

# Reconciling the concepts and measures of diversity, rarity and originality in ecology and evolution

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## ABSTRACT

The concept of biological diversity, or biodiversity, is at the core of evolutionary and ecological studies. Many indices of biodiversity have been developed in the last four decades, with species being one of the central units of these indices. However, evolutionary and ecological studies need a precise description of species' characteristics to best quantify inter-species diversity, as species are not equivalent and exchangeable. One of the first concepts characterizing species in biodiversity studies was abundance-based rarity. Abundance-based rarity was then complemented by trait- and phylo-based rarity, called species' trait-based and phylogenetic originalities, respectively. Originality, which is a property of an individual species, represents a species' contribution to the overall diversity of a reference set of species. Originality can also be defined as the rarity of a species' characteristics such as the state of a functional trait, which is often assumed to be represented by the position of the species on a phylogenetic tree. We review and compare various approaches for measuring originality, rarity and diversity and demonstrate that (i) even if attempts to bridge these concepts do exist, only a few ecological and evolutionary studies have tried to combine them all in the past two decades; (ii) phylo- and trait-based diversity indices can be written as a function of species rarity and originality measures in several ways; and (iii) there is a need for the joint use of these three types of indices to understand community assembly processes and species' roles in ecosystem functioning in order to protect biodiversity efficiently.

**Key words:** biodiversity measure, community assembly, conservation biology, distinctiveness, extinction risk, functional diversity, originality, phylodiversity, species abundance, trait-based diversity.

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## I. INTRODUCTION

One of the goals of the biological sciences is to identify ecological and evolutionary mechanisms driving community assembly that vary in space and time (Walker, 1992; Myers *et al.*, 2000; Pavoine & Bonsall, 2011). Indices of biological diversity (or biodiversity) are commonly used with this aim. Biodiversity has been defined in many ways. According to the Convention on Biological Diversity published in 1992, biodiversity means 'the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems'. We will focus here on ecological and evolutionary aspects of inter-species diversity.

Historically, species diversity was measured as a function of species number and abundance, and the concept of diversity was thus connected to those of species abundance, commonness and rarity (Patil & Tailie, 1982). The concept of rarity has generally been used in the last few decades in ecology to describe the low abundance, restricted range size or habitat specificity of a species (Rabinowitz, 1981). However, many researchers have claimed the need also to describe variety in species' attributes since species are not equivalent and exchangeable (Findley, 1973, 1976; Vane-Wright, Humphries, & Williams, 1991; Faith, 1992). For example, we can expect that a set of species with a crocodile, an emu and a lion has higher diversity than does a set with a lion, a cheetah and a domestic cat because the species of the first set are more distant in the tree of life than are the species of the second set and have very contrasting biologies. Indices of phylogenetic diversity and trait diversity have been produced (e.g. see Faith, 1992; Petchey & Gaston, 2002; Webb *et al.*, 2002; Hardy & Senterre, 2007; Helmus *et al.*, 2007; Villéger, Mason, & Mouillot, 2008; Pavoine & Bonsall, 2011). These measures of biological diversity synthesize the variety of species in terms of their different attributes: their phylogenetic relations (Vellend *et al.*, 2011; Tucker *et al.*, 2017) and their traits, including those that are qualified as functional (Petchey & Gaston, 2002).

Functional traits have been defined in the literature in different ways, notably as the traits that influence species' responses to environmental conditions (response traits) or that influence ecosystem properties (effect traits) (Lavorel & Garnier, 2002) and as 'the traits that are associated with species' ability to gain resources, disperse, reproduce, respond to loss and generally persist' (Weiher *et al.*, 2011, p. 2403). The diversity in species' functional traits was naturally named 'functional diversity' (Petchey & Gaston, 2002). As many studies used the term 'functional trait' to describe any measurable character of a species, we will consider here the diversity in species traits more generally, referred to as 'trait-based diversity' (Pavoine & Bonsall, 2011). The expression 'phylogenetic diversity' is used to describe both a concept of diversity in the evolutionary histories and relatedness among any set of taxa and a measure developed by Faith (1992) for conservation purposes. To avoid any confusion, we use 'phylogenetic diversity' to describe this concept.

In parallel, a few measures described the degree of isolation of a species in a phylogeny (May, 1990; Vane-Wright *et al.*, 1991; Nixon & Wheeler, 1992). More recent studies developed many alternative measures accounting for branch lengths leading to the focal species in dated phylogenetic trees (Redding, 2003; Pavoine, Ollier, & Dufour, 2005; Redding & Mooers, 2006; Isaac *et al.*, 2007; Redding *et al.*, 2008; Huang, Mi, & Ma, 2011; Redding, Mazel, & Mooers, 2014; Pavoine *et al.*, 2017). All these measures evaluate the originality of each species in a phylogenetic tree.

An issue of many general concepts used in science is that the word used to designate the concept also has a common use for a general audience and thus could have different meanings. Rarity and originality are no exception. In the most common sense, the words 'rarity' and 'rare' are usually associated with a low probability of encountering some specific entity. The term 'original' is also used to designate an unusual entity. When used in science, these words may refer to different definitions. In ecology, species rarity usually represents the low probability of encountering the species. Species' originality represents the low probability of encountering the species' biological characteristics (phylogenetic position or traits).

Several studies thus used the term ‘originality’ to describe a concept, a measure or both (e.g. Pavoine *et al.*, 2005; Buisson *et al.*, 2013; Redding *et al.*, 2014) to quantify the degree to which species may harbour or actually harbour rare characters. Since Webb *et al.* (2002), phylodiversity and originality have largely been used in ecological studies as proxies for trait-based diversity and originality, respectively. Recent approaches now recommend considering phylo- and trait-based measures as complementary: the former to reveal historical and evolutionary processes, and the latter to reveal ecological processes (e.g. Grandcolas, 1998; Pavoine & Bonsall, 2011; Kelly, Grenyer, & Scotland, 2014; Gerhold *et al.*, 2015; Mazel *et al.*, 2017).

Indeed, as ecology and evolution share a wide range of scientific questions about biodiversity, there is an increasing interest in inter-disciplinary studies. Ecologists try to understand how species interact with each other and with their environment as well as how these interactions can influence the assembly patterns of multispecies communities (e.g. Weiher, Clarke, & Keddy, 1998; Emerson & Gillespie, 2008; Cavender-Bares *et al.*, 2009). Evolutionary biologists work at different time scales and seek to understand the origins and history of biodiversity and its variation (e.g. Mergeay & Santamaria, 2012). At the frontier between these disciplines, studies in evolutionary ecology are developing frameworks to explain biodiversity patterns and dynamics, combining ecological causes of evolution and evolutionary implications in community assembly and ecosystem processes (e.g. Mouquet *et al.*, 2012). Such developments are now also needed to explain originality patterns. The use of phylogenies in community ecology, macroecology, and conservation biology reflects the shared recognition that accumulated evolutionary differences may explain trait variation and thus predict biological and ecological processes. Phylogenetic approaches have revolutionized these disciplines (Mouquet *et al.*, 2012; Tucker *et al.*, 2017).

Although the concepts of diversity, originality and rarity are fundamentally connected, they have often been treated independently in the past two decades in ecological and evolutionary studies. Even if attempts to bridge two of these concepts do exist (e.g. Pavoine *et al.*, 2005; Redding & Mooers, 2006), very few studies have tried to combine them all (e.g. Rosauer *et al.*, 2009; Cadotte & Davies, 2010). As a result, our three main objectives are: (i) to bring attention to the fact that a conceptual explanation of the links between the three concepts is still missing; (ii) to highlight the need to clarify some aspects of the complementarities between these concepts and their measurement; and (iii) to demonstrate why these three concepts should be used together in evolutionary, ecological and conservation studies.

## II. RARITY AND ORIGINALITY: TWO ENTANGLED CONCEPTS

Since the first ecological studies, one of the main challenges has been to determine the contribution of each species to

biodiversity. Those contributions are measured *via* species characteristics that can be expressed by species rarity or originality. Here, we provide an overview of the definitions of the rarity and the originality of a species. We highlight that these two words refer to the same core concept of being unusual and point out the importance of spatial scale for their definitions.

### (1) The concept of species rarity in ecology and evolution

The measurement of species rarity is relative, as its definition and units depend on the context, nature, quality and quantity of data, constraining every study to define what they mean by ‘rare species’ (Magurran, 2004; Hessen & Walseng, 2008). Many different definitions and viewpoints on rarity exist in the literature with biological aspects (e.g. abundance), threat aspects (e.g. extinction risk) and value aspects (e.g. ‘how special species are’) (Gaston, 1997). In a seminal paper, Rabinowitz (1981) proposed a typology of rare plant species by crossing three characteristics: local population size (high or low), geographic range (large or small) and habitat specificity (wide or narrow). She proposed seven forms of rarity by combining these three dichotomized criteria, excluding the case where a species has high local population size, large geographic range and wide habitat specificity. If local population size, geographic range and habitat specificity are all scarce (the most drastic form of rarity), then a species will be prone to be the most endangered and to extinction.

Because Rabinowitz’s (1981) classification requires a considerable amount of information for a given taxon that is often not available, many studies use only one criterion or a combination of two to determine species rarity (Kunin & Gaston, 1993). Most past studies have favoured a definition of rarity relying on abundance and range size (Gaston, 1997). However, even if a broad consensus has been reached on these two aspects of rarity, abundance and range size may be measured by many different approaches (Gaston, 1997). For example, the geographic range may be analysed in terms of extent of occurrence (EOO, total range extent even if unevenly occupied: Gaston, 1991; Kunin & Gaston, 1993), area of occupancy (AOO, amount of sites or grid squares inhabited: Gaston, 1991; Kunin & Gaston, 1993), or both. This distinction allows the identification of species that occur only in a restricted, localized area (low EOO) from species occupying a low proportion of the area within their otherwise large range boundaries (high EOO but low AOO) (Hartley & Kunin, 2003).

Regarding species abundance, Rabinowitz (1981) considered local abundance in terms of population size, which can be understood as the number of individuals in a population. In the context of biodiversity measurement, the number of individuals is also currently the most frequently used aspect of species abundance. Abundance, however, can be measured by different means (e.g. absolute and relative density, biomass, per cent cover), and these could also be included in species diversity analyses (e.g. Lyons, 1981).

In addition, the relevance of considering a single aspect of rarity as an indicator of all others is likely dependent on the phylogenetic and spatial scales considered. For example, although a positive correlation between species' range size and mean local population size at occupied sites has been reported by many studies across many different taxa and habitats (see Brown, 1984; Gaston, 1996), this correlation was sometimes found to be rather weak or even negative, particularly when the studied species were phylogenetically distant (Brown, 1984; Gaston, 1997; Johnson, 1998). Population size also varies depending on where in the range of the species it is measured, introducing a spatial contingency into defining rarity (Brown, 1984). Finally, part of this correlation may be due to sampling artefacts, as species with low local abundance are likely to be recorded from fewer sites than the number at which they actually occur (Gaston, 1997; Hessen & Walseng, 2008). Rarity is thus a multifaceted concept; and it is reasonable to argue that when data are available, several facets should be considered and compared (Gaston, 1997).

More recently, the concept of rarity has been extended to the functional and phylogenetic characteristics of species (Pavoine *et al.*, 2005). In his paper on the definition(s) of rarity, Gaston (1997) reported that taxonomic distinctness had been considered to define rare species. Pavoine *et al.* (2005) highlighted that phylogenetic distinctness may represent how rare a species' traits are, and Pavoine *et al.* (2017) reported that many recent studies measured distinctness directly from a finite set of traits (e.g. Mouillot *et al.*, 2013). Violle *et al.* (2017) subsequently proposed an expanded framework for rarity to study what they called 'functional trait rarity': a species is rare if it has a low abundance and distinct traits relative to the other species of an assemblage. They also stressed the need to study functional rarity from an evolutionary perspective by examining the phylogenetic signal of trait rarity. Overall, species rarity can thus be based on a variety of species attributes. Species' originality works with the phylogenetic and trait-based aspects of rarity.

## (2) The concept of originality or phylo- and trait-based rarity

Rarity is a concept widely used to determine a species' contribution to the diversity of a finite set of species. Nevertheless, fully to evaluate a species' contribution to phylo- and trait-based diversity, an additional measure of species characters is needed that can be made by means of species' originality. Here, we discuss the definition of species' originality, different types of originality measures and their link to abundance-based rarity.

The vocabulary employed to describe species' characters is continuously evolving and differs between evolutionary and ecological studies, leading to potential confusion when a term is employed without a clear definition or reference (Pavoine & Bonsall, 2011). Since the 1990s, various terms, such as 'originality', 'distinctness', 'distinctiveness', 'uniqueness' and 'isolation', have sometimes been used to refer to the same concepts but sometimes not. Thus, there is an inconsistency

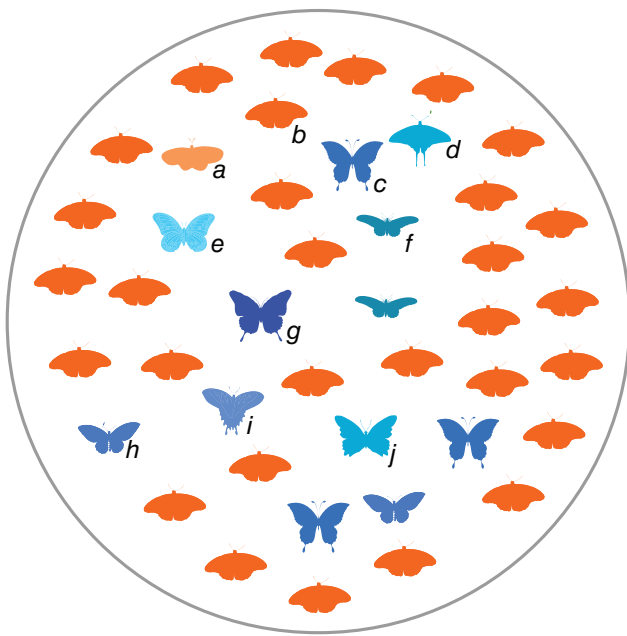
in the literature in the terms used to describe measures and concepts of species rarity and in how they should be used.

The term originality describes species' general rarity using characteristics linked to traits and phylogeny. Pavoine *et al.* (2017) defined originality as the rarity of species' characteristics in a given set of species, where a characteristic can be a position on a phylogenetic tree or the state of a functional trait. As recommended by Pavoine *et al.* (2017), we define 'phylogenetic originality' as synonymous with the terms 'evolutionary distinctiveness' (Isaac *et al.*, 2007), 'evolutionary isolation' (Redding *et al.*, 2014), 'phylogenetic rarity' (Winter, Devictor, & Schweiger, 2013) and 'phylo-based rarity'. A species without close sister species in a phylogenetic tree is likely to have high phylogenetic originality and thus a high contribution to phylodiversity (Redding *et al.*, 2008). In recent decades, particular attention has also been paid to species' functional traits that indicate species' roles in ecosystem functioning (e.g. Lavorel & Garnier, 2002; Mouillot *et al.*, 2008; Schmera, Erős & Podani, 2009; Buisson *et al.*, 2013; Mouillot *et al.*, 2013; Rosatti, Silva, & Batalha, 2015; Brandl *et al.*, 2016). The assumption that phylogenies indirectly comprise the evolutionary changes in species' characters may explain why the first originality approaches were inferred from phylogenetic trees.

These approaches were adapted to the analysis of species' functional traits, to measure what we hereafter refer to as 'functional originality'. We consider 'functional originality' a synonym of 'functional rarity' and 'rarity of functional traits'. More generally, we consider below 'trait-based originality' a synonym of 'trait-based rarity' and 'rarity of traits'. Hence, a species with very distinct trait values compared to those of other species is expected to have a higher contribution to trait-based diversity (Jarzyna & Jetz, 2016). Similar to abundance-based rarity, species' originality is relative to the values of the other species in a set. Following Pavoine *et al.* (2017), we define the uniqueness of a species as an unshared part of the species characteristics in a set. Strict uniqueness is thus an extreme case of originality in which a species does not share any of its characteristics. Finally, redundancy is antonymous with uniqueness and measures the number of shared characteristics of species. Therefore, originality is the full contribution of a species to the diversity of the set composed of species' unshared (uniqueness) and shared (redundancy) characteristics.

Commonness and rarity traditionally have been presented as the extremes of a gradient of the abundance-based rarity of species (Kunin & Gaston, 1993). Redundancy and uniqueness are the extremes of a gradient of species' originality, measured in terms of species' phylogenies and traits (Redding *et al.*, 2014). Some studies have analysed potential correlations between the two gradients, asking whether original species are rare in terms of abundance at different spatial scales (Mi *et al.*, 2012; Pigot *et al.*, 2016). Researchers found variable results showing that abundance-based rarity and phylo- and trait-based originality are not always correlated depending on the





**Fig. 1.** Theoretical illustration of the concept of abundance-weighted functional originality. Here, we consider an assemblage of butterflies. The drawings represent butterfly species of different shapes, for which colours are used to represent a functional trait: two species with similar colours have similar values for the trait. Species *a*, *d*, *e*, *g*, *i* and *j* are each represented by one individual; species *b* by 30 individuals; species *c* by three individuals; and species *f* and *h* by two individuals each. The species *a* and *b* are original because they are the sole species with shades of orange. The other eight species have different shades of blue and green. However, given that species *b* is very abundant (being represented by 30 individuals), the abundance-weighted originality of species *a* can be considered low, and if originality is measured at the individual level, instead of at the species level, then the originality of any individual of species *b* can be considered low.

spatial resolution of a study. Violle *et al.* (2017) combined both gradients to define what they called the ‘functional rarity’ of species (see Fig. 1 in Violle *et al.*, 2017): a species is functionally rare if it is both original and scarce. Their concept of functional rarity is not equal to our concept of functional rarity, which expresses the scarcity of species’ traits rather than the scarcity of the species themselves.

The measure of originality indeed can be weighted by abundance, leading to a third gradient of rarity where originality and abundance-based rarity are entangled. Along this gradient, a species is original in an assemblage if its characteristics are rare among the individuals of the assemblage (Fig. 1). Similarly, Violle *et al.* (2017) suggested an abundance-weighted measurement of functional trait distinctiveness, making it dependent on species scarcity (Box 2 in Violle *et al.*, 2017). Hence, originality (trait-based and phylo-based rarities) and abundance-based rarity are closely related concepts but use different types of data for characterizing species based on their abundance, traits or phylogeny (Fig. 2). More generally, other aspects of species

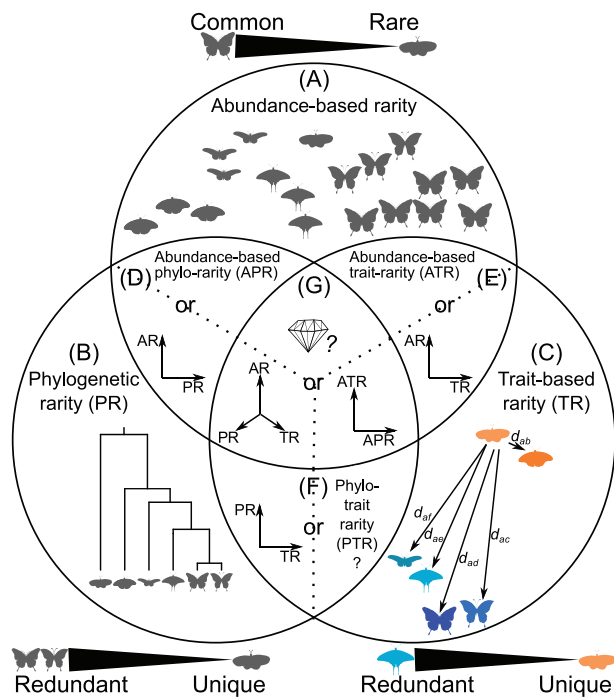
rarity could also be added to this framework, as, for example, the link between originality and range size has also been studied (Mouillot *et al.*, 2013; Grenié *et al.*, 2018).

### (3) The measurement of originality

The concept of species’ originality can be evaluated by different measures that rely on various types of data (see online Supporting information, Appendix S1). The first originality indices were developed on a tree structure and thus measured phylogenetic originality. However, they were applied to undated phylogenies ignoring the evolutionary time of change in taxa (May, 1990; Vane-Wright *et al.*, 1991; Nixon & Wheeler, 1992). Those indices used the number of internal nodes or the number of branches descending from each node to compute species’ originality. Unfortunately, they can hardly distinguish the originality between species from the same clade (Huang *et al.*, 2011; Redding *et al.*, 2014). These indices are useful when the branch lengths on a phylogenetic tree cannot be estimated.

With the improved access to dated phylogenetic trees, measures of phylogenetic originality have been developed that account for branch lengths. Several of these measures are derived from the Phylogenetic Diversity (*PD*) index of Faith (1992): the sum of branch lengths on a phylogenetic tree. Some of them are partly redundant, and their formulae are very similar [the indices of fair proportion (*FP*) (Redding, 2003), equal splits (*ES*) (Redding & Mooers, 2006) and evolutionary distinctiveness (*ED*) (Isaac *et al.*, 2007)]. Species with few relatives and deep terminal branches would be more original than species with many close relatives (Frishkoff *et al.*, 2014). Those indices can thus be used when one wants to know which species subtends most of the evolutionary history in a given set of species. According to Redding *et al.* (2014), technically, all tree-based indices of species’ originality combine two main aspects of originality: the average distance to another species on the tree [average phylogenetic distance (*APD*) (Redding *et al.*, 2014)] and the terminal branch lengths that connect the species to the rest of the tree [pendant edge (*PE*) (Redding *et al.*, 2008)]. Another framework of tree-based measures of species’ originality has been proposed that uses the genome evolution model of species characters called ‘character rarity’ (*CHR*; Huang *et al.*, 2011). Its advantage over other indices is that it incorporates models of dynamic processes, such as character changes and distribution along lineages during evolution. However, applications of this framework are still scarce.

With the accumulation of species’ trait information in large databases, a new type of study appeared that considered a limited number of traits (Violle *et al.*, 2007; Mouillot *et al.*, 2008; Hidasi-Neto, Loyola, & Cianciaruso, 2015; Ricotta *et al.*, 2016). As measures of originality already existed for phylogenetic trees, trait data were transformed into dendrograms (trees) to measure trait-based originality (Buisson *et al.*, 2013; Pavoine *et al.*, 2017). A new challenge appeared: how best to construct trait-based dendrograms from a finite set of traits and how to avoid the distortion of the original trait data (Petchey & Gaston, 2002; Mouchet



**Fig. 2.** Diagram illustrating the three types of rarity discussed herein. Each black circle represents one type of rarity. The areas where the circles cross designate studies where two or more aspects of originality are compared or combined. We illustrate each core concept with a theoretical data set, represented here by seven theoretical butterfly species. (A) Abundance-based rarity (AR) (as an illustration, it is here inversely related to the number of individuals of each species); (B) phylo-based rarity (PR) representing species evolutionary histories (here exemplified by a theoretical phylogenetic tree); (C) trait-based rarity (TR) reflecting species' trait dissimilarities. In C, butterfly colours represent species' traits. We illustrate the trait-based rarity (or originality) of species *a* by the dissimilarities *d* between this species and all the others. The gradient above the top circle represents the two extremes of AR: commonness and rarity. The gradients below the bottom left and right circles represent phylogenetic and trait-based originality, respectively, from redundancy to strict uniqueness. (D, E) PR and TR can be compared with AR using two-dimensional graphs. The phylogenetic and trait data can also be weighted by species' abundances, leading to abundance-weighted trait-based rarity (ATR) and abundance-weighted phylo-based rarity (APR) (see, e.g. Fig. 1). (F) Studies that analyse both TR and PR thus far have compared the two aspects by two-dimensional graphs. No mathematical measures have been developed that combine these two aspects, which could lead to phylo- and trait-based rarity (PTR). (G) The area where the three circles cross would permit identification of the rarest species. Depending on whether different aspects of species rarity are treated independently or are combined, such rare species could be defined as having high AR, TR and PR (identified by the three-dimensional plot), high ATR and APR (identified by the two-dimensional plot), or high abundance-weighted PTR (identified by the diamond). The red circles and question marks show where further research is critically needed to determine how and why phylogenetically and functionally original species emerged in the course of evolution and how this emergence has influenced species abundance.

*et al.*, 2008), as most traits do not possess any structured hierarchy. A common approach is to first calculate pairwise trait-based dissimilarities between species and then construct the dendrogram from these dissimilarities with a clustering algorithm. Numerous mathematical equations exist to calculate the dissimilarity between two species using various traits (Pavoine *et al.* 2009). Additionally, the choice of the clustering method influences the shape of the dendrogram and eventually influences trait-based originality values (Mouchet *et al.*, 2008; Maire *et al.*, 2015). Transforming trait values into dendrograms introduces the risk of distorting the information on traits (Pavoine *et al.*, 2017) but could be justified as a way to compare trait-based originalities to phylogenetic originalities for the same set of species. Thus, in theory, any of the phylogenetic tree-based originality measures can be applied to trait-based dendrograms.

The problem raised by deforming trait data when building functional dendrograms can be bypassed by using trait-based dissimilarity matrices. Originality measures have therefore been adapted to work with dissimilarity matrices. Indeed, the average (*AV*) and nearest neighbour (*NN*) indices, working directly with trait-based dissimilarities between species, are the alternatives of the tree-based *APD* and *PE* indices (Pavoine *et al.*, 2017; Violle *et al.*, 2017; see also Appendix S1). *AV* is the average dissimilarity to all other species, and *NN* is the lowest dissimilarity to all other species. By extension, these dissimilarity-based indices can, in turn, incorporate not only trait-based but also phylogenetic dissimilarities calculated, for example, as the sum of branch lengths in the smallest path that connects the two species on the phylogenetic tree or as the time since their most recent common ancestor (Pavoine *et al.*, 2017). Computing phylogenetic dissimilarities is useful for comparing equally the trait-based and phylogenetic originalities of the same set of species without taking the risk of distorting trait data.

Clustering methods have also been criticized in favour of the use of multidimensional space (Maire *et al.*, 2015). A multidimensional trait space is a geometrical space representing the distribution of species according to their trait values (Mouillot *et al.*, 2013). It can be constructed in several ways (see Appendix S1). The coordinates of the species projected as points along the axes of such a space could be used for measuring originality. For example, originality has been measured as the distance from a species to the centroid (mean position) of all species (Magnuson-Ford *et al.*, 2009; Buisson *et al.*, 2013). In theory, the multidimensional approach was created for the trait-based context but could also be applied to a phylogenetic space obtained, for example, with a principle coordinate analysis applied to phylogenetic dissimilarities between species (e.g. Sobral, Lees, & Cianciaruso, 2016).

Pavoine *et al.* (2005) introduced another family of originality measures by analysing the composition of theoretical species assemblages that would maximize an index of diversity. The first index of this family, the *QE*-based index (*Q<sub>b</sub>*), relies on Rao's quadratic entropy (*Q*) (1982). *Q* is an index of diversity equal, in our context, to the phylogenetic

or trait-based dissimilarity between two randomly selected species in an assemblage.  $Qb$  uses the abundance values that species should have to maximize the phylogenetic or trait-based dissimilarity between two randomly selected species (Huang *et al.*, 2011). Up to a certain degree, the more abundant the original species are, the more the diversity of a set is increased (Pavoine *et al.*, 2017). The hypothetical abundances of species that maximize  $Q$  thus reflect species' originality. Using the same approach, Pavoine *et al.* (2017) developed the  $Rb$  index using another index of entropy ( $R$  index) closely related to  $Q$ .  $Rb$  turned out to be similar, although not equal, to the  $AV$  index (the mean trait-based or phylogenetic distance to all other species), but it better discriminates original from redundant species. The  $Qb$  and  $Rb$  indices are discussed in detail in Section III.3.

Finally, a measure of originality based solely on species' phylogeny or traits does not account for other aspects of rarity such as population size or species range size. As shown in Fig. 2, species originality can be weighted by species abundance. Regarding phylogenetic data, Cadotte *et al.* (2010), for example, modified the  $FP$  index (see Appendix S1) to account for species abundance when species' originalities are calculated within a local community. To do so, at each tip (species) of a phylogenetic tree, they artificially added as many branches with a length of zero as there were individuals from the corresponding species in the local community. In other words, they weighted each terminal branch by the number of individuals it subtends. They then calculated originality using the  $FP$  index but replaced species with individuals, leading to their abundance-weighted evolutionary distinctiveness ( $AED$ ). Later, they modified their index, replacing individuals with populations or sites (Cadotte & Davies, 2010), leading to the biogeographically weighted evolutionary distinctiveness ( $BED$ ) index.

By doing so, Cadotte & Davies (2010) evaluated the originality of an individual or a population of a species. Other approaches have been proposed using different types of data. For example, Ricotta *et al.* (2016) proposed measuring the originality of a species as the abundance-weighted mean of the trait-based difference between this focal species and all other species in a set (weighted version of  $AV$  index). Laliberté & Legendre (2010) measured the distance in a functional trait space between a species point and the abundance-weighted centroid of all species points, which can be viewed as a measure of abundance-weighted originality. Other indices were also developed that weight originality by species' extinction risk (e.g. Steel, Mimoto, & Mooers, 2007).

#### (4) How should the originality measure be chosen?

Measures of species' originality are expressed by formulae, and their mathematical properties can influence the results and conclusions of a study. Several studies have compared some of these measures, seeking to establish the relations between them (Redding *et al.*, 2008, 2015; Huang *et al.*, 2011; Vellend *et al.*, 2011; Redding *et al.*, 2014; Pavoine *et al.*, 2017). According to these studies, some measures are more redundant than others in capturing species-specific

information and in their contribution to phylodiversity and trait-based diversity. Each type of originality measure has its own advantages and drawbacks. In general, tree-based indices would be influenced by tree topology (terminal and deeper branch lengths, unresolved nodes, root consideration), but trees without branch lengths fail to discriminate individual species.

If one wants to compare species' phylogenetic and trait-based originalities, then dissimilarity-based indices are a better choice than tree-based indices, as the former avoid the potential distortion of trait data. The use of a multidimensional trait space permits potential original species and their traits to be visualized. However, all axes need to be retained. For example, a common practice when measuring trait-based diversity is to apply a principal coordinate analysis to trait dissimilarities and then select the first few axes to calculate diversity, a constraint that may be forced by the mathematical properties of the diversity indices (e.g. Villéger, Mason, & Mouillot, 2008). This dimension reduction can hide some important species if their originalities are explained by traits on the non-visualized axes. Finally, originality indices, such as  $Qb$  and  $Rb$  (Appendix S1), predict species' originality expressed as the theoretical abundance of a given species that maximizes the diversity of a set. Note that, as originality is context dependent, its application to a set of two species would give equal originality to both species; the concept of originality is thus useful as soon as there are at least three species in a set.

#### (5) Spatial scale matters

Spatial resolution is essential in species' originality analyses that are relative to a reference set of species. Phylogenetic originality is usually measured at the level of an entire clade in an evolutionary context (e.g. Jetz *et al.*, 2014). This allows the identification of the most phylogenetically original species on Earth and the analysis of their biogeography (e.g. Safi *et al.*, 2013) and extinction risks (e.g. Isaac *et al.*, 2007). Such global phylogenetic originalities have been typically summed for all species present in a region to evaluate the worth of the region for conservation: how many globally original species occur in the region (e.g. Pollock, Thullier & Jetz, 2017), and how original are these species (e.g. Safi *et al.*, 2013; Jetz *et al.*, 2014)?

Such an approach has also been applied at local levels. In this case, phylogenetic originality was calculated within the species pool present at a regional (or continental) or global level. Then, these regional or global originalities were summed or averaged for all species within a local site to identify priority sites for conservation (e.g. Veron, Clergeau, & Pavoine, 2016) or to determine variations in the presence of original species among environments (e.g. Morelli *et al.*, 2018). Most of these studies on phylogenetic originality focused on the preservation of evolutionary history.

Another approach, which Redding *et al.* (2015) explored, is to calculate species originalities directly within a local site and to compare these local values with regional originalities of the species. They demonstrated that the correlation between



local and regional originality depends on the originality index used. Analysing Nearctic and Neotropical birds, they found that this correlation is spatially structured and may depend on the habitat, being notably higher in forested habitats. More studies of this type are needed to evaluate how local conservation projects based on local originalities could complement regional and global projects relying on large-scale originalities.

In contrast to phylogenetic originality, trait-based (especially functional) originality is rarely measured at the global level (see, e.g. Grenié *et al.*, 2018). Instead, it is usually evaluated at the regional and local levels, as species' characteristics are directly related to ecosystem functioning and depend mostly on field data (Da Silva, Silva & Batalha, 2012; Mouillot *et al.*, 2013; Rosatti *et al.*, 2015). Several of these studies have underlined the potential vulnerability of functionally original species (Mouillot *et al.*, 2013) and the negative impact of human disturbance on these species, with potential consequences on the sustainability of ecosystems (Rosatti *et al.*, 2015). However, these conclusions may depend on the taxa, traits and geographic areas analysed (Da Silva *et al.*, 2012; Brandl *et al.*, 2016).

Future studies could thus focus on determining and explaining scale-dependent patterns in both phylogenetic and trait-based originalities as local, regional and global originality scores may or may not be correlated depending on the processes that drive diversity patterns (Redding *et al.*, 2015).

### (6) Directions for future research on species' originality

We have shown that studies on species rarity recently have been improved by the addition of aspects of trait-based and phylogenetic originalities. Although many originality measures have been developed at the species level, they can be applied to other units of biodiversity, notably, to individual organisms (Pavoine *et al.*, 2017). For example, replacing trait-based dissimilarities between species with trait-based dissimilarities between individuals and replacing species points in multidimensional trait space by individual points allow all originality indices presented above to be transferred from the measure of the originality of a species to the measure of the originality of each individual (de Bello *et al.*, 2011; Violle *et al.*, 2012). For example, if information on estimated among-individual divergence is available on a phylogenetic tree, Cadotte *et al.* (2010, Appendix S2) proposed replacing species with individuals in the *FP* originality index to measure the originality of each individual. Thus, from a mathematical viewpoint, it is possible to apply all originality indices at an individual level and access the intraspecific variability of genes and traits. Applying such detail is limited by the scarcity of relevant data and by the relative cost of obtaining these data; however, this approach could provide more accurate results when trait variation is large within species.

Although we focused our review on inter-species diversity with aspects of phylo- and trait-based diversity, the concept of originality was also treated in genetics. For example, genetic

originalities can be calculated by replacing phylogenetic distances between species with genetic distances based on a genome evolution model (Thaon d'Arnoldi, Foulley, & Ollivier, 1998; Laval *et al.*, 2000; Huang *et al.*, 2011). Connecting these different fields of research could improve biodiversity analyses, allowing more continuous multiscale analyses, better to connect patterns to underlying processes in ecological and evolutionary studies.

In Section III, we demonstrate how the indices of originality relate to indices of diversity. We develop potential applications of originality indices with real case studies in Section IV.

## III. LINKS BETWEEN MEASURES OF DIVERSITY, ABUNDANCE-, PHYLO- AND TRAIT-BASED RARITY

A biodiversity measure is a calculation method expressed by a mathematical formula that allows specific values for the amount of variety in a biological system to be computed; in our case, these values are computed for a set of species. The oldest and most intuitive biodiversity measure is species richness, computed as the number of species (Magurran, 2004). Nevertheless, species richness has several drawbacks. First, it is strongly dependent on sampling effects: in a highly diverse community, the observed number of species may greatly underestimate the real number of species because species with very low abundance frequently will be absent from even very large samples (Lande, 1996). Second, it would give equal diversity to a region dominated by a single species with two rare species and a region with three species having even abundances (e.g. Magurran, 2004). Third, it does not include any information on species' traits and evolutionary histories. Fourth, it depends strongly on the definition of the concept of species (Gaston & Spicer, 2004; Groves *et al.*, 2017) and on taxonomic incompleteness (e.g. Delić *et al.*, 2017). To overcome these drawbacks, alternative diversity indices have been developed that include species' abundances, phylogenies and traits and thus incorporate various facets of species rarity. Diversity is measured at the level of the species set, while rarity and originality indices provide a value for each species that is linked to its contribution to the diversity of the set.

In the last two decades, the development of trait-based diversity and phylodiversity indices has expanded. This variety of indices is partly explained by the fact that one single mathematical formula cannot alone encompass all aspects of biodiversity in a set, especially phylogeny, functionality and abundance (Mason *et al.*, 2005; Mazel *et al.*, 2016). Several previous studies tried to define semantic frameworks for measurements of species' phylo- and trait-based diversities, in which they specified whether each measure of diversity was weighted by abundance data (e.g. Ricotta, 2007; Pavoine & Bonsall, 2011; Vellend *et al.*, 2011; Tucker *et al.*, 2017). Our aim here is not to review all mathematical indices of species' phylo- and trait-based diversities but to analyse a small set of

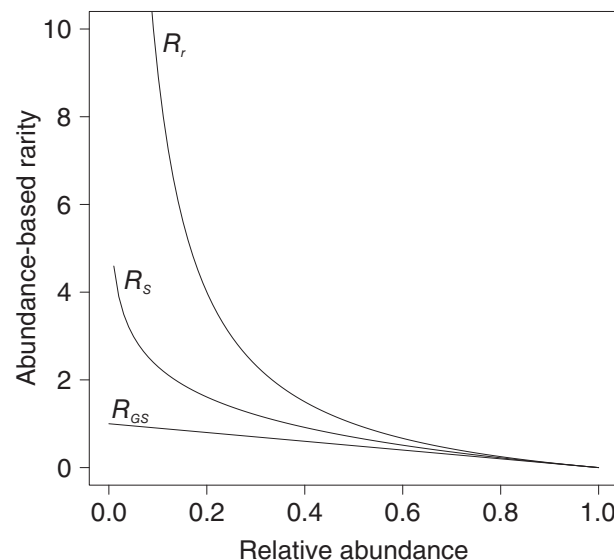


previous approaches for which we can try to distinguish the relative importance of abundance-based, phylogenetic and trait-based rarities. Although most of the diversity indices we discuss in this part were developed either for phylo- or trait-based diversity, all our reasoning could easily be adapted to be applied to both contexts.

### (1) Biodiversity as a mean of abundance-based rarities

Indices that relied on species number and species' abundances were named indices of species diversity. A myriad of such indices have been developed in the literature (e.g. Magurran, 2004). The most famous and most commonly used are the Gini–Simpson index (Gini, 1912; Simpson, 1949) and the Shannon index (Shannon, 1948). In Fig. 3, we provide Patil & Taillie's (1982) demonstration that species richness, the Shannon index, and the Gini–Simpson index can be written as the mean of species abundance-based rarity values. The three indices differ in their sensitivities to the presence of rare species. The most sensitive measure is species richness, as it gives equal importance to all species regardless of their abundance. The least sensitive is the Gini–Simpson index, which overweights common species relative to rare species (Lande, 1996). Thus, using abundance in indices of species diversity is actually a way to give a different value to each species. For example, giving the same value to each individual of a species forces us to give different values to the species, as species are represented by different numbers of individuals in a community. These well-known diversity indices illustrate that the first links between diversity measurement and rarity measurement date back to around 40 years ago, but these links concerned only abundance-based rarity. They did not refer to the phylogenetic or functional trait characteristics of the species.

The simplest approach for measuring aspects of phylo- and trait-based diversity naturally consisted of replacing species in the traditional diversity indices discussed above with trait-based or phylogeny-based entities. When the analysis of species' functional traits as an aspect of diversity measurement started to emerge in the ecological literature, the number of functional groups represented by the species in a community was the main measure of trait-based diversity (Petchey & Gaston, 2002). A functional group is a group of species united by their similarities in a given trait value or set of traits (Brandl *et al.*, 2016). The traditional diversity measures can be applied to the abundance of each functional group instead of to the abundance of each species (Hooper *et al.*, 2002). In that case, trait-based diversity can be related to the abundance-based rarity of functional groups. Such an approach could also be applied to clades in a phylogenetic tree, replacing functional groups with clades (Pavoine, Love, & Bonsall 2009). Although such approaches allow phylo- and trait-based diversity indices to be connected to abundance-based rarities, they do not connect them directly to measures of originality, that is, with trait-based and phylogenetic rarities.



**Fig. 3.** Functions of rarity associated with three traditional indices of diversity. A simple index to measure the diversity of a set is the number of species, or 'species richness'. A related index is the number of species minus one, for which an assemblage with only one species has null diversity. Indeed, the minimum value of many indices of species diversity is zero and is reached when a single species dominates the assemblage (its relative abundance is 1). Let  $S$  be the number of species in the assemblage;  $p_i$ , the relative abundance of species  $i$ ; and  $\mathbf{p}$ , the vector of species' relative abundances. Patil & Taillie (1982) emphasized that a richness-related ( $H_r$ ), the Shannon ( $H_s$ ) and the Gini–Simpson ( $H_{GS}$ ) indices can be written as follows:  $H_r(\mathbf{p}) = S - 1 = \sum_{i=1}^S p_i R_r(p_i)$ ,  $H_s(\mathbf{p}) = -\sum_{i=1}^S p_i \log(p_i) = \sum_{i=1}^S p_i R_s(p_i)$ , and  $H_{GS}(\mathbf{p}) = 1 - \sum_{i=1}^S p_i^2 = \sum_{i=1}^S p_i R_{GS}(p_i)$ , where  $R_r(p_i) = 1/p_i - 1$ ,  $R_s = -\log(p_i)$ , and  $R_{GS} = 1 - p_i$ . The functions  $R_r$ ,  $R_s$  and  $R_{GS}$  represent how rare a species is. In Patil & Taillie's (1982) framework, rarity means low abundance (for example, in terms of biomass or number of biological organisms).  $H_{CDT}$  entropy generalizes all these indices of diversity (Havrdá & Charvat, 1967; Daróczy, 1970; Tsallis, 1988). Its formula is  ${}^q H_{CDT}(\mathbf{p}) = \left(1 - \sum_{i=1}^S p_i^q\right) / (q - 1) = \sum_{i=1}^S p_i [{}^q R_{HCDT}(p_i)]$ . If  $q = 0$ , then the  $H_{CDT}$  index is  $H_r$ ;  $q$  tending to 1 gives  $H_s$ , and  $q = 2$  gives  $H_{GS}$ . The general form of the function of rarity associated with the  $H_{CDT}$  index is  ${}^q R_{HCDT}(p_i) = \left(1 - p_i^{q-1}\right) / (q - 1)$ . The sensitivity to rare species decreases with  $q$ . The figure shows how the functions of rarity  $R_r$ ,  $R_s$  and  $R_{GS}$  vary if  $p_i$  increases from zero to one.

### (2) Explicit link between originality and diversity indices

Because a myriad of species diversity indices have been developed since the 1970s, a myriad of phylo- and trait-based diversity indices could also be imagined by replacing species abundance in species diversity indices, such as the Gini–Simpson and Shannon indices, with species originality or abundance-weighted originality. This approach was adopted, for example, by Cadotte *et al.* (2010), Scheiner

(2012) and Scheiner *et al.* (2017). With such an approach, the diversity would be high if the number of species was high and if species' originalities were even. If originalities are weighted by abundance (Figs 1 and 2), then the diversity would be high if the distribution of abundance was imbalanced such that the most original species have the highest abundances (Cadotte *et al.*, 2010).

Ricotta (2004) previously proposed a different approach in which abundance and originality were treated as independent information on species (instead of using abundance-weighted originalities) and were combined into one measure of diversity. Further, he used taxonomy instead of a phylogeny, leading to taxonomic originality, where a species is original if there are no or relatively few species from the same genus, family, order, etc. We will see in Section III.3 that many diversity indices can also be considered as functions (e.g. sum, mean or abundance-weighted mean) of originality values, even if the indices were not developed with that goal in mind. The approach in which species' originality values and potential species abundances are combined in a mathematical formula is thus central to the measurement of biodiversity.

### (3) Most diversity indices only implicitly depend on species' originalities

Contrary to the few approaches presented in the previous Section III.2, species' originality, obtained through phylo- and trait-based rarities, was often only implicitly incorporated into measures of phylo- and trait-based diversity. We will show here that many of these measures of diversity can instead be seen as functions of species' originality or are largely linked in their formulae to a measure of species' originality, even if they were not developed explicitly as functions of species' originality.

#### (a) When diversity equals the sum or mean of originalities

Early on, Faith (1992) suggested replacing species in diversity measurements with features (or character states) of species. He then developed, as a proxy for feature richness, the *PD* index, which is the sum of branch lengths on a phylogenetic tree. His approach assumes that branch lengths reflect feature richness. Ten years later, Petchey & Gaston (2002) similarly proposed representing trait diversity as the sum of branch lengths on a trait-based dendrogram, an index named 'functional diversity' (*FD*). Two of the most used phylogenetic originality measures, the *FP* and *ES* indices (Appendix S1), can be written as additive decompositions of *PD* (Redding & Mooers, 2006; Isaac *et al.*, 2007). Thus, the sum of the originality values over all species in a set is equal to the *PD* of the set. If these originality indices, *FP* and *ES*, are calculated from a trait-based dendrogram rather than from a phylogenetic tree, then the sum of species' trait-based originality values over all considered species equals the *FD* index.

Two other commonly employed indices of community phylogeny, the mean pairwise distance (*MPD*) index

and the mean nearest taxon distance (*MNTD*) (Webb *et al.*, 2002), are means of species' originality values. The mean of the *APDs* (average phylogenetic distance to all other species) over all species in a set is equal to the *MPD* or the average phylogenetic distance between any two species in a set (Redding, Mazel, & Mooers, 2014). The minimum phylogenetic distance to another species is an index of strict uniqueness (see indices *NN* and *PE* in Appendix S1). Its mean over all species in a set is equal to the *MNTD* index used during the last two decades to detect the effects of competition in community assembly (Kraft *et al.*, 2007). Such reasoning could also be applied to trait-based dissimilarities between species. Indeed, indices such as *MPD* and *MNTD* were used early on by Findley (1973, 1976) to analyse the morphometrical diversity of bats. These indices do not integrate information on how abundant species are. However, other diversity indices can be seen as functions of abundance-weighted originalities.

#### (b) When diversity equals the sum or mean of originalities weighted by abundance

Regarding phylodiversity, the sum over all individuals of the *AED* value (individual's phylogenetic originality) of Cadotte *et al.* (2010) is equal to Faith's *PD* (phylogenetic diversity) of the species pool. Similarly, the sum over all populations of the *BED* value (the phylogenetic originality of each population of a species) of Cadotte & Davies (2010) is also equal to Faith's *PD* of the species pool. Furthermore, Cadotte & Davies (2010) suggested summing the *BED* values over all species in a site, leading to a measure of the relative originality of each site, and thus to its relative conservative worth within the studied regional area. This *BED* index was inspired by the index of phylogenetic endemism (*PE*) of Rosauer *et al.* (2009), which measures the spatial restriction of the evolutionary history in a site. *PE* is the sum of the ratios branch length/clade range for each branch of the phylogenetic tree pruned to retain only the species of a site. The clade range is the union of the ranges of all species descending from the branch. As such, *PE* combines notions of phylodiversity (if species were ubiquitous, *PE* would be maximal, which means that regional and local phylodiversity would be equal), range-based rarity (each branch length is divided by clade range), and originality (if a species with a small range descends from a long branch, it is likely to have a high contribution to *PE*). Cadotte & Davies (2010) developed *BED* to complement the concept of phylogenetic endemism with a measure that can be calculated at different levels: at the species, population, local-site or regional levels.

Pavoine *et al.* (2009) used clades (groups of all species descending from a specified ancestor) in a phylogenetic tree to obtain measures of phylodiversity. They divided a tree into time periods defined between two consecutive speciation events. They then applied the Havrda–Chavat–Daróczy–Tsallis (*HCdT*) diversity index (a generalization of the well-known species richness, Shannon and Gini–Simpson indices; Fig. 3) at each period, using the number of clades that descend from the period and their

relative abundances (the abundance of a clade is the sum of abundances of all its species). At the most recent period, clades are species. However, from the second period, at least one clade has more than one species. The associated index of diversity is equal to the length of the period (in million years of evolution) times the clade diversity (as measured by the *HCDT* index applied to clades). Such an approach brings an evolutionary dimension to traditional diversity analysis and has the advantage of considering species abundance when measuring the phylodiversity of a local community.

This approach is a generalization of the *HCDT* index for phylogenetic studies, which was at the core of the theory of Patil & Taillie (1982) to express diversity in terms of the mean of species' rarities (Fig. 3). In Patil & Taillie's (1982) theory, rarity was expressed as low abundance. In Table 1, we propose a new theory using the generalization of the *HCDT* index from Pavoine *et al.* (2009). In this new theory, rarity is measured as an abundance-weighted phylogenetic originality, and the measure of phylodiversity is quantified as the mean of these abundance-weighted originality values. This theory could also apply to trait-based diversity if a dendrogram is available.

Another currently widespread approach to measure biodiversity consists of defining trait-based or phylogenetic dissimilarities between species and taking their sum or their mean (e.g. Rao, 1982; Walker, Kinzig, & Langridge, 1999; Schmera, Erös, & Podani, 2009). The quadratic entropy index ( $Q$ ; Rao, 1982) is a diversity measure that can handle dissimilarities between species and species abundance. Shimatani (2001) demonstrated how to decompose  $Q$  into three underlying components: (i) the Gini–Simpson index (an index of species diversity that itself is a combination of species richness and species evenness (Fig. 3); (ii) the non-weighted mean of the (trait-based or phylogenetic) dissimilarities between species; and (iii) a measure of the balance between species' abundances and the (trait-based or phylogenetic) dissimilarities between species (which can be related to a covariance-like measure). Examining this decomposition reveals that  $Q$  increases with abundance evenness and with the number of trait-based or phylogenetic dissimilarities between species, and it increases when the most redundant species are rare and the most abundant ones have the highest trait-based or phylogenetic dissimilarities between them (Fig. 4).

We showed in Section III.1 that the first component, the Gini–Simpson index, can be viewed as a mean of abundance-based rarities and, in Section III.3a, that the second component, the non-weighted mean of the trait-based (or phylogenetic) dissimilarities between species, can be viewed as a mean of trait-based or phylo-based rarities. The third component, the balance component, relates abundance to trait-based or phylogenetic differences. More generally, if we measure the originality of a species as the abundance-weighted mean of the (phylogenetic or trait-based) dissimilarity to all species (including the species itself), then the mean of species' abundance-weighted originalities equals Rao's quadratic entropy (Ricotta *et al.*,

2016). Therefore, the quadratic entropy can be decomposed into independent values of abundance-based rarity and trait-based/phylogenetic originality or into more integrative values of abundance-weighted originalities. In Section III.3c, we also develop a distinct link between quadratic entropy and the notion of originality. We were thus able to extract multiple links between abundance-based rarity, originality and diversity indices from some of the mathematical formulae used to measure these concepts.

### (c) When species' abundances maximize diversity

To measure the trait-based diversity and phylodiversity of a species assemblage, Pavoine *et al.* (2005) and Pavoine *et al.* (2017) used the quadratic entropy index,  $Q$ , and a related index,  $R$ , with the following formulae:

$$Q = \sum_{i=1}^S \sum_{j=1}^S p_i p_j d_{ij} \quad (1)$$

$$R = \sum_{i=1}^S \sum_{j=1}^S \sqrt{p_i} \sqrt{p_j} d_{ij} \quad (2)$$

where  $p_i$  is the relative abundance of species  $i$  among  $S$  species and  $d_{ij}$  is a measure of phylogenetic or trait-based dissimilarity between species [see Pavoine *et al.*, 2005 for the use of  $Q$  with a restriction on dissimilarities, i.e. use of ultrametric dissimilarities]. As a measure of species' originality, the authors proposed the abundance that species should have in order to maximize the diversity (according to  $Q$  or  $R$ ) of a theoretical assemblage. The associated indices of species' originality, named  $Qb$  and  $Rb$ , thus correspond to the values of  $p_i$  that maximize  $Q$  and  $R$ , respectively, given that the trait-based or phylogenetic dissimilarities cannot vary (for details, see Pavoine *et al.*, 2017). The  $Qb$  and  $Rb$  indices illustrate that, up to a certain degree, trait-based diversity and phylodiversity are high if the most original species in a set (with the highest trait- and phylo-based rarities) have the highest abundance and thus the lowest abundance-based rarity (Fig. 5, Table 2). The indices  $Q$  and  $R$  thus reveal an important property that abundance-weighted indices of trait-based diversity and phylodiversity should have: a positive correlation between species' abundances and species' originalities tends to increase trait-based diversity and phylodiversity.

### (d) When diversity and originality depend on a multidimensional space

The previously discussed diversity indices either used a tree structure or used phylogenetic or trait-based dissimilarities among species directly. However, several diversity indices were also developed specifically for use in a multidimensional space, where axes reflect traits and points are species' positions according to their traits, as described in Section II.3. The distance of a species' point to the centroid of all points (mean position of all species from the reference set



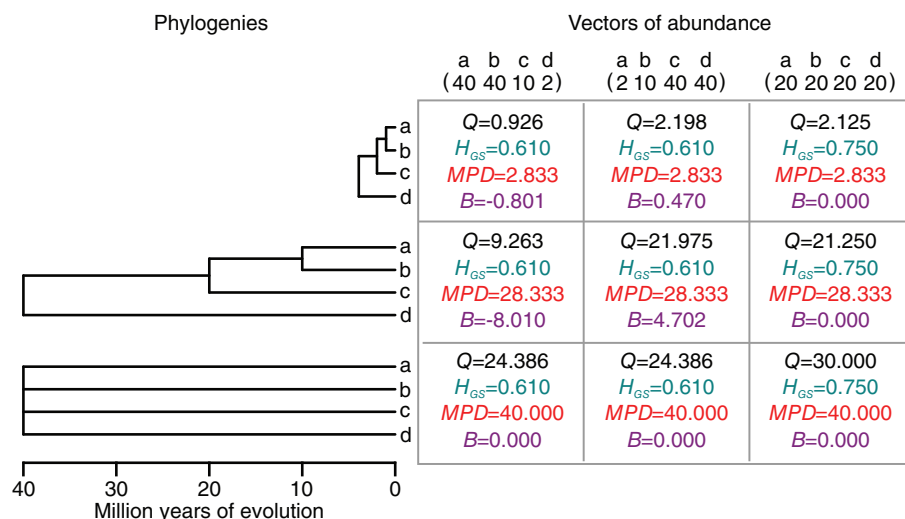
Table 1. Phylodiversity as a mean of phylogenetic rarities

	Function of diversity	Function of rarity <sup>a</sup>
General formula <sup>b</sup>	$I_q = \sum_{k=1}^K T_k \left[ \frac{1 - \sum_{b \in P_k} p_b^q}{q-1} \right] = \sum_{i=1}^S p_i O_q$	$O_q = \left[ \sum_{b \in C(i, \text{Root})} L_b \left( \frac{1 - p_b^{q-1}}{q-1} \right) \right]$
$q = 0^c$	$I_0 = PD - T = \sum_{i=1}^S p_i O_0$	$O_0 = \sum_{b \in C(i, \text{Root})} L_b \left( \frac{1}{p_b} - 1 \right)$
$q \rightarrow 1$	$I_1 = - \sum_{k=1}^K T_k \left[ \sum_{b \in P_k} p_b \ln(p_b) \right] = \sum_{i=1}^S p_i O_1$	$O_1 = \sum_{b \in C(i, \text{Root})} L_b \ln(1/p_b)$
$q = 2$	$I_2 = \sum_{k=1}^K T_k \left( 1 - \sum_{b \in P_k} p_b^2 \right) = \sum_{i=1}^S p_i O_2$	$O_2 = \sum_{b \in C(i, \text{Root})} L_b (1 - p_b)$

<sup>a</sup>The functions  $O_q$ ,  $O_0$ ,  $O_1$  and  $O_2$  represent the abundance-weighted originality of a species.

<sup>b</sup> $q$  is the parameter of the diversity index. It controls the importance given to species lineage abundances (from presence/absence if  $q = 0$  to the overweighing of the most abundant lineage if  $q \rightarrow \infty$ ).  $p_i$  is the relative abundance of species  $i$ .  $b$  is a branch of the phylogenetic tree.  $k$  is a period in the phylogeny,  $T_k$  is its length (time elapsed between two speciation events) and  $P_k$  is the set of branches that cross period  $k$ .  $K$  is the number of periods.  $C(i, \text{Root})$  is the shortest path from species  $i$  (tip) to the root of the tree.  $L_b$  is the length of branch  $b$ .  $p_b$  is the summed relative abundance of all species descending from branch  $b$ .  $S$  is the number of species. See Appendix S2 for a proof of this.

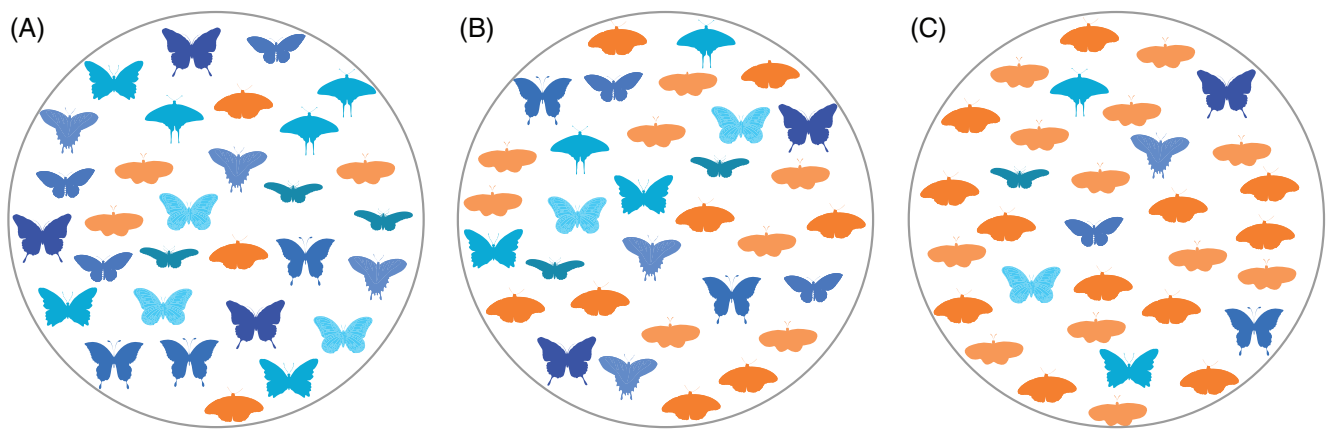
<sup>c</sup>For  $q = 0$ ,  $PD$  is the sum of branch lengths on the phylogenetic tree, and  $T$  is the height of the tree. The function of rarity is linked to the  $AED$  index of abundance-weighted phylogenetic originality in Cadotte *et al.* (2010): if  $p_i = N_i/N$ , with  $N_i$  being the number of individuals of species  $i$ , and  $N$  is the number of individuals across all species, then  $O_0 = AED \times N - T$ .



**Fig. 4.** The quadratic entropy ( $Q$ ) and its main components according to Shimatani (2001). Here, we considered nine theoretical examples formed by crossing three phylogenetic trees with species as tips and three vectors of species abundance. In each example, species are named a, b, c and d. We defined the dissimilarity  $d_{ij}$  between any two species  $i$  and  $j$  as the time since their first common ancestor. For example, in the top tree,  $d_{ab} = 1$  million years. The vectors of abundance give the number of individuals of each species in a community (the  $N_i$  values). We calculated the relative abundance of any species  $i$  as  $p_i = N_i / \sum_{i \in \{a, b, c, d\}} N_i$ . According to Shimatani (2001), the quadratic entropy ( $Q = \sum_{i, j \in \{a, b, c, d\}} p_i p_j d_{ij}$ ) is a function of the Gini–Simpson index of species diversity ( $H_{GS} = 1 - \sum_{i \in \{a, b, c, d\}} p_i^2$ ), the mean dissimilarity between two species ( $MPD = (\sum_{i, j \in \{a, b, c, d\}} d_{ij}) / (4 \times 3)$ ) and a balance component measuring a link between species' dissimilarities and species' abundances ( $B = \frac{1}{2} \sum_{i, j \in \{a, b, c, d\}} (d_{ij} - MPD) / [p_i p_j - H_{GS} / (4 \times 3)]$ ):  $Q = H_{GS} * MPD + B$ . The figure shows that  $B$  is negative if the most abundant species are closely related and that it is positive if the most abundant species are also the most dissimilar. It shows that  $B$  is zero in two cases: when the abundances are even and when the dissimilarities between species are even. The top and middle trees have similar topologies, but we multiplied branch lengths by 10 in the middle tree, which allowed us to emphasize that  $Q$ ,  $MPD$  and  $B$  are multiplied by any factor  $X$  (here, 10) if the dissimilarities between species are all multiplied by  $X$ .

in the space) is the main originality measure derived from this method (e.g. Magnuson-Ford *et al.*, 2009). Laliberté & Legendre (2010) proposed using the average distance to the centroid over all species as a measure of trait-based diversity (functional dispersion index,  $FD_{is}$ ). They defined two versions of this index: one unweighted (presence/absence data) and

the other weighted by species' relative abundances. In the unweighted version,  $FD_{is}$  values are high if species are all very original, i.e. have the highest distances to the centroid. In the weighted version, they used abundance-weighted distance to the centroid and thus abundance-weighted originality values. In this weighted version,  $FD_{is}$  will be high if the most original



**Fig. 5.** Theoretical illustration of the  $Q_b$  and  $R_b$  originality measures. Up to a certain degree, increasing the abundance of the most original species increases diversity. As in Fig. 1, we use different drawings of butterflies as theoretical species and differences in colours as indicators of functional/phylogenetic dissimilarities between species. Let us first consider a community in which each species is represented by three individuals (A). This butterfly community appears mostly blue. However, if we increase the abundance (in terms of number of individuals) of orange species, which are more original, then the colour diversity of the new community appears much higher (B). If we increase the abundance of orange species too much, then the butterfly community appears mostly orange, and the diversity decreases (C). The relative originalities of the species do not change from A to C if abundance data are discarded, but the relative abundance-weighted originalities of the orange species decrease, and those of the blue species increase from A to C. In other words, an orange species in C is original (species level), but an orange individual is not (organism level). The indices  $Q_b$  and  $R_b$  determine precisely the abundance that species should have to maximize diversity (see Table 2 for an example with the index  $R_b$ ).

Table 2. Illustration of the link between species' originality ( $R_b$ ) and the index of diversity named  $R$  in Pavoine et al. (2017)

Species <sup>a</sup>	Mass <sup>a</sup> (kg)	S1 (%) <sup>b</sup>	S2 (%) <sup>b</sup>	S3 (%) <sup>b</sup>	S4 (%) <sup>b</sup>	S5 (%) <sup>b</sup>
<i>U. arctos</i>	266.50	10	25	49.60	70	85
<i>V. vulpes</i>	5.60	30	25	16.61	10	5
<i>M. erminea</i>	0.90	30	25	16.89	10	5
<i>M. nivalis</i>	0.04	30	25	16.90	10	5
		↓	↓	↓	↓	↓
Body-mass diversity ( $R$ ) <sup>c</sup>		282	402	462	422	328

<sup>a</sup>We considered a theoretical set of four New World terrestrial carnivora species (*Ursus arctos*, *Vulpes vulpes*, *Mustela erminea* and *M. nivalis*) with estimates of each species' body mass obtained from Diniz-Filho & Törres (2002).

<sup>b</sup>We considered five case studies corresponding to five scenarios of species' relative abundances, from S1 to S5. S3 corresponds to the species' relative abundances that lead to the highest possible value for  $R$  and thus to the values of species' relative originalities ( $R_b$ ). This table shows that, up to a certain threshold (S3), increasing the abundance of the most different (original) species (here, *U. arctos*) more than that of others increases diversity.

<sup>c</sup>We consider the following formula for the index  $R$  applied to this data set:  $R = \sum_{i=1}^4 \sum_{j=1}^4 \sqrt{p_i} \sqrt{p_j} |M_i - M_j|$ , where  $p_i$  is the relative abundance given to species  $i$  in the set (for example, in terms of number of individuals), and  $M_i$  is the body mass of species  $i$  (in kg).

species have the greatest abundance, again highlighting that an inverse correlation between abundance-based rarity and originality increases diversity.  $FDi$  is closely related to quadratic entropy (their mathematical formulae are very similar, as shown in Pavoine & Bonsall, 2011).

Villéger, Mason, & Mouillot (2008) developed indices to describe three facets of trait-based diversity: functional richness, functional evenness, and functional divergence. None of these indices can be divided into continuous values of species' originality. However, they also implicitly depend on the notion of originality. The first one, functional richness ( $FRic$ ), is the volume of the convex hull of species' points (minimal space that includes all species' points) in the trait-based multidimensional space. From a certain

viewpoint, one can consider that the most original species support the convex hull, with less-original species lying inside the convex hull. The second index, functional evenness ( $FEve$ ), increases if species and their abundances are evenly distributed in the multidimensional space delimited by the most original ones (those at the vertices of the convex hull). The third index, functional divergence ( $FDiv$ ), is linked to the mean distances from species' points to a centroid, but this centroid is measured differently than in the  $FDi$  index developed by Laliberté & Legendre (2010). Villéger, Mason, & Mouillot (2008) considered only the species at the vertices of the convex hull, i.e. from a certain viewpoint, the most original species when finding the centroid coordinates. Their  $FDiv$  index relies on the difference between the

unweighted mean of the distance to the centroid and the abundance-weighted mean of the distance to the centroid. In this index, Villéger, Mason, & Mouillot (2008) did not use species abundance to define the centroid – originality and abundance-based rarity are thus treated separately – while Laliberté & Legendre (2010) did use species abundance to define the centroid of all points, thus obtaining an abundance-weighted originality.

$FDiv$  increases if the most peripheral species have the highest abundances (Fig. 6). Here, we can again observe an inverse link between abundance-based rarity and originality, if we consider the most peripheral species as the most original. However,  $FDiv$  is not an index of biodiversity: we identified that  $FDiv$  can be close to its maximum when a single species dominates in abundance, with the remaining species having residual abundance; for this to happen, this dominant species must be at the largest distance to the centroid of the convex hull (Fig. 6B). Diversity means variety. If intraspecific variations are omitted and if an assemblage is composed of a single species, then any measure of the trait diversity of the assemblage must attain its minimum. Similarly, if intraspecific variations are omitted and if a single species represents almost all the abundance of an assemblage, then, whatever its trait values, the trait diversity of the assemblage is bound to be close to the minimum, whereas in contrast,  $FDiv$  may be close to its maximum.  $FDiv$  thus describes a particular pattern of community functional compositions but is not an index of trait-based diversity.

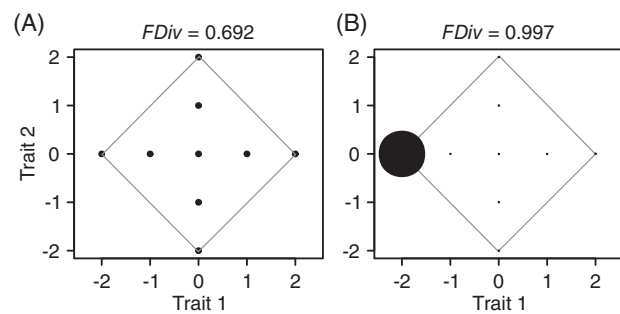
#### IV. RECONCILING THE DIVERSITY, RARITY AND ORIGINALITY CONCEPTS FOR THEIR USEFUL APPLICATIONS

In the previous sections, we have discussed the definitions of the concepts of rarity and originality. We have also demonstrated that fundamental links exist in the definition and in the measurements of the concepts of rarity, originality and diversity. Now we highlight, through many examples, how these concepts can be explored conjointly for the benefits of ecology and evolution.

Every organism is a product of its own individual evolutionary history and is shaped by the environmental conditions and interactions experienced by its ancestors (Cadotte & Davies, 2016). We observed that originality and rarity indices are designed to capture species-specific features, while diversity indices are applied to sets of species. Diversity, rarity and originality thus complement each other in describing the amount of biological variability in species assemblages. Here, we briefly develop some examples of fields where diversity, rarity and originality indices can be applied and underline the importance of their joint analysis.

##### (1) Understanding the evolutionary emergence of species' originality

No approaches have been developed thus far to analyse how trait-based and phylogenetic aspects of originality

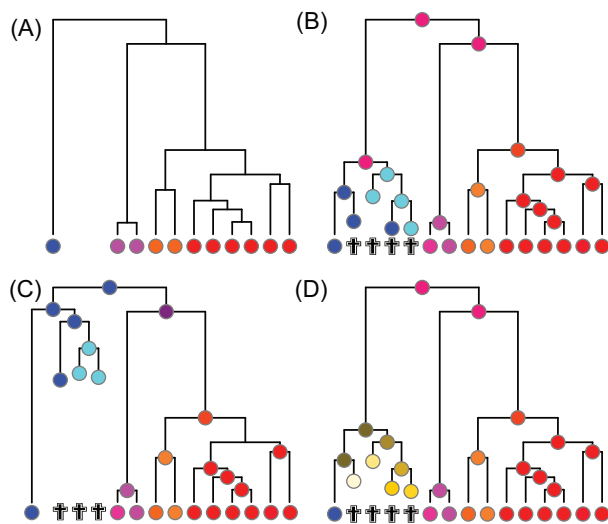


**Fig. 6.** A key property of the functional divergence ( $FDiv$ ) index of Villéger *et al.* (2008) is that it tends to the maximum (equal to 1) when a single original species dominates in abundance. Here, we use the theoretical example of Villéger *et al.* (2008) including a set of nine species (points) characterized by two traits (axes). The traits (positions in the functional space) of the nine species are similar in A and B. Each species is represented by a point, the size of which is proportional to the species' abundance. In A, species have even abundances: the abundance of a species equals  $1/9$ . In B, one of the species dominates in abundance: it has a relative abundance of 0.99, while other species have relative abundances equal to 0.00125 (given that  $0.99 + 0.00125 \times 8 = 1$ ). The convex hull of the set of points is represented by the grey square in the two panels, and the centroid of its vertices is simply its centre. As noted in the two panels, the  $FDiv$  value in case A is lower than that in case B, where the value of  $FDiv$  is close to the maximum (1). These relations hold because the dominant species is one of the original species located on the convex hull of all points, and this dominant species is one with the largest distance to the gravity centre of this convex hull.

are entangled. Often researchers have measured the two aspects independently and have then searched for statistical correlations between them (two-dimensional graph in Fig. 2F). A given species could have evolved, for example, a specific set of characteristics that are individually rare or rare in their combination. Such a species could be both phylogenetically original and original according to its traits, in which case the overall originality reflects the history of a species in terms of trait evolution and species relations [the phylo-trait rarity (PTR) case in Fig. 2F]. The correlation between phylogenetic and trait-based originality is expected if traits have a phylogenetic signal, which means that closely related species tend to share similar values of traits, while distantly related species tend to have different traits.

Inferring that a species is original both in the phylogeny and according to its traits requires observing a particular pattern on a phylogenetic tree (Fig. 7A). However, we must remember that past species extinction could blur the phylogenetic history of a trait state by suppressing many species displaying it (Fig. 7B). This inference also depends on the relevance of our present-day taxonomic sampling (Grandcolas, Natier, & Trewick, 2014). Rare, distinct traits can occur either on old, persisting branches (Fig. 7C) or on rapidly and recently evolved branches of a given phylogenetic tree (Fig. 7D). The combination of phylogenetic and trait-based originalities of a species is then

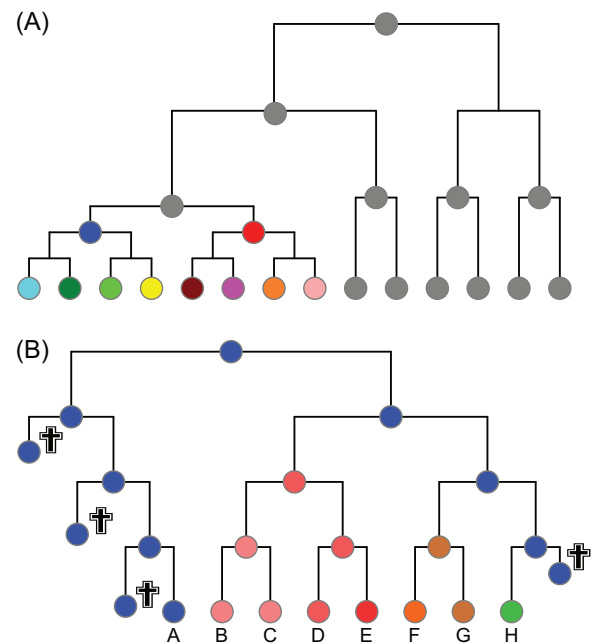




**Fig. 7.** Theoretical examples where a species is original according to both its traits and phylogenetic position. We considered a theoretical phylogenetic tree with 11 extant and up to four extinct species as tips and branch lengths expressed in time of evolution. A shows the tree with only extant species, and B, C and D represent potential scenarios of complete trees with extinct species and trait values for all species and their theoretical ancestors (interior nodes). Circle colours express different values of a theoretical trait (or a complex of traits). (A) Among all extant species, the current species with the blue trait is both the most phylogenetically original, because it is the most isolated, and the most trait-based original, because it is very different in its trait (colour) value from the other extant species. (B) A scenario where past extinction events have suppressed many species displaying the blue trait. (C) A scenario where the species with the blue trait is a relictual species that has kept an ancestral value of the trait (that at the root of the tree). (D) The case where the species with the blue trait has become original among extant species, although its trait value is a recent autapomorphy. In B to D, crosses indicate extinct species.

not explained only by the species' relictiness if it alone remains from a group that is mainly extinct (Grandcolas, Nattier, & Trewick, 2014). Species' originality can emerge from evolutionary autapomorphy, that is, from the appearance in a given taxon of a distinctive derived value of a trait that is unique to this taxon (Fig. 7D).

Species originality may also be used to replace intuitive characterizations that are still too often employed in evolutionary biology, such as 'evolved' or 'primitive' (Crisp & Cook, 2005; Grandcolas & Trewick, 2016). The comparison of a species to a reference species group could benefit from being carried out while considering speciation or extinction rates. For example, adaptive radiations are associated with both an increase in speciation rates and the adaptation of constituent species to a diversity of ecological niches (Gavrillets & Losos, 2009). This adaptation usually leads to high levels of diversity in the trait(s) on which selection for local adaptation acts. As a consequence, adaptation leads to species being original for the trait(s), relative to each other and to the remaining species of the clade. For example, the



**Fig. 8.** Theoretical examples of the potential effects of speciation and extinction events on species' originality and diversity. (A) Adaptive radiation. (B) Phylogenetically structured extinctions. As in Fig. 7, we considered theoretical phylogenetic trees with species as tips and with branch lengths expressed in time of evolution. Circle colours express different values of a theoretical trait (or a complex of traits). Each species and each of their hypothetical ancestors (interior nodes) has a defined value for the trait(s). In A, the ancestor at the root of the phylogeny has a grey colour. All of its descendants kept this trait value up to a given period when adaptive radiation yielded speciation events with rapid trait evolution. In B, the crosses indicate that four species are extinct. Extant species are named A to H. The colours in the circles represent the assumption that some extant species might have acquired traits (pink, orange and green) that render them either tolerant or adapted to new environmental conditions. We used different colours for the acquired traits as there may be multiple ways of being either tolerant or adapted to some specific environmental conditions. This shows that species A, which is phylogenetically distant from the other extant species, is also likely to be functionally original (here by remaining with the ancestral character state), but this may depend on the considered traits.

adaptive radiation in Darwin's finches led to an increase in the diversity of beak size and shape, making these species more original than their relatives (Grant & Grant, 2008). If speciation events occur in a short time period during such a radiation, then trait-based and species diversities are likely to increase by a much larger extent than phylodiversity. In such a case, trait-based originality is not always accompanied by phylogenetic originality (Fig. 8A).

Inversely, high extinction rates in a particular lineage could lead to the phylogenetic isolation of a relict species and thus to its phylogenetic originality among extant species. The trait-based originality of the relict species is likely dependent on the traits considered and on their evolution

(Fig. 8B). An example of a relict species is the present-day ginkgo (*Ginkgo biloba*) (Crisp & Cook, 2011). Phylogenetically clumped extinctions could thus decrease the diversity of a regional pool in terms of species number and phylogeny. At the same time, they could lead to a skewed distribution of phylogenetic originality across the study region, with a few very original species belonging to the species-poor lineages where extinctions occurred. Future research could thus concentrate on searching for how and why phylogenetically and functionally original species emerge in the course of evolution and at which spatial and taxonomic scales they emerge. Additionally, future studies could evaluate how the emergence of original species has influenced current patterns of diversity and distributions of species' abundances.

## (2) Analysing the dynamics of community assembly with rarity, originality and diversity

Species evolve in continuously changing communities governed by numerous ecological, evolutionary and stochastic processes. The ecological processes that have been most studied to explain species diversity are competition, in which biotic interactions between species regulate species' abundances; environmental filtering, where abiotic forces act to constrain certain species' traits within limits; and density dependence, where abundant species have lower individual performance than do rare species (e.g. Hubbell, 2001; Holyoak, Leibold, & Holt, 2005). Mathematical models have been developed in recent decades to synthesize knowledge on community assembly and diversity patterns (Hubbell, 2001; Holyoak, Leibold, & Holt, 2005; Munoz & Huneman, 2016). So far, most of them have focused on measuring and/or predicting patterns of species abundance (number of individuals) and patterns of species richness in communities (MacArthur & Wilson, 1967; Magurran, 2004; McGill *et al.*, 2007). These models have thus rarely focused on patterns of phylo- and trait-based diversity and originality, despite copious numbers of empirical and conceptual studies on community assembly in terms of functional and phylodiversity. A few recent models have, however, started to give insights into functional and phylodiversity (e.g. Münkemüller & Gallien, 2015; Munoz *et al.*, 2018).

There is a broad consensus now on the fact that several distinct processes, including niche-based and neutral ones, interact in species assemblages (e.g. Chase & Myers, 2011). However, despite this consensus, it was also shown that community assembly models based on contrasting underlying processes (e.g. niche-based *versus* neutral processes) may predict the same patterns of species abundance and diversity equally well (e.g. McGill *et al.*, 2007). Such equivalence hampers the direct inference of assembly processes from observed patterns of species abundance and diversity. In fact, mechanistic insights into patterns of community assembly may rely more on the originality of species rather than on their abundance alone (Cadotte & Davies, 2016). One of the oldest identified patterns in ecology is the hollow curve of the distribution of species abundance, with few dominant and many rare species (McGill *et al.*,

2007). The shape of this curve is usually described in terms of skewness. The skewness of an abundance curve is thus inversely related to species diversity, with the latter increasing with an increase in abundance evenness. A hollow curve can also describe the distribution of species' originality in the case of many redundant and few original species (Da Silva *et al.*, 2012). Both species abundance and originality could thus be described by the same tool: a hollow curve.

In parallel, since Webb *et al.* (2002), ecologists often use statistical approaches to associate the trait and/or phylogenetic structure of a community with scenarios of community assembly. This association can be accomplished by comparing observed patterns of trait-based diversity and phylodiversity with those expected by chance using a null model of randomly assembled communities from a regional species pool (Emerson & Gillespie, 2008; Hardy, 2008; Cavender-Bares *et al.*, 2009). Trait-based clustered communities, with many redundant species and low average originality, would reveal environmental filtering, while trait-based overdispersed communities, with the presence of highly original species, would indicate limiting similarity and interspecific competition (Webb *et al.*, 2002). These paradigms may, however, be an oversimplification as competition can sometimes lead to a reduction in functional diversity, particularly when traits are linked to species fitness (Mayfield & Levine, 2010).

The same statements were made for phylodiversity patterns under the assumption of the phylogenetic signal mentioned in Section IV.1 (Webb *et al.*, 2002; see also Saito *et al.*, 2018). Phylogenetic signal tends to decrease at local spatial scales in communities and for narrow taxonomic levels (Cavender-Bares, Keen, & Miles, 2006). Differences between trait-based diversity and phylodiversity patterns for the same community would indicate labile, convergent traits, character displacement between lineages (Gerhold *et al.*, 2015), or environmentally determined traits that vary more than others (Cadotte & Davies, 2016). Species' trait evolution must thus be quantified (see Section IV.1) to connect community trait-based diversity and phylodiversity patterns to the assembly processes (Losos, 2008).

Therefore, to date, the processes that shape community assembly have mostly been analysed based on the concepts of diversity, abundance and thus abundance-based rarity. The roles of trait-based (functional) and phylo-based rarities and thus of species' originality in community assembly have been far less studied. For example, during a colonization event from a regional pool to a local community, the local originality of a colonizing species relative to resident species could be decisive for the successful colonization of the species. The local originality could enhance the colonization success of those species if they can avoid competition with natives for resources due to their high originality ('Darwin's naturalization hypothesis'; Strauss, Webb, & Salamin, 2006; Pearson, Ortega, & Sears, 2012). Inversely, the species' local originality could hamper its colonization success if its high originality makes it less adapted to the local environmental conditions than are the native species (Strayer, 2012).

The local coexistence of species could influence the lineage diversification of the species (Gerhold *et al.*, 2015) and the distribution of the species' originalities. Overall, analyses of community species, phylo- and trait-based diversity, rarity and originality patterns at various spatial scales could therefore better indicate underlying ecological and evolutionary processes that influence species coexistence than analyses of species abundance could alone. A given process could impact only part of the species of an assemblage, which could result in patterns in the distributions of species' originalities. The joint use of rarity, originality and diversity indices could thus provide insights into which interactions among stochastic, ecological, biogeographical and evolutionary processes shape local communities and their dynamics.

### (3) Role of originality in ecosystem functioning

Many studies of biodiversity patterns are focused on common species because they consider common species to represent the largest part of the biomass of a community and thus to be essential for ecosystem functioning (Gaston, 2012). By contrast, rare species may be difficult to include in community-level analyses due to sampling limits. In cases in which knowledge of these species is poor, rare species can be even more difficult to include in trait-based and phylogenetic originality analyses. However, originality and abundance-based rarity were found to be correlated in some cases (e.g. Mi *et al.*, 2012). If low-density species possess the most distinct functional traits, then they could support vulnerable functions in ecosystems and be of particular importance to the community (Gaston, 1998; Mouillot *et al.*, 2013; Leitão *et al.*, 2016). The removal of such species from a community could result in a considerable reduction in ecosystem functioning (Mouillot *et al.*, 2008; Bender *et al.*, 2017), with no possibility for other species to compensate for their loss (Leitão *et al.*, 2016). For example, using species extinction simulations, Rosatti *et al.* (2015) showed that, under extinction scenarios based on abundance and fire tolerance, the probability of losing the most functionally original woody cerrado species was higher than that expected by chance, while the loss of phylogenetically original species was random. In this case study, trait-based functional originality could thus be an indicator of species vulnerability defined based on species rarity and fire sensitivity.

By contrast, two species are functionally redundant if they overlap in their functional niches, i.e. they maintain similar ecosystem functions (Brandl & Bellwood, 2014; Carmona *et al.*, 2016). However, any two species in a set are unlikely to be perfectly redundant but likely to be complementary, i.e. sharing parts of their functional niches and their roles in the ecosystem (Rosenfeld, 2002; Loreau, 2004). Contrary to trait-based originality, trait-based redundancy does not increase trait-based diversity, but it may increase the stability and resilience of communities of species and ecosystem functions. Determining redundant species can thus guide conservation measures. Indeed, local species extinctions caused by perturbations could be compensated for by the

persistence of species that are functionally similar to the lost species but that differ from them in their responses to changes in environmental factors or disturbances (Walker, 1992; Pillar *et al.*, 2013). For example, an increase in trait-based functional originality has been found in coral reef communities after a cyclone disturbance due to the local extinction of redundant species that had trait values similar to those of the surviving species (Brandl *et al.*, 2016). Ecosystem functioning, stability and resilience are dependent on the composition of species and those species' abundance-, phylo- and trait-based rarities. Inversely, species' characters, abundances and distribution patterns are shaped by many ecological processes. We should continue to consider this mutuality in future studies to better comprehend the complexity of ecosystem functioning.

### (4) Guiding conservation actions

Species are among the key units of biodiversity measurement. Their conservation is at the core of many national and international programmes that request effective methods for habitat prioritization and species preservation. Criteria related to ecosystem services evaluated as economic costs, aesthetic value, contribution to well-being, and species richness and rarity are often parts of these programmes. Should such programmes also include phylo- and trait-based diversity and originality? Even if conservation planning alternates between preserving particular units of biodiversity and preserving the processes that shaped those units, the most commonly employed method to design conservation priorities uses species richness ranked by species' abundance-based rarity and endemism (Mace, 2003). Conservation values are thus often given to geographical units, or biodiversity hotspots, that are not chosen with regard to species' traits and evolutionary histories (Veron *et al.*, 2017).

For example, Brum *et al.* (2017) reviewed currently protected areas determined by the International Union for Conservation of Nature (IUCN) risk classification system. They demonstrated that those areas do not harbour more phylo- or trait-based diversities of threatened mammals than would be expected if they were randomly selected. As shown in the previous sections, species are not equivalent, and the phylo- and trait-based diversities of an area are the products of numerous stochastic, evolutionary and ecological processes. Conservation planning would thus benefit from considering biodiversity as multidimensional by including the phylogenetic and trait-based originalities of species (Rodrigues & Gaston, 2002; Pellens, Faith, & Grandcolas, 2016). For example, Pollock, Thuiller, & Jetz (2017) showed that a 5% expansion of protected areas could more than triple the protected range of species or trait-based or phylo-based units.

Originality indices could be useful as a complement for conservation actions that target species rather than areas (Pavoine *et al.*, 2005; Isaac *et al.*, 2007; Jetz *et al.*, 2014; Laity *et al.*, 2015; Grenié *et al.*, 2018). Species are often ranked for conservation attention by their patrimonial,



abundance-based rarity and threat status, which is not sufficient to determine priorities (Mouillot *et al.*, 2008). These conservation attentions could nevertheless indirectly (non-intentionally) preserve original species. For example, Thévenin *et al.* (2018) showed that, although evolutionary considerations are unlikely to have driven explicitly the allocation of reintroduction efforts, reintroduced birds and mammals in Europe, North America and Central America tend to be more phylogenetically original than expected by chance.

Originality indices allow treating species within multiple facets of biological diversity. The explicit inclusion of such indices in conservation actions would be useful to evaluate each species' contribution to local and global phylo- and trait-based diversity (Jensen *et al.*, 2016; Pavoine *et al.*, 2017). The recommendation to safeguard species that are both original and threatened inspired some authors to extend pre-existing indices of originality to include additional species attributes: abundance, range size and probability of extinction (Isaac *et al.*, 2007; Rosauer *et al.*, 2009; Cadotte & Davies, 2010; Hidasi-Neto *et al.*, 2015). Although alternatives exist (Steel *et al.*, 2007; Jensen *et al.*, 2016), the most widely cited originality measure that also integrates species extinction risk is the evolutionary distinct and globally endangered (EDGE) species index (Isaac *et al.*, 2007). The EDGE index combines the phylogenetic originality of a focal species with its IUCN threat status. Given that it was designed for large-scale analyses, the EDGE index does not consider species' traits. However, conservation actions are often developed locally. Hidasi-Neto *et al.* (2015) thus modified the EDGE index and proposed the EcoEDGE index, which combines phylogenetic and functional components of species' originalities with those species' extinction risks.

Some studies found that low abundance and narrow range size are the characteristics of functionally original species that are threatened to extinction at the local scale in French breeding birds (Calba, Maris, & Devictor, 2014) and freshwater bivalve molluscs (Burlakova *et al.*, 2011) and at both local and regional scales in coral reef fishes, alpine plants and tropical trees (Mouillot *et al.*, 2013). At a global scale, phylogenetically original primate species were found to be more threatened with extinction than were other primates (Verde Arregoitia, Blomberg & Fisher, 2013; but see Redding, deWolff, & Mooers, 2010), but this was not true for the whole class of mammals (Verde Arregoitia *et al.*, 2013). The endangerment of original species could, however, lead to a drastic decrease in phylo- and trait-based diversity if it were also associated with the phylogenetic clustering of species extinction (Parhar & Mooers, 2011).

Therefore, the spatial distribution of original species may provide information on whether they are concentrated in low-diversity areas that are not targeted by current conservation actions (e.g. Jetz *et al.*, 2014; Veron, Clergeau & Pavoine, 2016). Additionally, using simulations, Redding *et al.* (2008) showed that prioritizing species by different originality indices measured globally tends to safeguard more local phylodiversity than is expected by the selection

of random species. Similarly, prioritizing Neotropical and Nearctic bird species with high average global phylogenetic originality scores could allow local phylodiversity to be safeguarded (Redding *et al.*, 2015). Clearly, species' originality identifies 'key' species for preservation priority that could be overlooked by classical abundance-based rarity and diversity methods.

## V. CONCLUSIONS

(1) Due to the emergence of myriad terms related to biodiversity, rarity, and originality in the ecological literature, it has become difficult to determine whether terms used by different studies refer to the same concepts and measures. Each concept encompasses different aspects of species assemblages and can be measured by several mathematical indices. We provided a semantic and historical overview of these three concepts – biodiversity, rarity and originality – at the level of an assemblage of species. We showed that mathematical links exist between their associated indices.

(2) Historically, rarity was explicitly integrated into diversity measures by means of species abundance. Later, diversity measures incorporated species' biological (trait or phylogenetic) differences, sometimes weighted by the species' abundances. Species identities can be interchanged without affecting diversity measurement based on the number and abundances of species. Phylo- and trait-based diversities have thus gone far beyond the vision of species diversity.

(3) The contribution of individual species to the phylo- and trait-based diversities of a reference species set is captured by the concept of originality. This concept brings together ecologists and evolutionary biologists because it can combine species' evolutionary histories, traits and abundances. It can be measured by various approaches based on phylogenetic trees and trait-based dendrograms, dissimilarity matrices and multidimensional space. Focused at the individual species level, originality complements the diversity measures that can then sometimes be written as simple functions of species' trait-, phylogeny-, and abundance-based rarities.

(4) The joint use of the concepts of diversity, rarity, and originality could aid in the understanding of the multiple mechanisms shaping communities at different spatial and temporal scales. At a large scale, the joint use of these concepts could help clarify general patterns of evolutionary events such as trait evolution, extinction, speciation, and adaptive radiation of species. At a local scale, it could aid in understanding community assembly and ecosystem functioning. At any scale, it could refine conservation strategies.

(5) It is widely accepted that no single mathematical formula could alone encompass all aspects of biodiversity. Here, we have shown that the joint use of diversity, rarity and originality measures has the potential to recompose accurately the complex picture of the diversity of a species assemblage.

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## VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.  
**Appendix S1.** List of main originality indices cited, with references, abbreviations and some of their key properties.

**Appendix S2.** Illustration associated with Table 1.

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