

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

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- 2 developments
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- 23
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26 ABSTRACT

In biodiversity studies a species is often classified as original when it has few closely related 27 species, a definition that reflects its phylogenetic originality. More recently, studies have 28 focussed on biological or functional traits that reflect the role(s) that species play within 29 communities and ecosystems. This has led many studies to an alternative evaluation of 30 species' originality: its functional originality. Most indices of species' originality were 31 developed to treat the hierarchical structure of a (phylogenetic) tree. The change in 32 perspective from measures of phylogenetic originality to measures of functional originality 33 thus raises methodological issues particularly around the need to develop indices explicitly 34 appropriate for evaluating functional trait-based originality. We compare indices of species' 35 originality including a new index which we develop to evaluate 1) whether phylogenetic 36 37 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 38 39 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) 40 whether different indices provide different views on how original species are from each other, 41 hence reflecting different ecological and evolutionary processes that generated patterns of 42 originality. Using simulations and a real case study, we show that: 1) the strong effects of the 43 choice of a clustering approach can affect reported levels of dissimilarities among species; 2) 44 45 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 46 47 functional originality measures when species have large amount of independent evolution. Overall, phylogenies may be used at large scales but cannot replace functional approaches 48 designed for depicting community assembly. Indeed, traits involved in ecological processes 49 50 may have various histories and thus moderate phylogenetic signals. Our comparative study

- 51 provides approaches and perspectives on the analysis of originality across biological scales of
- 52 organization from individuals, through populations, up to the originalities of communities and
- 53 regions.
- 54
- 55 *Keywords*:
- 56 Biodiversity; carnivores; conservation priorities; entropy; simulations; species distinctiveness

57 **1. Introduction**

58

59 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 60 61 seems reasonable to give priority to the taxonomically distinct form". May (1990) and Vane-62 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 63 not closely related to other living species, a concept also known as evolutionary isolation 64 (Jensen et al. 2016). Following Faith (1992), Pavoine et al. (2005) extended the concept of the 65 isolation of a species on a phylogenetic tree to that of originality. They defined originality as 66 the potential rarity of the species' features, where a feature means a particular state of a 67 character. They also considered 'strict uniqueness' as the number of features possessed by this 68 species yet not those shared with the others. Recently, there have been more studies directed 69 70 on the functional attributes of species: a finite number of physiological, anatomical, 71 behavioural or life-history 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; 72 73 Schmera et al., 2009a; Thompson et al., 2010; Buisson et al. 2013; Mouillot et al., 2013; Godet et al., 2015; Rosatti et al., 2015). 74

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 81 82 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 83 species. The fact of being taxonomically distinct was introduced by Atkinson as a concept but 84 "evolutionary distinctiveness" is often used to name an index also known as the "Fair 85 Proportion" measure (Isaac et al., 2007; Jensen et al., 2016; see also Table 1). The concept 86 associated with "evolutionary distinctiveness" was instead often referred to as evolutionary 87 isolation (Redding et al. 2014). 88

Hereafter we use originality as the core, unifying concept and strict uniqueness as a 89 special case. As a proposal for a unified semantic framework, we define the originality of a 90 given species in a set of species as the rarity of its biological characteristics. Originality can 91 92 emanate from any characteristics of the species. Notably, it can integrate the evolutionary history (phylogenetic originality) or the functional traits (functional originality) of species. 93 This definition generalizes the definition Pavoine et al. (2005) initially proposed. We consider 94 originality synonymous to the following expressions: distinctiveness (e.g. Atkinson, 1989); 95 isolation (e.g. Redding et al., 2014); degree of uniqueness (e.g. Brooks et al., 2015; Ricotta et 96 97 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 98 any other species in a set. We consider strict uniqueness as a special case of originality. From 99 100 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 101 102 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 106 107 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. 108 109 (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 110 species (herbivores) that tend to be more trophically original (they share no or few prey and 111 112 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 113 (Petchey et al., 2008). The concept of species originality has also been studied in ecology and 114 115 associated with key ecological processes, such as community assembly, ecosystem functioning, and species extinction. Original species could be more likely to invade or 116 117 colonize, and in addition may have less impact on resident species (Strauss et al., 2006; 118 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). 119 120 Unique functions of original species in their ecosystems reinforce the importance of originality indices for conservation biology. Developing and comparing measures of 121 originality is thus critical for their efficient use in conservation. 122

As highlighted above, species originality has been primarily measured from 123 phylogenetic trees. Consequently the methods that were first developed to measure species 124 125 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 126 127 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 128 a risk of distorting the information provided by functional traits. This is exemplified with the 129 130 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(OE)-based index 131 132 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 133 clustering methods. Here, we extend this OE-based approach to any (phylogenetic or 134 functional) dissimilarity matrix among species. We compare these originality indices related 135 to QE to a range of existing indices introduced in the literature in their ability to discriminate 136 species in terms of their functional originality (Table 1; May, 1990; Eiswerth and Haney, 137 1992; Redding, 2003; Ricotta, 2004; Redding and Mooers, 2006; see also Redding et al., 2014 138 for a review). We selected originality indices amongst the most used in the literature. We use 139 140 numerical simulations and a case study to evaluate the strengths and differences across the range of originality indices. In particular, we evaluate 141 1) whether measures of phylogenetic originality could serve as a proxy for measures of 142 functional originality in conservation and ecological studies; 143

2) whether the transformation of functional data into functional trees modifies the way species
are ranked according to their measured originalities compared to approaches that directly rely
on pairwise functional dissimilarities among species;

3) more generally, whether different indices provide different views on how original species
are from each other, hence reflecting the range of ecological and evolutionary processes that
generated patterns of originality.

We discuss our results in light of recent developments in the assessment and
measurement of a multidimensional view of biodiversity (Pavoine and Bonsall 2011), with the
aim to identify (and preserve) the ecological and historical processes that drive biodiversity
dynamics.

Table 1

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

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

2. Methods

2.1. A variety of originality indices

164 2.1.1. Phylogenetic originality indices

Vane-Wright et al. (1991) were probably the first to define a cladistic (taxonomic) measure of originality. Their measure was defined as inversely proportional to the number of internal nodes between the focal species (tip) and the root of the cladistic tree. An improvement to this originality measure (discussed in an earlier study by May, 1990) has considered the effects of unresolved nodes by counting not simply the number of nodes between tip and root but rather the number of branches descending all such nodes. This improved index of species' originality can be applied to any phylogenetic tree. Hereafter we will refer to it as index M.

172 More recently, other measures have been suggested that consider branch lengths on the 173 phylogenetic tree (Table 1; Fig. 1):

i) The pendant edge (*PE*, e.g. Redding et al., 2014) index is defined as the length of the

175 branch that connects a species to the rest of the tree.

ii) The fair proportion index (*FP*, Redding, 2003) distributes the phylogenetic diversity (sum
of branch lengths) contained within a tree uniquely among the species at the tips. This is
achieved by dividing the shared evolutionary history represented by a branch equally among
its *daughter species* at the tips.

iii) The Equal-Split index (*ES*, Redding and Mooers, 2006) also distributes the phylogenetic
diversity contained within the tree uniquely among the species at the tips. However, it
achieves this by dividing the shared evolutionary history represented by a branch equally
among its *daughter branches*.

184

185

Insert Fig. 1. Single-column fitting image

186

187 2.1.2. Dissimilarity-based originality indices.

Considering a set of N species, Eiswerth and Haney (1992) and Ricotta (2004) suggested an 188 189 alternative measure that allowed genetic and taxonomic distances to be included directly in measures of originality. It consists of computing pair-wise genetic or taxonomic distances 190 among species and then obtaining the average distance between a focal species and all others 191 (N-1 species) in the set. We refer to this measure as the average distance index (AV). It is clear 192 that this index has broader applications: it can be applied to any distances among species be 193 194 they genetic, taxonomic, phylogenetic, or functional. Index AV is related to Schmera et al. (2009b) functional value of a species (FV): FV = [(N-1)*AV]/N. The conclusions we obtain 195 below for AV also applies to FV because these two indices similarly order species from the 196 197 least to the most original one. Below, we compare AV to the shortest distance between the focal species and all others in the set (hereafter referred to as the 'nearest neighbour' index, 198 NN). 199

200

201 2.1.3 The special case of the QE-based index framework

To define the QE-based index (hereafter referred to simply as *Qb*), Pavoine et al. (2005) considered a matrix $\mathbf{D} = (d_{ij})_{1 \le i \le N, 1 \le j \le N}$ of dissimilarities among *N* species. The dissimilarity d_{ij} between any two species *i* and *j* was calculated on an ultrametric, phylogenetic tree as the sum of branch lengths between each of them and their most recent ancestor. These dissimilarities are ultrametric as they satisfy the following property: $d_{ij} \le \max(d_{ik}, d_{ik})$ for all *i*,*j*,*k*.

207 Let $\mathbf{p}=(p_1, ..., p_i, ..., p_N)$ be a vector of species' relative abundance $(\sum_{i=1}^N p_i = 1)$ in an

hypothetical assemblage. The average dissimilarity among individuals from this assemblage is
an established measure of diversity (Rao, 1982; Pavoine et al., 2009):

210
$$Q(\mathbf{p}, \mathbf{D}) = \sum_{i}^{N} p_{i} \sum_{j}^{N} p_{j} d_{ij}$$
.

- The index Qb of species' originality is the value of p_i a species *i* should have to maximize Q (Table 2). The value of p_i that leads to the maximum possible value of Q reflect the originality of species *i*. Indeed, to a certain extent, the more abundant original species are compared to redundant species, the more diversity there is in a set of species. However, this index Qb is critically dependent on the use of dissimilarities derived from an ultrametric tree (Table 2).
- 217
- 218

219 **Table 2**

- 220 Details on how to calculate the originality indices *Qb* and *Rb*.
- 221

Diversity index	Originality index
Q	Consider that D is a matrix of patristic distances between species derived
	from a phylogenetic or functional tree (Fig. 2). The value of p_i that lead to
	the maximum possible value of Q applied to D is equal to
	$Qb_i = \sum_{j}^{N} \delta_{ij} / \sum_{i}^{N} \sum_{j}^{N} \delta_{ij}$
	where δ_{ij} is the value at the <i>i</i> th row and <i>j</i> th column of the inverse of D .
	Pavoine et al. (2005) restricted Qb to ultrametric dissimilarities in D .
	Indeed without this property, the vector \mathbf{p} that maximizes Q may not be
	unique and could take null values (zeros) for several species.
R	Consider a given matrix $\mathbf{D} = (d_{ij})_{1 \le i \le N, 1 \le j \le N}$ of dissimilarities among N
	species with the only conditions that $d_{ij}=d_{ji}$ for any $i,j, d_{ij}>0$ for any $i\neq j$,
	and $d_{ii}=0$ for any <i>i</i> . The maximum of <i>R</i> over p is the first eigenvalue of D .
	Its unique maximizing vector is the squared first eigenvector of \mathbf{D} (proofs
	in Appendix A). This maximizing vector is our index <i>Rb</i> .

225 Originality can thus be defined as the amount of abundance a species should have in a 226 theoretical community to provide the maximally, theoretically possible biodiversity to this community. Such a reasoning however means that the measurement of species originality 227 depends on how biodiversity itself is measured. In their study, Pavoine et al. (2005) used Q as 228 the reference biodiversity index. A particularity of Q is that it preferentially weights common 229 species over rare species. However, recent studies have focused on profiles of diversity 230 231 indices where rare versus common species are weighted with more or less importance (Jost, 2006; Pavoine et al., 2009; Chao et al., 2010; Leinster and Cobbold, 2012). Changing the 232 relative importance given to rare versus common species in functional or phylogenetic 233 234 diversity measurements has an impact on the amount of abundance a species should have to provide the maximally, theoretically possible biodiversity to a community. 235

236 Most of these studies rely on the Hill numbers (Hill, 1973):

237
$${}^{q}D(\mathbf{p}) = \left[\sum_{i}^{N} (p_{i})^{q}\right]^{\frac{1}{1-q}}, q > 0, q \neq 1$$

238 where q modifies the relative importance given to rare versus common species: the sensitivity of ^qD to rare species decreases with q (Patil and Taillie, 1982). The limiting case $(q \rightarrow 1)$ 239 serves as a reference where species are weighted directly by their relative abundances $(p_i s)$ 240 without favoring either rare or common species (Jost, 2006). In the case where the d_{ii} 's are 241 defined in the range [0,1], 1/(1-Q) is a generalization of ²D that includes (functional or 242 phylogenetic) distances among species (Ricotta and Szeidl, 2009). The fact that the quadratic 243 diversity (Q) gives high weight to abundant species compared to rare species can be viewed as 244 a weakness when rare species are considered as key drivers of biodiversity of conservation 245

interest. Developing this, we propose an index to contrast quadratic diversity (*Q*) by weighing
rarity over commonness (see Appendix A):

248
$$R(\mathbf{p}, \mathbf{D}) = \sum_{i=1}^{N} \sum_{j=1}^{N} \sqrt{p_i} \sqrt{p_j} d_{ij}$$

In the particular case where the d_{ij} 's are defined in the range [0,1], *R*-1 is a generalization of Hill number ^{0.5}*D* that includes functional or phylogenetic dissimilarities among species (Appendix A).

Our new index, *R*, complements *Q*, both by the similarity of their formulas and by their relatedness to the Hill numbers. Both these indices (*Q* & *R*) are anchored within the broader literature on entropy, species diversity, and functional and phylogenetic diversity (see details in Appendix A). For example, when species have even relative abundances, i.e. $p_i=1/N$ for all *i*, then *R* equals *MFAD*, an index of diversity introduced by Schmera et al. (2009a):

257
$$MFAD(\mathbf{D}) = \frac{1}{N} \sum_{i=1}^{N} \sum_{j=1}^{N} d_{ij}$$

As for index Q, the values of p_i that lead to the maximum possible value of R also reflect 258 species originalities. Increasing the abundance of original species compared to redundant 259 species to a certain extent increases the diversity of the set of species (see Appendix A for a 260 simple example). Using the vector of p_i 's that maximizes R, instead of Q, should however 261 262 provide an alternative view on species' originalities (Table 2). We refer to this vector as *Rb*. Compared to *Qb*, an advantage of *Rb* is that it can be applied to any dissimilarities (even those 263 that are not ultrametric). However, whether *Rb* provides novel interpretation to species' 264 265 originality will be analyzed below.

266

267 2.3. Case studies

268	We use both simulation studies and an empirical dataset (on European carnivores) to
269	investigate the measurement of functional originality. For each case (simulation or empirical
270	dataset), we computed all the indices introduced in Table 1 as specified in Fig. 2. We
271	calculated functional dissimilarities among species from raw data using the Euclidean
272	distance metric with quantitative traits in the first case study; and Gower distance (Gower,
273	1971) with a mix of quantitative and nominal traits in the second case study. We obtained
274	functional trees from functional distances using UPGMA and Ward methods (R function
275	hclust, parameter "average" and "ward.D2", respectively; R Core Team 2016).
276	
277	Insert Fig. 2. Single-column fitting image
278	
279	2.3.1. Simulations
280	

For the simulation case study, our objective was to analyze functional originality when traits 281 evolved under a Brownian motion model. Indeed, the Brownian model of trait evolution 282 283 assumes constant rates of trait changes through time. Under this model, trait-based distances between species are expected to be strongly correlated with phylogenetic distances. We thus 284 285 chose the Brownian model to evaluate whether, in this extreme, simplified scenario, measures of phylogenetic originalities effectively acted as proxies for measures of functional 286 originalities. If phylogenetic and functional originalities are different even when traits are 287 simulated under a Brownian model of evolution, then the use of phylogenetic originality 288 289 measures as proxies for functional originality measures would be poor. We also wanted to evaluate whether the correlations between phylogenetic originality measures and functional 290 291 originality measures depended on methodological choices such as the originality index

chosen, the method used to obtain functional dendrograms, the number of traits considered.

Our a priori hypothesis was that, using *Rb*, *AV* and *NN*, functional originality measures would better reflect phylogenetic originality measures. Indeed, these indices are calculated using raw functional data with minimal methodological assumptions and thus minimal data distortion. In contrast, functional dendrograms may distort information obtained from raw traits. Originality indices based on functional dendrograms may thus depart more from the original signal driven by phylogenies.

We simulated four general phylogenetic trees: (i) a pure birth model (BIRTH model, 299 with birth rate of 0.1) leading to relatively well-balanced trees (function "sim.bd.taxa" in the 300 R package TreeSim; Stadler, 2015); (ii) trees with speciation events close to the root (ROOT 301 model); (iii) trees with speciation events near the tips (TIPS model) (using package geiger in 302 R - function "deltaTree" with $\delta = 10$ and 0.1, respectively, Harmon et al. 2008); and finally 303 (iv) asymmetric nonultrametric trees (NU model, where the distance from tips to root is not 304 305 constant). In the asymmetric trees the topology was generated by splitting randomly the edges (function "rtree" in ape package in R, Paradis et al., 2004) and branch lengths were simulated 306 using a log-normal distribution (with LogN(0,1)). Nonultrametric trees represent unequal 307 evolutionary rates in different parts of the phylogeny. They led to asymmetric distributions of 308 species' originalities with many redundant species and a few original ones. We simulated 309 1000 trees per model with 2^7 =128 tips. One, 25 or 50 traits were simulated for each 310 311 phylogenetic tree, according to a Brownian model with parameters $\sigma=1$ and $\theta=0$ (function "rTraitCont" in ape package). 312

Our analysis proceeds by first analyzing the effect of the clustering approach (either UPGMA or Ward) on functional originalities using Spearman correlations for each originality index. Next we analyzed the Spearman correlations between indices and detailed the correlations between *Rb* and the other indices calculated with functional data (using one, 25 or

50 traits) for each different trait evolution modes (BIRTH, ROOT, TIPS, or NU models of 317 318 trait evolution) under different functional (UPGMA vs Ward) dendrograms. For tree-based metrics, correlations with *Rb* were analyzed with centred Principal Component Analysis using 319 320 the number of traits, the model of trait evolution and the method for tree construction as supplementary variables (using package 'ade4' in R; Dray and Dufour, 2007). Then we 321 analyzed the Spearman correlations between phylogenetic originality measures and functional 322 323 originality measures for each originality index and simulation case. We used Spearman correlations in all cases as the high number of simulations restricted checking the shape of the 324 relationships between phylogenetic and functional originality measures for each scenario, 325 326 each originality index and between originality indices.

327

328 2.3.2. Functional and phylogenetic originalities of carnivore species in Europe

329

330 We investigated the phylogenetic and the functional originalities of European carnivores. We based our study on Temple and Terry (2007) who identified 38 European Carnivora species. 331 Among these species, four were introduced into Europe after 1500 A.D. (Herpestes javanicus, 332 Neovison vison, Nyctereutes procyonoides and Procyon lotor), and seven were defined as 333 marginal in Europe (Cystophora cristata, Erignathus barbatus, Martes zibellina, Odobenus 334 335 rosmarus, Pagophilus groenlandicus, Felis chaus and Mustela sibirica). The qualification of marginal occurrence was attributed to these latter species as less than 1% of their population 336 or of their range lies in Europe (Temple and Terry, 2007). We took phylogenetic data from 337 338 the Carnivora phylogeny established by Nyakatura and Bininda-Edmonds (2012). Trait data were obtained from the PanTHERIA database (Jones et al., 2009). Among the 53 traits 339 present in the database, we eliminated those for which values were missing for more than a 340

quarter of the species. To avoid circularity in our reasoning, we also discarded geographic 341 342 traits. Indeed, we made a difference in originality between marginal and non-marginal species, marginality being defined by the geographic distribution of species. Among 343 344 remaining variables, we removed missing values by using alternative data (MacDonald, 2009; Myers et al., 2015). As the trait database was still incomplete (due to missing values) we 345 could not analyze all traits individually. We thus combined traits for this illustration, in order 346 347 to measure the global functional originality of each species. We provide however in Appendix B a guide on how to deal with individual traits, particularly when some species have identical 348 values for those traits. We discuss also in Appendix B on potential impact of trait selection. 349

350 Before combining the traits we removed redundancy by excluding six of the traits with high correlations with body mass (Appendix B). We ended with 9 traits with only 6 missing 351 values: activity cycle (3 attributes: nocturnal only, diurnal only, others), adult body mass, age 352 at eye opening, diet breadth, habitat breadth, inter-birth interval, terrestriality (2 attributes: 353 354 fossorial and/or ground dwelling only versus above ground dwelling), trophic level (3 attributes: herbivore, omnivore, or carnivore) and weaning age. Body mass, as a 3-355 dimensional quantitative trait, was log-transformed to avoid extreme originalities. Indeed, we 356 357 expected extreme originalities to occur because of species with high body mass such as Odobenus rosmarus (walrus). The complete set of functional traits retained for this study is 358 given in Appendix C. 359

We evaluated phylogenetic signal in traits using Mantel correlations for the combined traits (Hardy and Pavoine, 2012; Pavoine and Ricotta, 2013); for individual quantitative traits we used Blomberg et al. (2003) *K** and Pavoine and Ricotta (2013) *Kw* while for individual nominal traits we used Maddison and Slatkin (1991). We first analyzed the effect of the clustering approach (either UPGMA or Ward) using Spearman correlations for each originality index. Next, we analyzed the Spearman correlations among indices calculated with

phylogenetic and functional data. Then, we analyzed the Spearman correlations between
phylogenetic originality measures and functional originality measures for each originality
index.

We complemented these analyses with some more specific questions related to the 369 conservation of Carnivora species. We distinguished introduced from native species. Among 370 371 natives, we distinguished species whose occurrence is marginal in Europe. We first assessed which species were more original using the median of originality values for each index and 372 group of species. For non-marginal native species only, we used an index of extinction risk 373 defined by the International Union for Conservation of Nature (IUCN) European Red List 374 where species are ranked as follows: 1=Least Concern, 2=Near Threatened, 3=Vulnerable, 375 376 4=Endangered and 5=Critically Endangered (IUCN 2015). We calculated a Spearman correlation between the (functional or phylogenetic) originality and the extinction risk index. 377

378

379 **3. Results**

380 3.1. Simulations

381 When only one trait was used the correlations between measured functional and phylogenetic originalities were always low (Fig. 3). When the number of traits increased, 382 383 correlations increased. They were especially high with PE and related indices (ES and FP, Redding et al., 2014) when the pure birth model was used to simulate phylogenies (with or 384 without the speciation events moved towards tips). When the speciation events were 385 concentrated close to the root only the three indices PE, ES and FP led to correlations 386 between measured functional and phylogenetic originality. The impact of the method used for 387 388 tree construction (i.e. Ward versus UPGMA) on originality depended on the model used to

389	simulate the phylogeny on which traits evolved. Correlations varied from ≈ 0.30 with <i>M</i> , <i>Qb</i> ,
390	<i>tb-AV</i> , and <i>tb-Rb</i> when 50 traits were simulated with the ROOT model to ≈ 1.00 with <i>PE</i> , <i>ES</i>
391	and FP (details in Appendix D). In general, correlations were higher with UPGMA than Ward
392	trees. When the simulated phylogenetic trees were not ultrametric (NU model), AV and Rb led
393	to the highest correlations between functional and phylogenetic originalities. UPGMA and
394	Ward transformations on functional distances thus decreased the connections between the
395	information within functional traits and the model used to simulate them.

- 396
- 397

Insert Fig. 3. 1.5-column fitting image

398

399 On average, the highest correlations (median>0.90) among originality indices were 400 between AV and Rb, between tb-AV and tb-Rb, between Qb and M, and between PE and NN (Table 3). High correlations (>0.70) were also obtained between *Qb*, *ES* and *FP*, between *ES*, 401 402 FP and PE, and between AV, Rb, tb-AV and tb-Rb. Correlations between our new index Rb and the other originality indices were moderate to high, with close-to-1 correlations with AV 403 (Fig. 4). The link between the square root of *Rb* and *AV* was close to linear (Fig. 4a). The 404 lowest correlations with Rb were obtained with PE, NN, and ES (Table 3 and Fig. 4b; see also 405 Appendix E for more details on these correlations). 406

407 Correlations between *Rb* and tree-based metrics tended to be higher when a single trait
408 was used and when traits were simulated using the *NU* model (Fig. 4c). The increase in
409 correlation with only one trait was especially high with *PE*, and related indices (*FP* and *ES*)
410 (Fig. 4c, PCA Axis 1). Correlations of *Rb* with *PE*, *ES* and *FP* were higher with Ward trees
411 and when speciation events were moved close to the root (compared to the pure birth model),

- 412 whereas those with the *tb-AV*, *tb-Rb*, *Qb* and *M* were higher with UPGMA and when the
- 413 speciation events occurred close to tips (Fig. 4c, PCA Axis 2).

415 **Table 3**

- 416 Median correlations among indices (correlations calculated with phylogeny, traits, and the
- two clustering approaches) below the diagonal for the Simulation case study and above thediagonal for the Carnivora case study.
- 419

	М	PE	ES	FP	Qb	tb-AV	tb-Rb	AV	Rb	NN
М		0.60	0.88	0.74	0.92	0.63	0.63	0.60	0.62	0.65
PE	0.36		0.83	0.84	0.77	0.56	0.56	0.60	0.62	0.96
ES	0.69	0.78		0.96	0.95	0.75	0.75	0.75	0.75	0.85
FP	0.61	0.76	0.89		0.96	0.84	0.84	0.84	0.84	0.81
Qb	0.93	0.52	0.79	0.78		0.83	0.84	0.76	0.78	0.80
tb-AV	0.69	0.23	0.42	0.55	0.77		1.00	0.93	0.90	0.55
tb-Rb	0.70	0.24	0.43	0.56	0.78	1.00		0.93	0.90	0.55
AV	0.55	0.24	0.42	0.54	0.62	0.72	0.73		0.99	0.59
Rb	0.54	0.24	0.42	0.54	0.62	0.70	0.71	1.00		0.62
NN	0.36	0.99	0.77	0.78	0.53	0.25	0.25	0.25	0.25	

420

Insert Fig. 4. 1.5-column fitting image

422

425	Compared to the simulation case study, the phylogenetic signal in functional traits was
426	not known a priori. Although phylogenetic signal was significant in all traits except activity
427	cycle (see details in Appendix B), we found low Mantel correlation between phylogenetic and
428	functional distances when using all combined traits (r=0.08, P=0.071). As expected from the
429	low Mantel correlation, correlations between the functional and the phylogenetic originalities
430	were also low (Table 4a). The correlation between the originality values obtained from the
431	two methods of tree construction (Ward and UPGMA) were high (Table 4b), which suggests
432	that the chosen clustering method had only a small impact on the originality estimates in this
433	case study. The highest correlations among originality indices were between FP, Qb, AV, Rb,
434	tb-AV and tb-Rb (Table 3). More precisely, our new index Rb was correlated with all indices
435	in our case study but particularly strongly with AV (Table 3).

Introduced species generally had higher phylogenetic and functional originalities than 436 native species (Fig. 5). Among native species whether the marginally European or the other 437 species were the least phylogenetically and functionally original depended on the index used. 438 There was no evidence for a correlation between the phylogenetic originality of native species 439 and their extinction risk (Table 4c). Correlations with functional originality were higher but 440 still moderate (Table 4d). The highest correlations were obtained with PE and NN, both 441 characterizing strict functional uniqueness. In this case study, using the clustering approaches 442 decreased the correlation between strict uniqueness and extinction risk and its significance 443 (P=0.068 using PE but P=0.039 with NN). All other correlations were not significant (P>0.1). 444

446 **Table 4**

447 Spearman correlations obtained with the Carnivora data set: a) between originality measures

448 obtained using phylogenetic data and those obtained using functional data; b) between

449 functional originality measures obtained with Ward algorithm indices and those obtained with

450 UPGMA; c) between phylogenetic originality measures and IUCN status; d) between

451 functional originality measures and IUCN status. When functional originality is measured, we

452 indicated for each row of the table whether we used raw dissimilarities (noted 'Raw'), Ward

453 trees, or UPGMA trees (see Fig. 2). The notations "(PE)NN", "(tb-)AV" and "(tb)-Rb" mean

- 454 that we applied indices PE, tb-AV and tb-Rb to trees (phylogenies, Ward and UPGMA
- 455 functional trees), and indices NN, AV and Rb to raw dissimilarities (see Fig. 2).

	М	(PE)NN	ES	FP	Qb	(tb-)AV	(tb-)Rb
a) cor(phylogenet	ic originalit	y, functiona	l originalit	y)			
Raw	-	0.19	-	-	-	0.11	0.06
Ward	0.06	0.14	0.30	0.26	0.20	0.21	0.21
UPGMA	-0.19	0.15	0.30	0.24	0.20	0.19	0.19
b) cor(Ward funct	ional origin	ality, UPGN	A functio	onal origina	ality)		
Ward-UPGMA	0.72	1.00	0.92	0.99	0.94	0.96	0.96
c) cor(phylogenet	ic originalit	y, extinctior	n risk)				
Phylogeny	0.01	0.14	0.14	0.08	0.05	-0.12	-0.13
d) cor(functional	d) cor(functional originality, extinction risk)						
Raw		0.40				0.26	0.29
Ward	0.24	0.36	0.32	0.26	0.27	0.12	0.13
UPGMA	0.18	0.36	0.24	0.27	0.22	0.14	0.14

4. Discussion

4.1. Is phylogenetic originality a proxy for trait-based originality?

463	The concept of species originality for conservation has been effectively applied to define
464	conservation priority most successfully through the Evolutionarily Distinct and Globally
465	Endangered (EDGE) program (<u>http://www.edgeofexistence.org/conservation/</u> ; Isaac et al.,
466	2007). Within the EDGE program, Isaac et al. (2007) proposed focusing on those species that
467	are both phylogenetically original and threatened with extinction. To date, mammals,
468	amphibians, birds and reef coral species have been assessed through this method (Isaac et al.,
469	2007, 2012; Collen et al., 2011; Huang, 2012; Jetz et al., 2014). The approach is known to
470	depend only on a single originality index (FP) and different priority schemes would be
471	expected when using other indices (Redding et al., 2014). The use of phylogenies to measure
472	species originality was justified by the assumption that phylogenetic originality reflects how
473	many character states (including observed and unobserved characters) species share (Faith,
474	2002; Pavoine et al., 2005; Isaac et al., 2007; Cadotte et al., 2010).
475	Using a phylogeny to predict diversity has been particularly important for establishing
476	broad-scale prioritizing schemes in conservation biology (e.g. Barker, 2002; Isaac et al.,
477	2007). In more fundamental ecological studies, for example, Strauss et al. (2006) showed that
478	invaders are more likely to be successful if they are phylogenetically distinct from the natives
479	in the assemblage. According to Strauss et al. (2006), not specifying traits might be useful, in

this context, because of the large diversity of mechanisms that underpin invasion success.
However, in community or evolutionary ecology, we might be interested in an identified,
finite set of traits that confer functions to species, in relation, for instance, with biotic
interactions or abiotic filters (Hooper et al., 2005; Violle et al., 2007). Variation in these focal
traits may be more or less predicted by the phylogenetic distances between species (Losos,
2008; Faith, 2015b) depending on the traits.

In our simulations of Brownian trait evolution, correlations between phylogenetic and trait-based strict uniqueness (as measured by *NN* and *PE*) were generally high. However, correlations obtained with other originality indices varied more according to the type of phylogenetic tree simulated and according to the clustering approach applied to traits. Our simulations suggest that a topological index (*M*) should be avoided when the aim is to use phylogenetic originality as a proxy for functional originality. However, it should be noted that the applicability of alternative indices depends on the quality of branch length estimations.

While we might expect that strict phylogenetic uniqueness can act as a proxy for strict 493 functional uniqueness, more generally phylogenetic originalities may rarely act as proxies for 494 trait-based originalities in real case studies. We obtained moderate to high correlations 495 496 between phylogenetic and trait-based originalities only when several traits were simulated. This latter point supports previous arguments that phylogeny-based approaches in ecology are 497 498 integrative: they are applicable in a macroevolutionary context to model many traits or 499 features (Webb et al., 2002). They are less likely to be applicable to specific species' functions 500 associated with community assembly (e.g. Gerholds et al., 2015). We indeed found low correlations between phylogenetic and functional originalities in the real case study where 501 502 traits revealed low (although significant) phylogenetic signals. Functionally but not phylogenetically strictly unique Carnivora species tended to be the most threatened in Europe. 503 These species were notably the nearly threatened *Lutra lutra* (European otter), the vulnerable 504

505 Ursus maritimus (polar bear) and Gulo gulo (wolverine), and the critically endangered
506 Mustela lutreola (European mink) and Monachus monachus (Mediterranean monk seal).

507

508 4.2. How to choose an index of functional originality?

509

In some respects the problem of choosing an index of functional originality is a simple 510 extension of choosing an index of phylogenetic originality. However, indices of functional 511 512 originality are more complex in that traits do not have the intrinsic tree structure on which most current originality indices rely. Our case study on European carnivores highlights that 513 the choice of an originality index can alter the conclusions of a study such as whether original, 514 515 native species are threatened with extinctions. We found low correlations between part of the indices in the simulation and Carnivora case studies. There is thus no one single way to define 516 and codify originality. This highlights that the choice of an originality index is critically 517 dependent on the research question under scrutiny. 518

According to Redding et al. (2014), many originality indices depend on two basic 519 measures: the strict uniqueness (as measured by PE or NN) and the average distance to all 520 521 other species in a set (as measured by tb-AV or AV). As Faith (2008) highlighted, strict uniqueness might be too restrictive as a measure of originality: the originality of the focal 522 species also depends on how many species share its evolutionary history (and/or its functional 523 trait states). For instance, Strauss et al. (2006) found that "the presence or absence of multiple, 524 closely related species and not just a single most closely related species may more effectively 525 526 limit the success of an invader once it has become established". That said, the originality indices most correlated with species' extinction risks in European carnivores were those 527

528 measuring strict functional uniqueness. Strict uniqueness might thus be an important criterion 529 to consider when defining priorities of conservation. However, the generality of this result 530 requires further work controlling for the traits selected to measure functional originalities, the 531 taxa considered and the spatial scale.

Redding et al. (2014) thus considered the average distance to all other species in a set 532 (AV or tb-AV) as the second basic component of species' originalities. Although derived from 533 the same theory as Qb, our case studies clearly highlight the high correlations between the 534 new index introduced in this paper (Rb) and AV. The advantage of AV and the new index Rb 535 over alternative, tree-based indices is that they can both be applied to any dissimilarity matrix 536 without the need to transform them into ultrametric distances, or into trees. An advantage of 537 AV over Rb is the simplicity of its formula. A drawback of AV however, identified by Pavoine 538 et al. (2005), is that it provides very close values for all species. *Rb* being linearly related to 539 the square of AV better discriminates among the species: it better distinguishes species with 540 541 high originality from species with close-to-zero originalities.

The other indices discussed in this paper combine information on strict uniqueness and the average distance to all other species in a set (Redding et al., 2014). When applied to functional dissimilarity, all these indices rely, however, on the use of clustering approaches. The question of choosing an originality index for functional data might then be simplified into whether strict uniqueness or average distance is most important for the question at hand, and whether transforming data by a clustering approach is reasonable (i.e., does the transformation allow information in traits to be retained?).

549 Our hypothesis was that *Rb*, *AV* and *NN* calculated directly on trait dissimilarities 550 should better reflect phylogenetic originalities than indices that require functional trees. This 551 hypothesis failed when traits were simulated from ultrametric trees but was confirmed when

traits were simulated from non-ultrametric trees. In the Carnivora case study, correlations
between *Rb* and *tb-Rb* (and similarly between *AV* and *tb-AV*) were high when analyzing all
traits together; however these correlations may vary with the traits considered (Appendix B).
Only with ultrametric phylogenies and Brownian evolution, a tree-based approach might
better reflect the process(es) that generated traits. However, these assumptions of constant
rates of evolution for all species need to be thoroughly verified.

The largest differences between the two clustering approaches (Ward and UPGMA) appeared when species had large amount of independent (compared to shared) evolutionary histories (ROOT model). More generally, the UPGMA approach led to higher correlations between phylogenetic and functional originalities whichever the index of originality was used. When a tree-based approach is adopted, a UPGMA functional tree could thus be the most appropriate. However, further research is needed specifically comparing a larger range of clustering approaches (Mouchet et al., 2008).

565

566 4.3. Enlarging the perspectives: measure more than species originality

567

Other criteria that may influence the choice of an index is the possibility to use other attributes (than phylogeny or traits) to define species originalities. For example, Faith (2008, 2015a), Rosauer et al. (2009), Cadotte et al. (2010) modified the *FP* index by weighting species by probabilities of extinction, range size and abundance, respectively. Whether these modified measures of phylogenetic originalities can be applied to functional trees is questionable. Indeed they were developed for rooted phylogenetic trees with branch lengths representing shared evolutionary histories. Further research is needed on how to include

additional information such as threat, endemism and/or abundance into indices of functional
originality (See Ricotta et al. 2016 first developments in this direction).

More generally, as dealing with functional originality led us to treat data that are not 577 necessarily connected to a hierarchy (in contrast to phylogenetic trees), the conclusions drawn 578 in this paper have the potential to be extended to assess different types of originality. Indeed 579 580 the concept of originality can be derived at any scale: using dissimilarities between individuals (measuring data per individual), between populations, between species, or 581 between sites (or assemblages, plots, regions, etc.). The concept of originality could then be 582 adapted for establishing conservation priorities across multiple scales. For example, 583 dissimilarities among communities, even when phylogenetic information is used (e.g. Ives 584 and Helmus, 2010; Chiu et al., 2014; Pavoine, 2016), are rarely derived from trees. At the plot 585 and regional scales, our methodology can also be extended to measure the environmental 586 originality of plots within regions, and of regions. This can be done simply by replacing 587 588 biological with environmental data when calculating dissimilarities between plots and between regions. Our study thus opens the way to new directions of research where the 589 biological originalities of areas will be compared to their environmental originalities. 590

591

592 **5. Conclusions**

593 Originality indices provide critically important but different interpretations to 594 measuring biodiversity. The use of these sorts of indices requires more integrative approaches 595 in both space and/or time. Here we have highlighted methodological similarities between 596 functional and phylogenetic originality. We analyzed alternatives for measuring species 597 originalities that do not depend on the clustering approach. We demonstrated the importance 598 of methodological choices in determining species' originalities. These choices are likely to

impact both the probability of observing significantly original species and the chance to 599 understand the local ecological processes driving species originality. Our new index (*Rb*) 600 strongly correlates with the average distance to all other species in a set, and its framework is 601 closely related to indices based on quadratic entropy (OE). In contrast to Rb, the OE-based 602 index (Qb) is influenced both by the effects of average distance and strict uniqueness. Both 603 these indices (*Rb* and *Ob*) are derived from the concepts of diversity (in terms of effective 604 number of species) and entropy. They highlight direct links between originality and the 605 606 contribution each species has to both diversity and entropy. Applications to field observational and experimental studies, as well extending theoretical models, are still 607 necessary to evaluate the future impact of species originality as a dimension of community 608 structure in conservation ecology. 609

610

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616

617 Appendixes A-E. Supplementary data

618

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Fig. 1. Tree-based indices used in this paper: a) the theoretical tree used in all panels with
indication of branches and branch lengths, tips (species from A to F), and root; b) Pendant
Edge (PE) index; c) Fair Proportion (FP) index; d) Equal-Split (ES) index. In each panel,
"Total" indicates the originality values attributed by each index to each species. Letters and
numbers above and below branches on the tree indicate how much each branch contributes to
the originality of each species. For example, in b) only terminal branches contribute to the PE
measure of originality.

	Functional trait data			 Phylogenetic data		
	Raw → dissimilarities	Functional tree	→Patristic dissimilarities	Phylogenetic tree	→Patristic dissimilarities	
ality indices	NN	ES FP M Qb	PE=tb-NN	ES FP M Qb	PE=tb-NN	
Origin	AV Rb		tb-AV tb-Rb		tb-AV tb-Rb	

Fig. 2. Link between data type (functional or phylogenetic data) and the originality indices 821 822 applied to the data. Patristic dissimilarities designate the distance between two leaves (species) measured along the tree: here, half the sum of branch lengths on the shortest path 823 that connects the two species on the tree. We computed Rb, AV and NN directly on the defined 824 functional dissimilarities among species. We also computed them indirectly from the 825 826 established functional trees using patristic distances. In this latter case, the indices Rb and AV 827 were named tb-Rb and tb-AV, respectively, where 'tb' stands for 'tree-based' to explicitly specify that their calculation depended on a functional tree. NN computed indirectly on a tree, 828 noted *tb-NN*, corresponded to *PE* (the pendant edge). 829



Fig. 3. Box plots of correlations between functional and phylogenetic originalities for each
originality index, simulation type [clustering approach (UPGMA, Ward, or raw distances = no
clustering), number of traits (1 trait, 25 traits, or 50 traits), and phylogenetic tree model
(BIRTH, ROOT, TIPS, or NU)].

Fig. 4. Relationships between *Rb* and the other originality indices used in the simulations. a) 838 Typical links obtained between AV and Rb (this example was simulated with BIRTH model 839 and 25 traits). b) Box plots of the Spearman correlations between *Rb* and the other originality 840 indices in the simulation case study. c) Principal component analysis of the Spearman 841 842 correlations between Rb and tree-based originality indices (see also Appendix E for a summary table of the correlations). In c) the coordinates of indices and simulation types are 843 given on axes 1 (57% of variation; horizontal axis) and 2 (26%; vertical axis); supplementary 844 variables (underlined in panel c) were added on the map at the centre of their associated 845 simulation types: the clustering approaches (U=UPGMA, W=Ward), the number of traits (1, 846 847 25, or 50), and the phylogenetic tree model (BIRTH, ROOT, TIPS, or NU)].

Fig. 5. Carnivore case study: box plots of the relative species originalities grouped into 850 851 introduced species (noted 'I' on the left of each panel), native species with marginal occurrence in Europe (noted 'M' at the middle of each panel) and other native species (noted 852 'N' on the right of each panel). Originality was calculated using a) phylogenetic data, b) raw 853 functional dissimilarities, c) functional data and Ward clustering, d) functional data and 854 855 UPGMA clustering. Codes for the originality indices used are indicated at the top of the 856 figure. The notations "(PE)NN", "(tb-)AV" and "(tb)-Rb" mean that we applied indices PE, 857 tb-AV and tb-Rb to trees (phylogenies, Ward and UPGMA functional trees), and indices NN, AV and Rb to raw dissimilarities (see Fig. 2). 858