Original Articles

# From phylogenetic to functional originality: Guide through indices and new developments

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## ARTICLE INFO

## ABSTRACT

In biodiversity studies a species is often classified as original when it has few closely related species, a definition that reflects its phylogenetic originality. More recently, studies have focussed on biological or functional traits that reflect the role(s) that species play within communities and ecosystems. This has led many studies to an alternative evaluation of species' originality: its functional originality. Most indices of species' originality were developed to treat the hierarchical structure of a (phylogenetic) tree. The change in perspective from measures of phylogenetic originality to measures of functional originality thus raises methodological issues particularly around the need to develop indices explicitly appropriate for evaluating functional trait-based originality. We compare indices of species' originality including a new index which we develop to evaluate (1) whether phylogenetic originality could serve as a proxy for functional originality in conservation and ecological studies; (2) whether the transformation of functional data into functional trees modifies the way species are ranked according to their originality measures compared to approaches that directly rely on pairwise functional dissimilarities among species; and more generally, (3) whether different indices provide different views on how original species are from each other, hence reflecting different ecological and evolutionary processes that generated patterns of originality. Using simulations and a real case study, we show that: (1) the strong effects of the choice of a clustering approach can affect reported levels of dissimilarities among species; (2) the tree-based approaches could better reflect the trait-generating processes under constant (Brownian) rates of evolution; and (3) phylogenetic originality measures can depart from functional originality measures when species have large amount of independent evolution. Overall, phylogenies may be used at large scales but cannot replace functional approaches designed for depicting community assembly. Indeed, traits involved in ecological processes may have various histories and thus moderate phylogenetic signals. Our comparative study provides approaches and perspectives on the analysis of originality across biological scales of organization from individuals, through populations, up to the originalities of communities and regions.

## 1. Introduction

Atkinson (1989) recommended that "given two threatened taxa, one a species not closely related to other living species and the other [a] widespread and common species, it seems reasonable to give priority to the taxonomically distinct form". May (1990) and Vane-Wright et al. (1991) therefore developed equations to measure how taxonomically distinct a species is compared to a reference set of species. A species was then defined as distinct if it is not closely related to other living species,

a concept also known as evolutionary isolation (Jensen et al., 2016). Following Faith (1992), Pavoine et al. (2005) extended the concept of the isolation of a species on a phylogenetic tree to that of originality. They defined originality as the potential rarity of the species' features, where a feature means a particular state of a character. They also considered 'strict uniqueness' as the number of features possessed by this species yet not those shared with the others. Recently, there have been more studies directed on the functional attributes of species: a finite number of physiological, anatomical, behavioural or life-history

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traits reflecting the roles that species play within communities and ecosystems (e.g. Petchey et al., 2007; Mouillot et al., 2008; Magnuson-Ford et al., 2009; Schmera et al., 2009a; Thompson et al., 2010; Buisson et al., 2013; Mouillot et al., 2013; Godet et al., 2015; Rosatti et al., 2015).

This diversity of approaches led different authors to use the terms distinctiveness, originality and uniqueness in different meanings. Sometimes two expressions have been used to designate the same concept and sometimes a single word was used to mean two different things. Also in the literature there is confusion between the concepts and the methods used to associate quantitative measures to these concepts. Notably originality was used by Pavoine et al. (2005) to design a concept. It was then used again by Buisson et al. (2013) to designate a measure: the distance, in a functional space, between a species position and the centroid of the space. Generalizing Buisson et al. (2013) framework, Redding et al. (2014) used the expression "originality" to designate the average phylogenetic (patristic) distance to all other species. The fact of being taxonomically distinct was introduced by Atkinson as a concept but "evolutionary distinctiveness" is often used to name an index also known as the "Fair Proportion" measure (Isaac et al., 2007; Jensen et al., 2016; see also Table 1). The concept associated with "evolutionary distinctiveness" was instead often referred to as evolutionary isolation (Redding et al., 2014).

Hereafter we use originality as the core, unifying concept and strict uniqueness as a special case. As a proposal for a unified semantic framework, we define the originality of a given species in a set of species as the rarity of its biological characteristics. Originality can emanate from any characteristics of the species. Notably, it can integrate the evolutionary history (phylogenetic originality) or the functional traits (functional originality) of species. This definition generalizes the definition Pavoine et al. (2005) initially proposed. We consider originality synonymous to the following expressions: distinctiveness (e.g. Atkinson, 1989); isolation (e.g. Redding et al., 2014); degree of uniqueness (e.g. Brooks et al., 2015; Ricotta et al., 2016). We consider originality antonymous to the concept of redundancy (e.g. Buisson et al., 2013; Ricotta et al., 2016). We define strict uniqueness as the minimum difference with any other species in a set. We consider strict uniqueness as a special case of originality. From a biodiversity perspective, strict uniqueness is the amount of diversity that is solely supported by the focal species (driven by unshared characteristics of the species). In contrast, originality is the full contribution of the species to the biodiversity of the set (Pavoine et al., 2005).

Both phylogenetically original and endangered taxa have recently been the focus of conservation actions (Isaac et al., 2007). Depending on the shape of the phylogenetic tree (imbalance and 'tippiness', Heard and Mooers, 2000), the loss of entire species-poor clades that contain original species could indeed lead to dramatic loss in taxonomic/phylogenetic diversity (Purvis et al., 2000). In contrast, as far as we are aware, very few conservation actions have focused on functionally original and endangered species. Yet, Mouillot et al. (2008), for example, found that protecting the most functionally original species protects high functional fish diversity in the Bonifacio Strait Natural Reserve. In food webs, intermediate species (herbivores) that tend to be more trophically original (they share no or few prey and predators with other species) might be more prone to secondary extinctions. Furthermore, their loss might have great effects on trophic diversity due to their relative originality (Petchey et al., 2008). The concept of species originality has also been studied in ecology and associated with key ecological processes, such as community assembly, ecosystem functioning, and species extinction. Original species could be more likely to invade or colonize, and in addition may have less impact on resident species (Strauss et al., 2006; Strayer et al., 2006). Species original in their functional traits might make a large contribution to ecosystem functions and services, such as gross photosynthetic rate (Petchey et al., 2004). Unique functions of original species in their ecosystems reinforce the importance of originality indices for conservation biology. Developing and comparing measures of originality is thus critical for their efficient use in conservation.

As highlighted above, species originality has been primarily measured from phylogenetic trees. Consequently the methods that were first developed to measure species originality from a phylogeny are now being adapted and applied to the analysis of functional traits. This translation raises new issues on the measurement of functional originality. Indices of phylogenetic originality rely on the tree structure of the phylogeny. Adapting these indices to functional originality thus requires the definition of functional trees (or dendrograms) with a risk of distorting the information provided by functional traits. This is exemplified with the clustering approach used to define the functional tree (Mouchet et al., 2008; Petchey et al., 2009). Among the indices of phylogenetic originality, the quadratic entropy(QE)-based index developed by Pavoine et al. (2005) was defined for (ultrametric) phylogenetic trees, where the distance from tips to root is constant, which also is a property of functional trees obtained by clustering methods. Here, we extend this QE-based approach to any (phylogenetic or functional) dissimilarity matrix among species. We compare these originality indices related to QE to a range of existing indices introduced in the literature in their ability to discriminate species in terms of their functional originality (Table 1; May, 1990; Eiswerth and Haney, 1992; Redding, 2003; Ricotta, 2004; Redding and Mooers, 2006; see also Redding et al., 2014 for a review). We selected originality indices amongst the most used in the literature. We use numerical simulations and a case study to evaluate the strengths and differences across the range of originality indices. In particular, we evaluate

**Table 1**
Originality indices discussed in this paper. All indices are measures of originality; but only *PE* and *NN* are measures of strict uniqueness.

| Short name | Full name | Dependence on | | Refs. |
|---|---|---|---|---|
| | | a tree structure | a dissimilarity matrix | |
| *AV* | Average distance to other species | | X | Eiswerth and Haney (1992) |
| *ES* | Equal-Split (branches in a tree are split equally among descending clades) | X | | Redding and Mooers (2006) |
| *FP* | Fair Proportion (branches in a tree are split fairly among descending species) | X | | Redding (2003) |
| *M* | May's topological index (number of branches emerging from internal nodes in the path between a species and the root of a tree) | X | | May (1990) |
| *NN* | Distance to the nearest neighbour | | X | This paper |
| *PE* | Pendant Edge (terminal branch of a tree) | X | | Redding et al. (2014) |
| *Qb* | Species' proportions that maximize the quadratic entropy diversity index | X | X | Pavoine et al. (2005) |
| *Rb* | Species' proportions that maximize the *R* diversity index | | X | This paper |
| *tb-AV* | *AV* index applied on tree-based distances among species | X | X | This paper |
| *tb-Rb* | *Rb* index applied on tree-based distances among species | X | X | This paper |