5% of extant mammal PD is expected to be lost worldwide within the next 50 years; again these losses are not greater than if extinction probabilities were independent of the phylogeny. However, this prediction also differs across orders: Chiroptera and Rodentia may lose less PD than expected from random extinctions whereas Cetartiodactyla, Diprotodontia, Perissodactyla, and Primates are likely to lose more PD (Jono & Pavoine, 2012).

Phylogenetic diversity loss across mammals has also been analysed spatially (Fritz & Purvis, 2010*a*; Huang *et al.*, 2011), and, similar to taxonomic losses, only a small proportion of regions would lose more PD than expected if extinctions were random. Nonetheless, regional differences can be dramatic. In particular Southeast Asia and Amazonia would lose more PD than expected under random extinctions, due to predicted extinctions of evolutionarily distinct species in Amazonia and because of phylogenetically clustered extinction risks in South Asia (Fritz & Purvis, 2010*a*; Huang *et al.*, 2011).

Recently, using a still underemployed index of phylogenetic endemism, Rosauer & Jetz (2015) identified 12 centres of mammal phylogenetic endemism – areas where PD is restricted to small ranges and thus of high conservation concern. These centres were located, in decreasing order of phylogenetic endemism, in Madagascar, Papua New Guinea and part of Indonesia including Sulawesi, parts of Mexico,

Sri Lanka, equatorial Africa, Borneo and Brunei, parts of Australia, Rwanda, Cuba, and Costa Rica. Madagascar, in particular, exhibited very high phylogenetic endemism given the level of species endemism and phylogenetic diversity. In a biogeographical context, phylogenetic endemism might reveal the role of persistent environmental barriers in isolating old mammal lineages with narrow ranges. However these centres may differ according to the mammal order considered as more narrowly distributed centres of phylogenetic endemism were found for example for Chiroptera (Rosauer & Jetz, 2015).

(b) Identification and localization of evolutionarily distinct and threatened mammal species

The extinction risks and evolutionary distinctiveness of mammals were initially quantified through the EDGE index by Isaac *et al.* (2007) and then updated by Collen *et al.* (2011) using newly available data from the third edition of *Mammal Species of the World* (Wilson & Reeder, 2005), the updated supertree of mammals (Bininda-Emonds *et al.*, 2007; Fritz *et al.*, 2009) and updated IUCN threat status (IUCN, 2008) (see EDGE, 2014). Safi *et al.* (2013) mapped the regions of the top 5% priority mammal EDGE species. They used mammal range distribution data from the IUCN and a combination of two approaches, the first based on the richness of the top-ranking species and the second identifying regions with higher accumulated ED and EDGE scores than expected by chance for the same number of species. Regions which harbour higher EDGE scores are within Southeast Asia whereas regions with higher ED scores are in East and South Africa. This result indicates that Southeast Asian mammals tend to be globally more threatened whereas mammals in East and South Africa may be less at risk but are globally more evolutionarily distinct. This study also demonstrates that endangered and evolutionarily distinct species represent a unique set of species different from those which are only evolutionarily distinct or only at high risk of extinction. Moreover, comparing the distribution of PD*loss* against EDGE values reveals Amazonia and Indonesia to be regions where both PD*loss* and EDGE scores are higher than expected by chance (Fritz & Purvis, 2010*a*; Huang *et al.*, 2011; Safi *et al.*, 2013). Yet, with the exception of these two regions, geographical patterns of PD*loss* and of the sum of species' EDGE scores (accumulated EDGE scores) generally differ from one another (compare Huang *et al.*, 2011; Safi *et al.*, 2013). Those differences emphasize that PD loss is not only driven by the loss of evolutionarily distinct species but also by other processes including the balance of the phylogenetic tree and the phylogenetic clustering of extinction risks, as discussed above.

Among mammals, evolutionarily distinct and threatened species were also evaluated separately in Primates (Redding *et al.*, 2010), terrestrial and marine Cetartiodactyla (May-Collado & Agnarsson, 2011), and terrestrial and marine Carnivora species (Agnarsson *et al.*, 2010; May-Collado & Agnarsson, 2011). Across these clades, it

was found that high-ED primate species are not more threat-ened than others (Arregoitia *et al.*, 2013), but Carnivora and Cetartiodactyla species with higher ED values are more likely to be in decline (May-Collado & Agnarsson, 2011). Causes for those declines are mainly hunting, illegal trade and high anthropogenic pressure on habitats (May-Collado & Agnarsson, 2011). However, as the trend for declines is more common in populations than for entire species, it would be interesting to investigate evolutionary reasons for population declines (May-Collado & Agnarsson, 2011, see also Section III.7).

(2) Birds

(a) *Recent and future bird PD loss*

Comprehensive global bird phylogenies have been built only recently (Jetz *et al.*, 2012). The first analyses examining loss of evolutionary history in birds were thus conducted using genetic-distance-based taxonomy (Sibley & Monroe, 1990, 1993). Purvis *et al.* (2000*a*) showed that among 2100 genera of birds, 38 extra bird genera would be lost compared to random extinctions. Von Euler (2001) estimated bird phylogeny by assuming that genetic distinctiveness between lineages in Sibley & Monroe's (1990, 1993) taxonomic classification was proportional to absolute time. Using this approach, he highlighted that the rate of losses of bird richness and phylogenetic diversity have been similar since 1600. Predictions of bird extinctions showed that the relative rate of PD loss in the future should decrease but remain high ($\geq 80\%$ of the species extinction rate). Von Euler (2001) also illustrated the negative effect of clustered bird extinctions: in a scenario of random extinction the relative rate of PD loss would decrease to 72–75% of species' extinction rate and even less in the case of a well-balanced tree (see Section II). Moreover, because data-deficient species were assessed as non-threatened, estimates of PD loss are likely conservative (von Euler, 2001). In a more recent analysis, Szabo *et al.* (2012) reported that 227 bird species have been lost through extinctions since 1500, and that these losses were disproportionately concentrated in species-poor families, indicating possible large past PD loss. Present-day patterns of taxonomic clustering are less pronounced, probably because susceptible taxa have already been lost, and because a higher proportion of threatened taxa are found on continents, where genera and families are more species rich. Notably, the main drivers of past extinctions in birds were human colonization and invasive alien species, which disproportionately impacted island communities, while current extinction risks are mainly from hunting and agriculture (Szabo *et al.*, 2012).

Few studies have analysed geographic patterns in bird PD loss although there is evidence that PD loss could vary among regions. Using Sibley & Monroe's (1990) genetic-distance-based taxonomy, Mooers & Atkins (2003) showed, for example, that Indonesia, which harbours 15% of the world's bird species, may lose 751 My of PD of which 288 My is not found anywhere else. Using the phylogeny of Jetz *et al.* (2012); Jetz *et al.* (2014) analysed the geographic distribution of ED bird species and suggested that prioritizing regions with high numbers of ED species restricted to small ranges could help in preserving PD globally. In particular, they showed that islands, such as Madagascar and New Guinea, as well as the Northern Andes, harbour a high proportion of geographically restricted and evolutionarily distinct species.

Although less widely used, other metrics have also been used to evaluate bird evolutionary history at risk. For example, Sobral *et al.* (2014) used mean phylogenetic distance (Webb, 2000) to show that the Brazilian protected area network did not capture bird evolutionary history adequately.

(b) *Evolutionarily distinct and threatened bird species*

In their assessment of bird evolutionary distinctness, Jetz *et al.* (2014) also considered extinction risks, comparing ED and EDGE scores of the 9993 extant bird species from a recent phylogeny (Jetz *et al.*, 2012). They found that 9 of the top 10 EDGE species were also among the top 10 ED species. However, the top ED bird species are not more imperiled, i.e. classified as EN and CR in the *IUCN Red List* (see Appendix), than other species, with only 4 of the 50 top ED bird species being either critically endangered or endangered (Jetz *et al.*, 2014). Geographic patterns of imperiled ED are unevenly distributed across the world with Indonesia, Brazil, New Zealand, Australia and the Philippines sheltering, in that order, the most distinct imperiled bird species (Jetz *et al.*, 2014).

(3) Plants

(a) *Contradictory predictions of plant PD loss at global and regional scales*

We only found one study which assessed plant (angiosperms only) PD loss at a global scale, probably because of the low resolution of large supertrees for plants and of the very high number of species (Vamosi & Wilson, 2008). The data used were an updated phylogeny from Davies *et al.* (2004) and the extinction status assessed in the 1997 and 2007 *IUCN Red List*. Under a scenario of extinction probabilities in the next 100 years, Vamosi & Wilson (2008) showed that extinctions were clustered in species-poor families which would lead to an extra loss of 1165 My of evolution compared to taxonomically random extinctions.

The pattern reported by Vamosi & Wilson (2008) conflicts with regional and local studies which did not find higher PD loss than expected under a model of random extinctions (Schwartz & Simberloff, 2001; Lozano & Schwartz, 2005; Davies *et al.*, 2011). Indeed, in regions such as the Mediterranean basin and North America, it was found that rare plant species, those with low abundance and considered vulnerable, were clustered in species-rich taxa (Schwartz & Simberloff, 2001; Lozano & Schwartz, 2005). A similar pattern was observed in the Cape region of South Africa where, additionally, extinction risks are

clustered in young and rapidly evolving lineages (Forest *et al.*, 2007; Davies *et al.*, 2011). Apparent contradictions in regional *versus* global assessments could be, in part, due to different phylogenetic resolutions, with more resolved phylogenies available for the former, and by the difference between regional rarity assessments and IUCN threat status (Vamosi & Wilson, 2008; Davies *et al.*, 2011). Davies *et al.* (2011) also argued that there could be two classes of globally threatened angiosperm, with different extinction processes in young and old lineages (see also Gaston, 1994). Species in old lineages might be remnants of once more-diverse clades, and thus prone to high extinction, which would result in large losses of phylogenetic diversity. By contrast, species in young lineages might be at high risk because they may not yet have had opportunity to expand geographically, but their extinction would result in little loss of phylogenetic diversity (Davies *et al.*, 2011). If this explanation is correct, it might not be surprising, therefore, that extinction risks in the plant phylogeny seem not to be explained by anthropogenic drivers alone (Davies *et al.*, 2011). Daru *et al.* (2013) even found a negative correlation between mangrove species extinctions and human pressure.

(b) *Few analyses of plant evolutionarily distinct species*

While there have been few studies exploring the evolutionary distinctness in plants at large scales, Vamosi & Wilson (2008) used an ED index developed by Pavoine *et al.* (2005), to show that angiosperm extinction risks were not clustered in ED species, but that the loss of currently threatened species could nonetheless result in high loss of PD. The relationship between extinction risk and evolutionary distinctness might depend on the spatial level of the analyses (global, regional, local) and on the habitat considered. For example, at a regional level, Daru *et al.* (2013) found a clustering of extinction risks in old and unique mangrove plant lineages whereas in the Cape flora, discussed above, extinction risks are clustered in young lineages (Davies *et al.*, 2011).

(4) Amphibians

(a) *Global and regional amphibian PD loss*

Amphibians face high extinction pressure mainly due to human impacts: 32% of the world's amphibians are currently threatened and 42% are declining in population indicating that future extinctions are likely (IUCN, 2008). However, the relative impacts of amphibian extinctions on amphibian PD are poorly understood, a problem compounded by the fact that amphibians are not well documented in species-rich areas (Whittaker *et al.*, 2013). As in other groups, some amphibian families are more threatened than others, which could endanger the future of whole clades (Baillie *et al.*, 2004; Corey & Waite, 2008). However, the distribution of extinction risks seems to be spread between both species-rich families and some species-poor and evolutionarily unique families (Baillie *et al.*, 2004). At a regional scale, Crawford, Lips & Bermingham (2010) found that from 33 to 61%

of original PD in a central Panama amphibian community could be lost due to a single epidemic disease caused by the fungal pathogen, *Batrachochytrium dendrobatidis*. However, Batista *et al.* (2013) showed that the extinction of all currently threatened species among the New World anurans would not lead to greater PD loss than if extinctions were random. Yet, once again predictions vary dramatically across regions with northern Mexico, the Brazilian Caatinga and the Atlantic forest expected to lose more PD than expected by chance.

(b) *Evolutionarily distinct amphibian species*

Isaac *et al.* (2012) reconstructed the phylogeny for 5713 amphibian species from which they derived EDGE scores (EDGE, 2014), later mapped by Safi *et al.* (2013). High ED and EDGE scores were observed in the large temperate zones of North America and Europe. However, some regions, particularly in Central and South America, show relatively lower ED scores than EDGE scores indicating that in these regions less evolutionarily distinct species face greater extinction risk. Interestingly, Howard & Bickford (2014) argued that data-deficient species may be more threatened than IUCN-assessed amphibian species. If true, this trend would indicate that amphibian evolutionary history is more threatened than currently assumed and could highlight new areas of risks. For example, Isaac *et al.* (2012) showed that assigning threat status to data-deficient species would identify a high number of new priority EDGE species.

(5) Corals

(a) *Coral PD loss*

Corals constitute a highly threatened group particularly sensitive to bleaching, disease and local anthropogenic impacts (Carpenter *et al.*, 2008). Despite their sensitivity, only a few studies have explored the impact of anthropogenic threats on coral PD. Huang & Roy (2013) reconstructed a phylogenetic tree for 975 scleractinian coral species and evaluated the loss of PD for different anthropogenic threats. They showed that the magnitude of PD loss would vary widely according to the threat considered. Notably, bleaching, disease and predation by crown-of-thorns starfish (*Acanthaster planci*) would remove a greater amount of PD than other threats such as a restriction or fragmentation of their range. In this order, PD loss is predicted to be higher than expected if extinctions were random as a consequence of the asymmetry of the phylogenetic tree and the phylogenetic clumping of some extinction risks (Huang & Roy, 2013).

As shown for other taxonomic groups, the amount of Scleractinia PD loss is likely to vary with the spatial units considered. In a more recent analysis using an updated phylogenetic tree, Huang & Roy (2015) showed that Johnston Atoll, East Hawaii, Pacific Costa Rica and Panama could lose more PD than expected if extinction risks were randomly distributed on the phylogenetic tree. However, the expected PD loss in species-rich regions would not be higher than under a model of random extinctions.

The magnitude of PD loss may also vary according to the phylogenetic scale considered. In one of the few studies to use a probabilistic framework to quantify Expected PD*loss*, Faith & Richards (2012) explored the impact of climate change on corals and found that Expected PD*loss* was low in comparison to species loss within the genus *Acropora*. However, at a finer phylogenetic scale, some parts of the tree showed clumped threats, resulting in higher Expected PD*loss*.

(b) Recent evaluation of evolutionarily distinct coral species

Coral reef EDGE species were assessed in 2011 by the ZSL EDGE program (EDGE, 2014), and again by Huang (2012) for 1293 species of the order Scleractinia. Interestingly, the top 30 rankings differed substantially between studies perhaps due to the use of a less-complete phylogeny in the EDGE program (Huang, 2012; Curnick *et al.*, 2015). Huang's (2012) ranking is topped by *Ctenella chagius* and two species from the genus *Orbicella*; top ranks also include three of the four critically endangered coral species. Species of high EDGE priority are found in Panama, Chagos Archipelago, Mauritius and La Réunion (Huang, 2012). Comparing ED scores with species' extinction risks, Huang (2012) found that the highest extinction risks were not clustered in the most evolutionarily distinct species; however the species which are the most susceptible to threats such as bleaching or crown-of-thorns starfish predation may be close relatives, and this might endanger deeper branches in the coral phylogeny.

Phylogenetic diversity and ED may not be the only dimension of coral evolutionary history at risk. Huang & Roy (2015) identified areas of high coral phylogenetic species variability (PSV), which measures the degree of disparity among species (see Section II.1; Helmus *et al.*, 2007). They showed that Pacific Costa Rica and Panama, Lakshadweep, Honshu, the Gulf of Martaban and Clipperton Atoll may lose a high proportion of their PSV if currently threatened species are lost. The reduction of PSV would mean that assemblages likely contain more functionally similar species.

(6) Fishes and other groups

The phylogenetic patterns associated with extinction risk are understudied in most non-charismatic groups. For example, in fish, which have been well studied for other ecological and evolutionary questions, only a few clades and species have been analysed in terms of relatedness and extinction risk. Magnuson-Ford *et al.* (2009) found that threatened marine rockfish species (genus: *Sebastes*) have significantly higher ED scores than species which are less vulnerable and are less intensively fished. In these more vulnerable species, high ED scores were associated with larger body size, which make those species more a target for fisheries. In coral reef fish species, D'agata *et al.* (2014) highlighted that human density may strongly impact PD loss. In particular, parrotfish PD (family: Scaridae) decreases dramatically above a threshold human density of 25 individuals per km^2. The ZSL EDGE program will soon assess rankings for sharks (EDGE, 2015). New advances in fish phylogenetics, especially within hotspot areas (Vélez-Zuazo & Agnarsson, 2011; Meynard *et al.*, 2012; Naylor *et al.*, 2012), would facilitate further studies of fish PD at risk.

(7) Synthesis and general trends in ED and PD loss

Knowledge of ED and PD loss is still poor for most groups as few taxa have been analysed, and even for better-known taxa most studies are incomplete due to limited data availability (Table 1). Despite these limitations, several important patterns in ED and PD loss emerge: (*i*) for many groups, if all currently threatened species were driven to extinction, the expected PD loss would be higher than if extinctions were random. However this pattern depends on the taxon, taxonomic level, and spatial scale (global, regional, local) considered. For example, higher than expected PD loss was inferred for Aves but not Mammalia, however, several orders within Mammalia, such as Primates, might still experience disproportionate losses. (*ii*) PD loss is often associated with clustered extinctions in the phylogenetic tree. This clustering has several explanations: closely related species could share traits that render them more sensitive to threats (Purvis *et al.*, 2000*b*); threatened species in currently species-poor clades might be remnants from previously species-rich clades that experienced high extinction in the past (Davies *et al.*, 2011); closely related species may tend to co-occur geographically and thus may be impacted by similar local threats (Jono & Pavoine, 2012). These explanations are not mutually exclusive and determining the causes of high PD loss requires detailed knowledge of species' spatial distributions and population trends. (*iii*) The loss of ED species could have a major impact on the tree of life as ED species capture high PD. Prioritizing species according to their ED scores could thus help to conserve PD efficiently, at least for certain taxa such as birds. However, irrespective of taxon, areas (regions or localities) with high PD may differ from areas with a high number of top-ED species. This suggests that both ED and PD should be considered when identifying conservation priorities.

This multi-taxon overview illustrates the strong taxonomic bias in our current knowledge on PD loss and evolutionarily distinct and threatened species (see online Table S1). This bias also has consequences for recommending conservation actions across spatial scales.

IV. APPLICATIONS: DO CONSERVATION ACTIONS PROTECT AND PRIORITIZE EVOLUTIONARY HISTORY?

Phylogenetic diversity and species losses may show different patterns – the extinction of a high number of species may not always result in high PD loss and the reciprocal is also true (Mace *et al.*, 2003; Diniz-Filho, 2004). Basing conservation actions on a silver-bullet strategy aimed at simultaneously capturing both of these biodiversity components may thus not be possible. Here we show how and to what extent

Table 1. Recently available phylogenetic trees used for PD and ED loss analysis

	References	Number of species	Dated?	Proportion of species/ taxonomy (%)	Taxonomy	Degree of completeness (% of resolved tips)	Method
Birds	Jetz et al. (2012)	9993	Yes	100	del Hoyo et al. (1992–2011) and Birdlife V3 (www.birdlife.org)	67	Supertree
Mammals	Fritz et al. (2009)	5020	Yes	92	Wilson & Reeder (2005)	50	Taxonomic lumping from Bininda-Emonds et al. (2007)
	Bininda-Emonds et al. (2007)	4510	Yes	99	Wilson & Reeder (1993)	47	Supertree
Carnivora	Nyakatura & Bininda-Emonds (2012)	286	Yes	100	Wozencraft (2005)	93	Supertree
	Bininda-Emonds et al. (1999)	271	Yes	100	Wozencraft (1993)	78	Supertree
Amphibians	Fritz & Rahbek (2012)	6111	No	95	Frost (2009)	13	Supertree
	Isaac et al. (2012)	5713	Yes	97	Frost (2007)	18	Supertree
	Pyron & Wiens (2011)	2871	Yes	42	Amphibia Web Database (amphibiaweb.org)	100	Molecular phylogeny; three mitochondrial and nine nuclear genes
Reptiles (squamates)	Pyron & Burbrink (2014)	4161	Yes	44	The Reptile Database (http://www.reptile-database.org/)	100	Molecular phylogeny; seven nuclear loci and five mitochondrial genes
Scleractinian corals	Huang & Roy (2013)	975	Yes	63*	Updated from Veron (2000); Wallace (1999); Gittenberg, Reijnen & Hoeksema (2011)	46	Supertree derived from the updated mitochondrial data set of Huang (2012)
	Huang (2012)	1293	Yes	83*	Updated from Veron (2000); Wallace (1999); Gittenberg et al. (2011)	36	Supertree constructed from mitochondrial DNA markers
Mediterranean teleost fish	Huang & Roy (2015)	1547	Yes	100	Huang et al. (2014)	46	Supertree
	Meynard et al. (2012)	372	Yes	62	Lasram & Mouillot (2009)	100	Molecular phylogeny; two nuclear and four mitochondrial genes
Sharks	Vélez-Zuazo & Agnarsson (2011)	229	Yes	45	Heinicke, Naylor & Hedges (2009)	100	Molecular phylogeny; one nuclear and four mitochondrial genes
Sharks and rays	Naylor et al. (2012)	595	No	50	Compagno (2005)	92	Molecular phylogeny based on one mitochondrial gene
Plants- angiosperms	Davies et al. (2004)	457 (families or higher taxa)	Yes	100	Angiosperm Phylogeny Group (2003)	93	Supertree
Mangrove species	Daru et al. (2013)	54	Yes	77	FAO (2007)	96	Molecular phylogeny based on two nuclear genes and one chloroplast gene
Cape flora	Forest et al. (2007)	735	Yes	78	Angiosperm Phylogeny Group (2003)	100	Molecular phylogeny from one plastid gene

*Percentage calculated from the taxonomy in Huang et al. (2014).

conservation actions have considered phylogeny, and if current actions aiming at species, ecosystem or habitat protection also adequately cover PD and ED species.

(1) How many conservation and prioritization actions focus on preserving PD and ED species?

In spite of the numerous calls to conserve PD and/or to identify zones of high evolutionary priority (Barker, 2002; Isaac *et al.*, 2007; Cadotte & Davies, 2010), little attention has been paid to evolutionary history by conservationists (Mace *et al.*, 2003; Sitas, Baillie & Isaac, 2009; Santamaría & Mendez, 2012; Safi *et al.*, 2013; but see some regional examples: Fay & Thomas, 1983; Faith & Baker, 2006).

The EDGE of Existence is one of the most active programs in placing phylogeny into a practical conservation framework. It aims at raising awareness of evolutionarily distinct and endangered species, provides support for the study of poorly known EDGE species, and has already led 12 projects for species conservation (EDGE, 2014). A benefit of the EDGE approach is that it can be used by conservationists to prioritize species based on both their degree of evolutionary distinctiveness and extinction status, and also to design reserves to protect key biodiversity areas that contain high-ranked EDGE species (Magnuson-Ford *et al.*, 2009; Agnarsson *et al.*, 2010; Safi *et al.*, 2013; Brooks *et al.*, 2015). Nonetheless, evolutionary distinctiveness is still rarely considered in practice. For example, Collen *et al.* (2011) found that 64 of the top 100 EDGE mammal species were given little or no attention by conservationists, and in amphibians, only 15% of the top 100 EDGE species received active protection (Isaac *et al.*, 2012).

In a recent paper, Winter *et al.* (2012) asked why evolutionary history is so rarely considered by conservationists. They suggested that arguments to preserve evolutionary history, including functional (Forest *et al.*, 2007) and evolutionary potential aspects (Mouquet *et al.*, 2012), suffer from a lack of empirical support (Diniz-Filho, 2004; Winter *et al.*, 2012; Davies & Yessoufou, 2013; but see Faith, 2013). Although the use of phylogenetic diversity as a proxy of functional diversity has been supported in some studies (Forest *et al.*, 2007; Cadotte *et al.*, 2008; Srivastava *et al.*, 2012), contradictory results have been found (Losos, 2008; Pavoine *et al.*, 2013). Winter *et al.* (2012) also criticized the 'jungle' of phylogenetic indices for which there is no clear guideline as to when and in which circumstances one should be used over another. Some indices have been defined without any clear indication of how they could be used in conservation. Different indices are nonetheless necessary because the information represented by phylogeny is multidimensional and any one measure can only capture a subset of these dimensions (Forest *et al.*, 2015).

Conservation biologists have to make compromises between ideal and practical measures of biodiversity. Recent advances, such as more readily available phylogenies and easy-to-use software (Rosauer & Mooers, 2013), should improve the use of phylogenetic diversity for conservation. However, there remains a need to investigate the value of different phylogenetic measures better, to present clear guidelines for the use of existing indices, to raise awareness and to enhance communication among and between conservationists and stakeholders (Winter *et al.*, 2012, 2013).

(2) Do current prioritization and conservation actions indirectly protect PD and ED species?

Phylogenetic diversity and species richness can sometimes be strongly correlated, therefore protecting species richness (SR) could also protect PD. Rodrigues *et al.* (2011) argued that, in the field of area-based conservation, a phylogenetic approach would not result in large differences in recommended actions because of the limited possible species assemblages and their corresponding PD. Several empirical analyses have supported the conjecture that SR provides a good surrogate to capture PD, most notably in birds and mammals (Rodrigues & Gaston, 2002; Rodrigues, Brooks & Gaston, 2005; Fritz & Purvis, 2010*a*; Rodrigues *et al.*, 2011). However, in other taxa, several studies have shown that prioritization and conservation actions based on SR do not always adequately capture PD (Tucker *et al.*, 2012; D'agata *et al.*, 2014). For instance, in the Cape biodiversity hotspot, protecting areas that maximize gain in SR would not maximize the gain in PD (Forest *et al.*, 2007; Tucker *et al.*, 2012). These contradictory results mean that it is not clear when SR could be used to design protected areas that would preserve PD. Indeed, the PD protected by current conservation areas is highly variable among groups and places. In Spain, for instance, Abellan *et al.* (2013) highlight that the PD of aquatic Coleoptera within National Parks was lower than under a random selection of species. In Europe, Zupan *et al.* (2014) demonstrated that networks of protected areas retain less PD for birds and mammals than if the areas were distributed randomly, but retained more PD for amphibians.

To address these contradictory findings, Tucker & Cadotte (2013) proposed a framework based on evolutionary and ecological processes that provided an estimate of when SR and PD should be congruent. Small pools of species, many polytomies, coarse scales, and old, highly divergent communities comprised of distantly related species should strengthen the congruence between SR and PD. By contrast, clusters of closely related species, recent divergence events and phylogenetic imbalance should weaken this congruence. Tucker & Cadotte (2013) suggested that the findings of high congruence reported by Rodrigues *et al.* (2011) might be in part explained by the numerous polytomies in the phylogeny used, spatial patterns of species occupancy, spatial autocorrelation in species' occupancy and rarity. One simple recommendation is that when the congruence between SR and PD is expected to be low, PD should be considered explicitly in conservation planning (Tucker & Cadotte, 2013).

Conservation areas currently capture ED poorly, and this is particularly true for ED at risk. Safi *et al.* (2013) reported that only 15.6 and 4.7% of the amphibian and mammal priority EDGE zones, respectively, intersected with currently protected areas. Similarly for birds, Jetz *et al.* (2014) identified

conservation gaps due to the concentration of high ED and imperiled birds, i.e. species classified as EN and CR in the *IUCN Red List* (see Appendix), outside species-rich areas. They found that 60% of the priority area for the conservation of the rarest evolutionarily distinct birds had less than 10% of their land protected (Jetz *et al.*, 2014). Among European tetrapods, amphibians were found to be the only group for which ED, but also PD (Zupan *et al.*, 2014), was captured better by the distribution of currently protected areas than if protected areas were distributed randomly (Thuiller *et al.*, 2015).

To tackle the lack of consideration of PD and ED at risk in protected areas, Brooks *et al.* (2015) proposed that PD should be included as a criterion in the definition of Key Biodiversity Areas (KBAs) – sites contributing significantly to the global persistence of biodiversity. KBAs would thus represent sites 'holding a threshold proportion of the compositional or phylogenetic diversity of species whose restricted ranges collectively define a center of endemism' (Brooks *et al.*, 2015, p. 4). In addition, Brooks *et al.* (2015) recommended consideration of EDGE in KBAs. Establishing such a framework would be a first important step to conserving Earth's evolutionary history.

Key issues relevant to preserving evolutionary history include: (*i*) the need to consider PD and ED directly in conservation and prioritization actions both at the area and species level and their interaction with species vulnerability or rarity; (*ii*) the failure of existing conservation and prioritization schemes to adequately capture PD or ED; (*iii*) differences in the patterns of loss of phylogenetic diversity and of other dimensions of biodiversity, such as species richness.

V. GAPS AND GOALS TO ENHANCE APPLICATION OF EVOLUTIONARY HISTORY IN CONSERVATION

(1) Phylogenetic bias and solutions

As highlighted in the previous sections, expected PD loss has been assessed for only a few taxa, representing a small proportion of the tree of life (Nee, 2005). Yet, thanks to recent methodological advances and to an increase in availability of molecular data, the number of phylogenies has increased dramatically and global phylogenies are now available for some species-rich taxa through, for example, the use of supertree or supermatrix approaches (for specific reviews of these approaches see Sanderson, Purvis & Henze, 1998; Bininda-Emonds, 2004; Roquet *et al.*, 2013). Supertrees usually incorporate only topological information from a set of previously published trees, but sometimes also include estimations of branch lengths. A main advantage of the supertree approach is that, by combining phylogenies rather than characters, they allow us to assemble together a larger portion of the global phylogenetic database (Bininda-Emonds, 2009). However,

supertree methods have a number of shortcomings (e.g. see Pisani & Wilkinson, 2002), and supertrees have been criticized because they are not connected directly to character data (Gatesy & Springer, 2004; Bininda-Emonds, 2004, 2009). The supermatrix approach is based on the joining of individual character data sets, including nucleotides, amino acids, and morphology. The main benefit of the supermatrix approach is thus the direct connection between the character data and the resulting phylogeny. The approach used to be limited because it was time-consuming, but recent optimized algorithms such as RAxML (Stamatakis, Hoover & Rougemont, 2008), have largely overcome this particular limitation. Today the main limitation of the supermatrix approach remains the large amount of missing data (Roquet *et al.*, 2013). Even with the rapid accumulation of molecular data and improvements in phylogenetic methods, complete phylogenies for species-rich groups are still scarce. Many existing trees are not fully resolved (Isaac *et al.*, 2012) (Table 1) and/or are poorly supported because of reconstruction methods and data uncertainties, or difficulties in estimating topologies (Gribaldo & Philippe, 2002) and incongruence between morphological and molecular estimates of divergence times (Isaac *et al.*, 2007). Here we review some biases in estimations of PD and ED that might be due to uncertainties in phylogenies and how they can be overcome.

(*a*) Effects of soft polytomies

Polytomies occur when a node supports more than two descendant branches. When polytomies reflect unresolved nodes rather than true evolutionary processes they are referred to as soft polytomies, and represent uncertainties about evolutionary relationships. The mammal (Bininda-Emonds *et al.*, 2007; Fritz *et al.*, 2009) and bird (Jetz *et al.*, 2012) phylogenies are 50 and 67% resolved, respectively, but some recent phylogenies for large groups, such as amphibians (Pyron & Wien, 2011) and reptiles (Pyron & Burbrink, 2014), do not contain polytomies (see Table 1). Soft polytomies can bias ED scores (Isaac *et al.*, 2007). They may cause only slight bias in measuring PD, as this index is not based on clade membership but on shared and unique branch lengths, but errors can be introduced indirectly from poorly inferred branch lengths. Indeed, Swenson (2009) demonstrated only a small effect of polytomies on PD but showed that the effect increases as the number of polytomies increases. Errors will be greater when polytomies are placed far from the tips because PD is more sensitive to basal polytomies than to terminal ones (Swenson, 2009). In addition, PD errors due to low phylogenetic resolution tend to increase with an increasing number of taxa (Swenson, 2009). Although different methods exist to resolve polytomies (Davies *et al.*, 2008; Kuhn *et al.*, 2011; Roquet *et al.*, 2013), their consequences on the selection of conservation priorities have been poorly explored. However, resolving polytomies using multiple methods or permutations can provide a sensitivity analysis to determine how PD estimates are influenced by polytomies.

(b) Missing tips or wrong placement

It is not always possible to place all the species of a study in a phylogeny, for example, because molecular data may be lacking (Roquet *et al.,* 2013). Other species can be very unstable in the tree (rogue taxa) and may have very different potential placements with similar support (Sanderson & Shaffer, 2002). Rogue taxa can result from incomplete data, or idiosyncratic evolutionary events resulting in atypical genetic sequences –for example polyploidization or release from stabilizing selection (e.g. Ren, Chin & French, 2014). Missing data can strongly affect evolutionary analyses and raise technical and philosophical problems for conservation planning (Isaac & Purvis, 2004). In particular, missing taxa may cause incorrect estimation of sister taxa and may overestimate divergence time (Gittleman, Jones & Price, 2004). However, Curnick *et al.* (2015) showed that imputing missing species from taxonomies in outdated coral phylogenies performed well, and led to ED scores that were closely correlated to the ED scores calculated from the most recent phylogeny (Huang & Roy, 2013). This correlation increased with data completeness (Curnick *et al.,* 2015). Moreover expert opinion was also found to be a valuable method to assess ED scores of missing species (Curnick *et al.,* 2015). As for PD loss, empirical analyses found that different placements of species did not greatly affect estimates of PD loss in amphibians, indicating that partially resolved phylogenies might give reliable estimates of PD loss (Batista *et al.,* 2013). In addition, some studies have shown that missing or wrongly positioned species do not substantially alter evolutionary distinctiveness rankings (Collen *et al.,* 2011; Isaac *et al.,* 2012). However, this may be true only if missing species are well dispersed in the phylogeny or if wrong placement occurs among closely related taxa within clades. By contrast, if missing species are numerous or phylogenetically clustered, ED rankings may change substantially.

(c) Branch length uncertainties

In the absence of sufficient molecular coverage, supertree methods (Sanderson *et al.,* 1998) are often the only option for generating large, more inclusive, phylogenies. However, estimates of branch lengths are often based on a restricted number of genetic markers, or inferred assuming some modelled branching process, and may not represent the true degree of relatedness (Roquet *et al.,* 2013). As stated above the resolution of polytomies may also cause poor branch length estimations. The effect of errors in branch lengths can be dramatic in estimated PD loss. Mooers *et al.* (2011) showed that some models underestimated the lengths of pendant edges and thus underestimated the impacts of species loss on PD (see also Pybus & Harvey, 2000; Morlon *et al.,* 2011). By contrast, Collen *et al.* (2011) found that errors in branch lengths had only little impact in the ranking of mammal EDGE scores. This might be due to the fact that EDGE scores in the ZSL EDGE program are calculated as the geometric mean of three sets of branches corresponding to the mean estimates of the branch lengths and to the upper and lower 95% confidence intervals around these dates (Isaac *et al.,* 2007).

Conservation biologists must be aware of the possible biases in phylogenetic data to understand the uncertainties in their models, estimate sensitivities to missing information and potentially to correct for them. Recent and future methodological advances as well as more available molecular data will help both to build more complete and reliable trees and reduce biases in derived metrics (Bininda-Emonds, 2009; Roquet *et al.,* 2013).

(2) Uncertainties and challenges in extinction probabilities

Lack of data about the threat status of numerous species may lead to large variation in estimates of PD*loss,* Expected PD*loss* as well as in EDGE and HEDGE rankings as has been shown for amphibians (Isaac *et al.,* 2012) and mammals (Purvis *et al.,* 2000a; Collen *et al.,* 2011; Jono & Pavoine, 2012). In addition, current IUCN threat status does not take into account 'latent' risks, i.e. species which are not yet assessed as threatened but that will probably be at risk in the future because of features which make them vulnerable (Cardillo *et al.,* 2006). The use of predictive models can help to identify those species with high 'latent' risk and better quantify extinction risks of non-assessed and data-deficient species (Cardillo *et al.,* 2006; Faith, 2008; Machado & Loyola, 2013). Many studies have searched for biological traits and environmental factors to explain and predict extinction risks (Cardillo *et al.,* 2008; Lee & Jetz, 2010; Isaac *et al.,* 2012; Machado & Loyola, 2013; MacKee, Chambers & Guseman, 2013). Musters, Kalkman & van Strien (2013) assessed threat status of non-evaluated species by comparing their traits with traits of already evaluated taxa. It may also be possible to quantify extinction risk using data on phylogenetic relationship and spatial proximity, for example, by employing generalized linear modelling approaches that incorporate both factors (Jetz & Freckleton, 2015) or by using methods of phylogenetic eigenvector regression (Diniz-Filho, de Sant'Ana & Bini, 1998) and spatial eigenvector filters (Diniz-Filho & Bini, 2005) to allow simultaneous modelling of spatial, phylogenetic and environmental information (Safi & Pettorelli, 2010).

Once the extinction status has been assessed for all species in a given clade at a given geographic scale, researchers most often explore extinction scenarios assuming the simultaneous loss of entire sets of species (for example all species classified as EN and CR, see Appendix) or less frequently the probabilities of extinctions of all species within a specified period of time. However, consideration of how extinction events happen through time suggests that the order in which species become extinct may be important. If species capturing a large amount of PD are lost first, then extinctions of few species could lead to faster loss of PD. On the other hand, if species capturing low PD go extinct first, it may minimize PD loss at a short timescale (Batista *et al.,* 2013). Moreover, in assessments of PD and ED loss, species extinctions are usually regarded

as independent events (Isaac *et al.*, 2007; Collen *et al.*, 2011; Jono & Pavoine, 2012), whereas species interact in their environment and the extinction of one species might result in co-extinctions or even extinction cascades. Dunn *et al.* (2009) argued that co-extinctions due to symbiotic relationships may be phylogenetically clustered which could further elevate loss of PD. Addressing impacts of correlated extinctions remains a major challenge. Witting, Tomiuk & Loeschcke (2000) proposed one method which accounts for the complete extinction processes of interacting species and allows for the optimization of PD conservation. However, its use with large data sets is precluded by the increasing number of parameters that have to be estimated (Witting *et al.*, 2000). Billionnet (2012) proposed an alternative method which determines the best allocation of resources to maximize expected PD under the assumption that conservation strategies are applied globally and that species extinctions are correlated. However, at a global scale, species interactions are challenging to consider as some species may interact in one place but not in others. Studies that account for spatial variation in dependent extinction probabilities or correlated extinctions and their impacts on predicted PD or ED loss are still scarce (but see Rezende *et al.*, 2007; Dunn *et al.*, 2009).

As discussed above, most studies of PD and ED loss have evaluated impacts of extinctions using species threat status. The *IUCN Red List* is of great value for conservation as it applies clearly defined criteria for assessing species extinction risks (Hoffmann *et al.*, 2010; Tucker & Cadotte, 2013). Moreover, the *IUCN Red List* is the only effort that attempts to assess extinction risks at a broad scale (Redding & Mooers, 2006). Nevertheless assessments also contain uncertainties. For example, information is biased towards some taxa and threat status assignments may be subjective (Possingham *et al.*, 2002; Mace *et al.*, 2008; Clements *et al.*, 2011). Further, it is not clear how to assign extinction probabilities to threat status (Collen *et al.*, 2011), and several important questions still need to be addressed: does a change in threat status reflect a continuous or nonlinear change in extinction probability? What time framework should be considered to assess species extinctions? Until these questions are resolved, extinction probabilities are extremely difficult to interpret and should be viewed as only crude approximations (Jetz *et al.*, 2014). For example, using models, Redding & Mooers (2006) estimated that a vulnerable species had a probability of extinction of 0.05 in 50 years but of 0.1 in 100 years; endangered species were estimated to have a probability of 0.42 to be extinct in 50 years but of 0.667 in 100 years. May-Collado & Agnarsson (2011) showed that rankings were significantly modified for both EDGE and HEDGE, sometimes dramatically, by the time frame considered. As suggested by Mooers *et al.* (2008), the appropriate time horizon for the probability of extinction should depend on the dynamics of the species and time frame for conservation actions, practitioners should need also to be aware of the uncertainties in extinction probabilities. Among the many possible models, the 'pessimistic' scenario, defined by Mooers *et al.* (2008) for which even 'least-concern' species have moderate probabilities of extinction, may better

reflect the ongoing biodiversity crisis (Kuntner *et al.*, 2011; May-Collado & Agnarsson, 2011). These uncertainties apply at both global and regional scales to local analyses of extinction risks.

(3) Assessing PD loss at the population level

Population decline is a prelude to species extinction, and with the ongoing biodiversity crisis numerous populations have already been lost with more local extinctions expected (Ceballos & Ehrlich, 2002; MacLaughlin *et al.*, 2002). Phylogenetic information at the population level has already been incorporated into conservation planning through concepts such as evolutionarily significant units (Ryder, 1986), management units (Moritz, 1994) and distinct population segments (Waples, 1991), which are based on population isolation and genetic distinctiveness. Recently, Volkmann *et al.* (2014) considered the possibility of extending evolutionary distinctiveness indices to populations. To do so, they used a method of phylogenetic networks (that allow for reticulate events, such as events where horizontal gene transfers are involved) to represent migration events and gene flows among populations. These authors then proposed algorithms equivalent to the fair-proportion index that quantify the genetic differentiation between populations as is currently done for species on phylogenetic trees. Applying this method to two species, *Strix occidentalis* and *Burramys parvus*, they were able to identify the most distinct populations and analyse their geographic structure. Equivalent population indices for phylogenetic diversity have also been proposed. For example, Minh, Klaere & von Haeseler (2009*a*) and Minh *et al.* (2009*b*) defined algorithms that maximized a measure of phylogenetic diversity, called split diversity (SD), on phylogenetic networks. Their method additionally corrects for phylogenetic uncertainty when estimating PD at the population level, and is able to identify the optimal set of species populations maximizing SD under given budget constraints. However, to our knowledge, this approach has rarely been tested on field data (but see Volkmann *et al.*, 2014), and SD scores could be improved by considering a range of possible species- and population-loss scenarios, for example, from the loss of one random population to the loss of all populations (Volkmann *et al.*, 2014).

VI. CONCLUSIONS

(1) Our knowledge of expected PD and ED loss is still limited, as only few taxa have been included in reconstructed phylogenetic trees (Nee, 2005). Yet recent studies on available data have increased our understanding about the potential losses of evolutionary history, particularly in charismatic groups such as mammals, birds and corals. Initial analyses have provided tools and established guidelines for pursuing phylogeny-based conservation strategies. We have also gained some general insights from this early body of work. For example, it is possible that at a global scale PD loss will not be much higher than if extinctions were

random (Huang *et al.,* 2011; Batista *et al.,* 2013), but that patterns may be very different across regions and taxonomic groups. Identifying in which areas and in which groups PD is most at risk will be important not only to preserve Earth's evolutionary heritage, but also its feature diversity and the ecosystem services it supports (Forest *et al.,* 2007; Cadotte *et al.,* 2011; Faith, 2013).

(2) Although a large variety of indices of phylogenetic diversity and evolutionary distinctiveness have been developed, few have been evaluated thoroughly using field and simulation studies, and fewer still have been implemented in conservation actions. A probabilistic extinction framework that considers species relatedness with regard to the preservation of deeper branches on the tree of life has many advantages, but is still rarely employed. We advise the increased use of such indices, for example, Expected PD and HEDGE.

(3) Expected PD and ED loss are measures that complement each other for conservation. Both measures fit within both an area-based and a species-based approach, yet practitioners rarely consider PD and ED in their efforts. Clear guidelines about the use of phylogenetic metrics, more empirical evidence linking PD to ecosystem services, and better communication between stakeholders may help bridge this gap between theory and application.

(4) Predictions of PD and ED loss strongly depend on data availability and quality, in particular, on species phylogenetic relationships and extinction probabilities. Important progress has been made, although challenges remain, including the construction of complete and resolved trees, the evaluation of threat status for data-deficient species, and the consideration of co-extinctions. We believe that such improvements will enable more complete and accurate predictions which will support the use of phylogenetic diversity and evolutionary distinctiveness in conservation practices.

VII. ACKNOWLEDGEMENTS

VIII. REFERENCES

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IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.
Table S1. Overview of current knowledge on PD loss and evolutionarily distinct and threatened species.

X. APPENDIX:

GLOSSARY

Phylogenetic tree: A phylogenetic tree is a diagram representing the evolutionary relationships between species and their ancestors. A tree can be rooted when a common ancestor is found for all species. In our study the species are represented by tips or external nodes, whereas ancestors are represented by internal nodes. Branches represent time or amount of evolution; **Supertree**: Supertrees are estimates of phylogeny assembled from sets of smaller estimates (source trees) sharing some but not necessarily all their taxa (Sanderson *et al.*, 1998); **International Union for the Conservation of Nature (IUCN) threat status**: The *IUCN Red List* is a program which evaluates the conservation status of plant and animal species. Eight conservation categories have been defined at a global scale according to specific threat criteria (IUCN, 2014). The classification is as follows, from most to least threatened: extinct (EX), extinct in the wild (EW), critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC). A last category, data deficient (DD), corresponds to taxa for which information is inadequate to make a direct, or indirect, assessment of its risk of extinction; **Probability of extinctions**: Phylogenetic diversity (PD) and evolutionary distinctiveness (ED) loss analyses sometimes require the conversion of each IUCN threat status as a probability of extinction, i.e. the probability that a species becomes extinct within a given period of time. The more threatened a species, the higher its extinction probability. The most commonly used probabilities of extinctions have been reviewed by Mooers *et al.* (2008) and reflect alternative extinction scenarios at 50, 100 and 500 years as well as a pessimistic scenario of extinction; **Tree imbalance**: The extent to which some branches lead to many species (or higher taxa) while their sister branches lead only to a few (Holman, 2005); **Polytomies**: Polytomies occur when a node supports more than two descending branches. When they reflect unresolved nodes rather than evolutionary processes they are called soft polytomies; **Evolutionary distinctiveness and uniqueness**: Evolutionary distinctiveness and uniqueness are two different measures, although they are sometimes confused. Evolutionary distinctiveness (ED) quantifies how few relatives a species has and how phylogenetically distant they are (Redding, 2003). Examples of evolutionary distinctiveness indices are fair-proportion (Redding, 2003; Isaac *et al.*, 2007), equal splits (Redding & Mooers, 2006) and originality (Pavoine *et al.*, 2005). Evolutionary uniqueness measures the unshared evolutionary history of a taxa, an example of an evolutionary uniqueness index is the pendant edge index (Altschul & Lipman, 1990); **Option value**: Biodiversity value that provides benefits and uses, often unanticipated, for future generations (Forest *et al.*, 2007; Faith, 2008; Faith *et al.*, 2010; Faith & Pollock, 2014).