

# Measuring biodiversity to explain community assembly: a unified approach

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## ABSTRACT

One of the oldest challenges in ecology is to understand the processes that underpin the composition of communities. Historically, an obvious way in which to describe community compositions has been diversity in terms of the number and abundances of species. However, the failure to reject contradictory models has led to communities now being characterized by trait and phylogenetic diversities. Our objective here is to demonstrate how species, trait and phylogenetic diversity can be combined together from large to local spatial scales to reveal the historical, deterministic and stochastic processes that impact the compositions of local communities. Research in this area has recently been advanced by the development of mathematical measures that incorporate trait dissimilarities and phylogenetic relatedness between species. However, measures of trait diversity have been developed independently of phylogenetic measures and conversely most of the phylogenetic diversity measures have been developed independently of trait diversity measures. This has led to semantic confusions particularly when classical ecological and evolutionary approaches are integrated so closely together. Consequently, we propose a unified semantic framework and demonstrate the importance of the links among species, phylogenetic and trait diversity indices. Furthermore, species, trait and phylogenetic diversity indices differ in the ways they can be used across different spatial scales. The connections between large-scale, regional and local processes allow the consideration of historical factors in addition to local ecological deterministic or stochastic processes. Phylogenetic and trait diversity have been used in large-scale analyses to determine how historical and/or environmental factors affect both the formation of species assemblages and patterns in species richness across latitude or elevation gradients. Both phylogenetic and trait diversity have been used at different spatial scales to identify the relative impacts of ecological deterministic processes such as environmental filtering and limiting similarity from alternative processes such as random speciation and extinction, random dispersal and ecological drift. Measures of phylogenetic diversity combine phenotypic and genetic diversity and have the potential to reveal both the ecological and historical factors that impact local communities. Consequently, we demonstrate that, when used in a comparative way, species, trait and phylogenetic structures have the potential to reveal essential details that might act simultaneously in the assembly of species communities. We highlight potential directions for future research. These might include how variation in trait and phylogenetic diversity alters with spatial distances, the role of trait and phylogenetic diversity in global-scale gradients, the connections between traits and phylogeny, the importance of trait rarity and independent evolutionary history in community assembly, the loss of trait and phylogenetic diversity due to human impacts, and the mathematical developments of biodiversity indices including within-species variations.

*Key words:* Functional diversity, environmental filtering, limiting similarity, metacommunity, neutral models, niche-based models, phylogenetic diversity, spatial scales, species richness, trait diversity.

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## I. INTRODUCTION

One of the oldest challenges in ecology is to elucidate the processes that underpin the composition patterns of multispecies communities. Studies of community assembly have often focused on patterns in biodiversity. However, biodiversity is often equated with species richness and/or evenness, while other components associated with diversity have been less well explored.

One of the main objectives of diversity analysis in ecology has been to explain these patterns in species richness and evenness. At broad scales, patterns in species richness are determined across geographic gradients such as those associated with changes in latitude and/or elevation. For plants and animals, species richness often increases near the equator and decreases with elevation or peaks at intermediate elevation. The potential mechanisms identified are numerous and no consensus has so far been reached (e.g. time from colonization, rates of diversification and extinction, zonation of habitats, dispersal limitation; Harrison & Cornell, 2007). At intermediate scales, immigration and regional extinction processes are likely to interact with the processes of speciation and species biotic and abiotic interactions (Harrison & Cornell, 2007).

A range of alternative models and approaches have been proposed to understand these patterns and processes of

community assembly (Magurran, 2004; Chase *et al.*, 2005). Rank-abundance plots, where species are ranked from the most abundant to the least abundant, have been widely used and the original models of species abundance were built from statistical rules on niche partitioning. These approaches are now considered too simplistic (Magurran, 2004) and more recently, species-sorting models have been developed to explore how niche-based processes such as habitat quality and dispersal can affect the composition of local communities. However, patterns in species richness and evenness can often be predicted by more than one model framework (Chase *et al.*, 2005). The failure to reject contradictory models together with access to more detailed species traits and phylogenies, and the development of numerous mathematical diversity measures has led to novel approaches in characterizing the ways in which communities are assembled.

Biodiversity is a complex multifaceted concept that includes scales in space and time, and entities such as species, traits and evolutionary units. Recent research on community assembly has shifted the emphasis away from simple measures of species diversity to trait- and phylogenetic-based determinants of diversity (Webb *et al.*, 2002; Silvertown *et al.*, 2006; Hardy & Senterre, 2007; Cavender-Bares *et al.*, 2009; Pavoine, Baguette & Bonsall, 2010). However, species, trait and phylogenetic diversity patterns are often found to differ. Previous attempts to

replace one measure of diversity with another (e.g. trait diversity with phylogenetic diversity, phylogenetic diversity with taxonomic diversity, trait and phylogenetic diversity with species diversity) have led to strong criticisms (Chave, Chust & Thébaud, 2007; Losos, 2008).

We first compare the vocabulary and methods used to analyse functional *versus* phylogenetic diversity. Then, we review the studies that have compared species, trait and phylogenetic diversity to understand the determinants of community structure and diversity. Although we draw from a wide range of methodological, observational and experimental studies on plants and animals in both aquatic and terrestrial systems, we limit our discussion to diversity within a trophic level. We will not review all mathematical models of community assembly as this has been extensively developed elsewhere (Holyoak, Leibold & Holt, 2005). Our first step is to provide an integrative review of the recent developments in trait and phylogeny measures of diversity and their applications in identifying community assembly rules. The consideration of traits and phylogenies in community assembly studies has required the establishment of new semantics, indices and tools to measure and analyse trait and phylogenetic diversity. Accordingly, we first highlight discrepancies in the vocabulary and semantics used in evolutionary *versus* ecological studies. Next, we identify methodological similarities and differences in approaches to measuring species, trait and phylogenetic diversity. We advocate that general ecological theories of community assembly will only emerge by combining species, trait, and phylogenetic diversity across spatial scales, and this combination provides an exciting range of new prospective research areas. We then consider empirical results that demonstrate how species, trait and phylogenetic diversity patterns can be used concomitantly to reveal large-scale historical, biogeographic and local-scale ecological processes underpinning community structures.

## II. SEMANTIC CONFUSIONS

There is a long history of developments in biodiversity measures. This history has been punctuated by philosophical debate about the basis for measures of diversity. For instance, Hurlbert (1971) claimed that, given the semantic, technical and conceptual problems in the literature on species diversity, the concept of species diversity has become meaningless and the term should be abandoned. However, this term persisted due to numerous attempts to find a unified framework for distinct indices of species diversity (Hill, 1973), to compare the indices (Moullot & Lepêtre, 1999), to identify basic properties that diversity indices should satisfy (Routledge, 1979) and to distinguish richness (number of species) and evenness (species abundance) components of diversity (DeJong, 1975). More recently, the adoption of a multivariate approach to species diversity has quantified and synthesized different characteristics of community structure (Ricotta, 2005; Liu *et al.*, 2007). In this Section, we highlight

that new developments that include trait and phylogenetic diversity also raise questions of definition, vocabulary, and the relevance of the measures developed.

### (1) The consequences of the myriad of biodiversity indices

Many observational and experimental studies have explored phylogenetic and trait diversity patterns in spatially extended communities to understand assembly rules. The difficulty when gathering the results of these studies into a single framework is that phylogenetic and trait diversity have been measured using a wide variety of metrics. The vocabulary used to classify indices 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.

### (2) An example: confusion with “trait evenness”

An example of semantic confusion concerns the definition of “trait evenness” (or “functional evenness”). Trait diversity indices have recently focused on three aspects: trait richness, trait “evenness” and trait divergence (Mason *et al.*, 2005). Although trait richness has a clear definition (the amount of niche space filled by species in the community; Mason *et al.*, 2005), trait divergence and trait evenness still lack appropriate definitions.

Under one definition, trait evenness applies to evenness in the abundance of traits, just as species evenness applies to the evenness of the abundances of species (Mason *et al.*, 2005). More recently, trait evenness has been redefined to include regularity in the distribution of abundance together with the regularity of the traits themselves in niche space (Moullot *et al.*, 2005*b*). Mason *et al.* (2008*a*) underlined this ambiguity by arguing that trait evenness denotes the regularity of the species within niche space *or* evenness of abundance within niche space.

Another source of confusion is that “phylogenetic evenness” has recently been introduced into community studies where species within local communities are less related than expected by chance. This definition was previously referred to as “phylogenetic overdispersion” and, although the use of phylogenetic overdispersion appears more frequently in the literature, it was suggested that this phrase should be abandoned and replaced with “phylogenetic evenness” (Kraft *et al.*, 2007). Similarly, in this context (and in contrast to Mason *et al.*, 2005), “trait evenness” or “trait overdispersion” defines a situation where species within local communities have less similar traits than expected by chance, for instance due to competition (Cavender-Bares, Keen & Miles, 2006).

### (3) Semantic framework

Here, we outline an approach that unifies the different definitions for the aspects of biodiversity. This builds on Ricotta’s (2007) useful attempt to classify indices of diversity

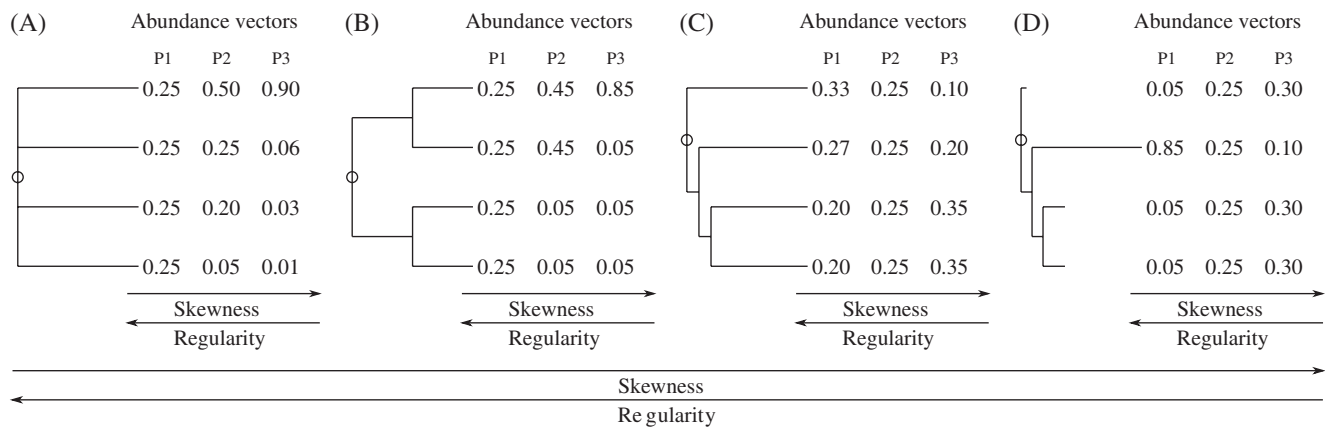
into semantic classes and Mouillot *et al.*'s (2005*b*) distinction between richness, regularity and divergence in functional diversity. In addition, we distinguish the classical richness (i.e. number of species, number of genera etc.), from new multivariate indices. This leads us to six classes. The first three classes are classical (Magurran, 2004):

- (1) Richness. This designates the amount of diversity units (e.g. taxa, functional groups, trait states, niche space coordinates, and evolutionary history units).
- (2) Evenness. This defines the equitability of abundance distribution between diversity units.
- (3) Abundance-weighted diversity indices. These should include all indices (e.g. Shannon, 1948) that combine both richness and evenness.

These first three classes were traditionally used to characterize distinct aspects of species diversity. However they have also been used to measure functional diversity and higher taxa diversity. Regrouping species into functional groups and applying these indices to those functional groups has led to functional diversity estimates (e.g. Stevens *et al.*, 2003). Regrouping species into higher taxa classification has led to taxonomic diversity estimates that have been used to predict species diversity (Williams & Gaston, 1994) but might incorporate phylogenetic components if the diversity in several taxonomic levels is considered (Shimatani, 2001).

More recently, these simple measures of functional and phylogenetic indices have been replaced by more complex, multivariate indices as using traditional indices leads to a loss of information. For instance, in classifying functional groups, differences among species are omitted and any differences between functional groups are always considered to be evenly distributed. Higher taxa diversity is a poor estimate of phylogenetic diversity as it is based on systematic trees without considering temporal evolutionary processes. The next three classes contain synthetic measures based on multivariate distances, sets of points or trees:

- (4) Multivariate richness. This designates measures related to the volume of niche spaces and the length of phylogenetic trees (sum of branch lengths).
- (5) Regularity (Fig. 1). This designates how evenly spread species are in niche space, across a phylogenetic tree or within a functional tree. Here, niche space and phylogenetic or functional trees are defined from the limited set of species considered (e.g. species within a local community) (Weiher, Clarke & Keddy, 1998; Stevens *et al.*, 2003; Mason *et al.*, 2005, 2008*a*; Mouillot *et al.*, 2005*b*; Ricotta & Moretti, 2008). Accordingly, they do not refer to a larger set of species. Regularity of trees implies that the tree is balanced (i.e. rather symmetric) (Clarke & Warwick, 2001; Webb & Pitman, 2002; Heard & Cox, 2007; Helmus *et al.*, 2007*a*). In



**Fig. 1.** The concepts of “regularity” versus “skewness”. For this illustration, we consider theoretical trees with species as tips and theoretical species abundance distributions. The trees could have been obtained with phylogenetic or functional data. We applied the indices of regularity or skewness given in Table 1 to these data (results are given in Appendix S1 and summarized here). For the indices based on distances among species (or minimum spanning trees constructed from the distances among species), we used the sum of branch lengths in the smallest path that connects two species as an evaluation of the distance between them. When species abundances are not taken into account then the regularity depends on the balance of the tree or on the evenness of the distances among species depending on the index used. Arrows indicate the direction according which each index (regularity versus skewness) increases. Most indices agree that the regularity increases from strongly unbalanced trees (case D), comb-like trees (case C), symmetric trees (case B), to equidistant species (case A). The regularity is not impacted by the size (i.e. global height) of the tree. On the contrary, some indices are sensitive to branch length and/or to the number of species (Table 1). The regularity might be changed if the species are weighted by their abundance. Any uneven abundance distribution decreases regularity if the species are equidistant (case A). In that case, the regularity only depends on the evenness of species abundances. The same is true for case B with symmetric trees, except that the regularity will be more reduced if both species within and among clades have distinct abundances (instead of among clades only). When the tree is unbalanced (cases C and D), the regularity might be increased, in comparison with species having equal abundances, if the most distinctive species (most distant from all other species) have the highest abundances. Inversely, the regularity is decreased when the most distinctive species have the lowest abundances.



contrast to regularity, skewness defines the irregularity in the spread of species in niche space, across a phylogenetic or within a functional tree (Heard & Cox, 2007). Regularity might be weighted by species abundances (see Fig. 1).

- (6) Divergence. This designates a dissimilarity measure that is computed from inter-species distances unweighted (unweighted divergence), or weighted by relative abundances (abundance-weighted divergence) (Ricotta, 2007). These distances could be calculated on trait states (Pavoine *et al.*, 2009b) or on the phylogeny (as sum of the branch lengths or nodes in the smallest path that connect two species on the phylogenetic tree, e.g. Pavoine *et al.*, 2008). Among the unweighted divergence indices, Ricotta (2007) distinguished indices normalized by a component of richness. We do not make this distinction here as the level of correlation with species richness is still unknown for most newly developed indices. In addition, we restrict this category of “divergence” to those indices that are related to a multivariate measure of variance.

All these definitions focus on diversity within a community without reference to a larger set of species. On this latter point, two alternatives have been proposed (Webb *et al.*, 2002) to designate higher levels of phylogenetic diversity within a community than that expected by chance from a larger species pool. These are “phylogenetic overdispersion” and “phylogenetic repulsion”. Kraft *et al.* (2007) highlighted that the term “overdispersion” has been used to imply uniform dispersion but may also mean aggregation, which is in contrast to high local diversity. These authors suggested that “phylogenetic overdispersion” should be abandoned and replaced with “phylogenetic evenness”. However, as highlighted above “evenness” is historically used in biodiversity studies to designate uniform abundances, and “repulsion” has the drawback of implying a process where we measure a pattern. Accordingly, we suggest (and use here) that “phylogenetic overdispersion” (and its homologue “trait overdispersion”) designates high local phylogenetic (trait) diversity. Conversely, phylogenetic (trait) clustering defines a situation where the phylogenetic (trait) diversity within local communities is lower than that expected from the larger species pool (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2006; Kraft *et al.*, 2007).

### III. TOWARDS UNIFIED MEASURES OF SPECIES, TRAIT AND PHYLOGENETIC DIVERSITIES

One of the preliminary steps in biodiversity analysis is to determine how diversity should be measured. Research on different measures of species diversity indices has been extensive. Trait and phylogenetic diversity measures have emerged from the idea that the degree of differences among species can be included in biodiversity indices as species are inherently different (Cousins, 1991). Previous reviews of

diversity indices have focussed on species (e.g. Magurran, 2004), traits (e.g. Petchey, O’Gorman & Flynn, 2009) or phylogeny (e.g. Cavender-Bares *et al.*, 2009; Vamosi *et al.*, 2009) but very few have ever dealt with these three aspects of diversity simultaneously (but see Magurran, 2004, for species, trait and taxonomic diversity) and none of them has attempted to compare the wide variety of recent developments for these three aspects of biodiversity.

#### (1) Connections between trait and phylogenetic measures - a generalization

Approaches to trait and phylogenetic diversity still lack an integrated framework. The choice for a diversity index will depend on mathematical properties that confer distinct biological interest. For instance, diversity indices might have distinct connections with species richness (Solow & Polasky, 1994; Petchey & Gaston, 2002; Schmera, Eros & Podani, 2009), power to detect ecological processes (Kraft *et al.*, 2007), and/or behaviour at their maximum (Pavoine & Bonsall, 2009). Accordingly, the use of distinct indices to assess species, trait and phylogenetic diversity measures could confound effects due to biologically inherent differences among species, a set of traits and a phylogeny. Table 1 provides an overview of the multivariate mathematical indices used to measure trait and phylogenetic diversity. While very few indices have been developed through knowledge transfer between the trait and phylogenetic literature, some examples do exist. For instance, Faith’s index of phylogenetic diversity (named PD) (Faith, 1992) has been adopted as a measure of functional diversity (with an index named FD) (Petchey & Gaston, 2002).

This lack of interactions between areas of complementary research has led to repeated independent developments in the biodiversity literature. For instance, measures using quadratic entropy were developed independently in functional ecology (Hendrickson & Ehrlich, 1971; Ganeshaiah, Chandrashekhara & Kumar, 1997), genetics (Nei & Li, 1979), taxonomy (Warwick & Clarke, 1995) and most recently in economics (Stirling, 2007). Other practical indices have been introduced independently in trait diversity and then phylogenetic diversity. This is the case for instance for the average distance and average nearest neighbour approach (Table 1). The lack of integrated development of functional and phylogenetic indices of diversity is striking as functional and phylogenetic data have similar structure. For instance, any index based on species distances could be applied to both functional and phylogenetic distances. Any index based on a phylogenetic tree could also be applied to a functional tree and so on. Accordingly, some indices developed in trait literature can be usefully adapted to characterize phylogenetic diversity. For instance, the MFAD index (Table 1) developed in a functional context as the sum of pairwise trait distances among species divided by the number of species (Schmera *et al.*, 2009), could be adapted for use with phylogenetic distances among species. An interesting feature of this index is that it is less correlated with species richness than indices of trait or phylogenetic richness although it retains the core assumption that its value

Table 1. Indices developed and/or used for measuring functional trait diversity or phylogenetic diversity. We indicate (with crosses) whether each index is based on trees (T) such as phylogenetic trees and functional dendrograms, minimum spanning trees (M), points in a Euclidean space (S) (e.g. niche space), or distances among species (D). The latter category (i.e. the indices that consider directly the distances among species) could be computed from any type of distance, even those distances obtained from trees and points in Euclidean space. The other categories are more exclusive. For instance, indices based on trees work on the tree structure and branch length. We also indicated whether the index is known to be strongly influenced by species richness (column Ri) and whether it depends on the scale of the distance (or tree height) (column Sc) and/or on the absolute abundances of the species (instead of relative abundances) (column Ab). While the list might not be exhaustive, it highlights the level of redundancy and, more importantly, the low level of interactions between the literature on functional and phylogenetic studies

Measure	Code <sup>1</sup>	Functional	Phylogenetic	T	M	S	D	Ri	Sc	Ab
<b>Richness</b>										
Convex hull	<i>ConvH</i>	Cornwell <i>et al.</i> (2006)				×			×	
Exponent of the relation between edge rank and corresponding cumulative edge length in a minimum spanning tree	$\alpha$	Ricotta & Moretti (2008)			×				×	
Sum of branch lengths in a tree	<i>FDPD</i>	Petchey & Gaston (2002)	Faith (1992)	×				×	×	
<b>Skewness/Regularity<sup>(2)</sup></b>										
<b>Unweighted skewness</b>										
Variance in the nearest species distance	$s_{\text{NND}}^2$	Weiher <i>et al.</i> (1998)					×		×	
Variance in the distances among species	$\Lambda^+$		Clarke & Warwick (2001)				×		×	
Standardized sum of differences in species richness between the two subclades defined by each internal node in a tree	Ic		Heard & Cox (2007)	×						
<b>Unweighted regularity</b>										
Diversity in evolutionary distinctiveness among species	HED		Cadotte <i>et al.</i> (2010)	×				×		
Evenness in evolutionary distinctiveness among species	EED		Cadotte <i>et al.</i> (2010)	×						
<b>Weighted skewness</b>										
Relative deviation from null expectation of phylogenetically balanced abundances	IAC		Cadotte <i>et al.</i> (2010)	×						×
<b>Weighted regularity</b>										
Evenness in the branch lengths of a minimum spanning tree	FEve	Villéger <i>et al.</i> (2008)			×					
Evenness in species uniqueness	PAE		Cadotte <i>et al.</i> (2010)	×						
Diversity in species distinctiveness	HAED		Cadotte <i>et al.</i> (2010)	×				×		
Evenness in species distinctiveness	EAED		Cadotte <i>et al.</i> (2010)	×						×
<b>Divergence</b>										
<b>Unweighted divergence</b>										
Sum of distances among species	FAD	Walker <i>et al.</i> (1999)					×	×	×	
Sum of distances among species divided by the number of species	MFAD	Schmera <i>et al.</i> (2009)					×		×	
Mean distance among species	<i>meanD</i>	Weiher <i>et al.</i> (1998)	Webb (2000); Clarke & Warwick (2001)				×		×	
Mean distance to the nearest species	<i>meanNND</i>	Weiher <i>et al.</i> (1998)	Webb (2000)				×		×	
Variability in the distance between the interior nodes and the root in a tree	PSV		Helmus <i>et al.</i> (2007a)	×					×	
Index PSV multiplied by the number of species	PSR		Helmus <i>et al.</i> (2007a)	×				×	×	

Table 1. (Cont.)

Measure	Code <sup>1</sup>	Functional	Phylogenetic	T	M	S	D	Ri	Sc	Ab
<b>Weighted divergence</b>										
Averaged distance among species and their barycentre	FDis	Laliberté & Legendre (2010)				×			×	
Standardized averaged distance among species and their barycentre	FDiv	Villéger <i>et al.</i> (2008)				×				
Variability in the distance between the interior nodes and the root in a tree weighted by species abundance	PSE		Helmus <i>et al.</i> (2007a)	×					×	
Sum of entropic abundance-weighted diversity over the interior nodes of a tree	Hp		Allen <i>et al.</i> (2009)	×					×	
Mean distance among species weighted by species abundance	QE	Pavoine <i>et al.</i> (2004); Botta-Dukát (2005)	Pavoine <i>et al.</i> (2005); Hardy & Senterre (2007)				×		×	
Sum of abundance-weighted diversity over the depth of a tree	Ia	Pavoine <i>et al.</i> (2009a) <sup>3</sup>	Pavoine <i>et al.</i> (2009a)	×					×	
Average conflict among species	Q <sub>α</sub>	Ricotta & Szeidl (2006)	Ricotta & Szeidl (2006)				×		×	

<sup>1</sup>We have tried to keep the names given by the developers. If the developers did not give a short name or if several developers gave distinct names, we attributed a code in italic.

<sup>2</sup>As highlighted in the main text skewness is used in contrast to regularity. Skewness indices increase with skewness (and thus decrease with regularity); whereas regularity indices increase with regularity (and thus decrease with skewness).

<sup>3</sup>Developed with phylogenetic trees but suggested for use with functional trees.

increases with the addition of a new species. By contrast, several indices developed in the phylogenetic literature can be adapted to characterize trait diversity. For instance, two indices have been developed to measure phylogenetic diversity from the Shannon index (Allen, Kon & Bar-Yam, 2009; Pavoine, Love & Bonsall, 2009a). They could be easily applied to a functional dendrogram tree to measure trait diversity. Likewise, Webb (2000) standardized the average phylogenetic distance among species and the average phylogenetic nearest species by their maximum expected value for a given number of taxa and a given phylogeny. These metrics could be very usefully applied to trait distances among species to associate trait diversity patterns with potential ecological processes (e.g. environmental filtering, limiting similarity). More generally, even if each index was developed either on phylogenies or on traits, we propose that any measure presented in Table 1 could be adapted to integrate both trait and phylogenetic diversity simply because the data structures are so similar.

Developing a new index of biodiversity is reasonably straightforward as there are many possible ways of characterizing biodiversity. Consider, for example, the many different metrics that have been developed for characterizing differences among species based on distance (e.g. Legendre & Legendre, 1998). If  $d$  is a function of distance among species, then  $d^\alpha$  is also a function of distance among species with  $\alpha$  in  $[0, \infty[$ . Once the distances have been chosen, they can be integrated with several diversity indices which might be

connected. Appendix S1 outlines such links among different indices. For instance, we demonstrate that an index based on quadratic entropy (QE) can be written as  $\sum_{i=1}^S p_i \|M_i G\|^2$  (Pavoine, Dufour & Chessel, 2004) while an index for functional diversity can be expressed as  $\sum_{i=1}^S p_i \|M_i G\|$  (Laliberté & Legendre, 2010), where  $S$  is the number of species,  $p_i$  the relative abundance of species  $i$ ,  $M_i$  are points that represent species in a multivariate space with a vector of coordinates  $\mathbf{m}_i$ , and  $G$  is the average point (representing an average theoretical species) with coordinates  $\sum_{i=1}^S p_i \mathbf{m}_i$ . From this, we can deduce that a more general index would be  $\sum_{i=1}^S p_i \|M_i G\|^\alpha$ , with  $\alpha$  in  $]0, \infty[$ . In addition, several modifications could be applied to existing indices as there are alternative ways to measure other aspects of diversity such as skewness and regularity. Furthermore additional modifications might be to replace measures based on means with medians (which, as is well-known, are less sensitive to extreme values, see Appendix S1). Given that the possibilities of developments are infinite, we advocate the following points:

- (1) *Focusing on unified frameworks for species, trait and phylogenetic diversity.* New developments should focus on measures that can be adapted to aspects of both functional and phylogenetic diversity. New indices should also extend traditional species diversity indices, to ensure that the differences between species, functional and phylogenetic diversity patterns are not

mathematical artefacts (due to differences between formulae). Such general frameworks of biodiversity do exist. For instance, if species are equidistant, the quadratic entropy that might measure functional and phylogenetic diversity is equal to the traditional Simpson index of species diversity (Pavoine *et al.*, 2004). With particular phylogenies, Faith's (1992) index of phylogenetic diversity (extended to measure functional diversity by Petchey & Gaston, 2002) is related to species richness, and Helmus *et al.*'s (2007a) PSE index is related to the McIntosh index of species evenness. Other indices of phylogenetic and functional diversity encompass species richness, and the Shannon and Simpson indices of species abundance-weighted diversity (Ricotta & Szeidl, 2006; Pavoine *et al.*, 2009a).

- (2) *Basing each index on appropriate assumptions.* Each index must be based on biological [e.g. expected amount of trait states (Faith, 1992); variability in neutral traits (Helmus *et al.*, 2007a)] or biologically relevant statistical arguments (e.g. expected difference between two species in a community; Pavoine *et al.*, 2004). The mathematical properties of each new index must be studied (Pavoine & Bonsall, 2009), so that the connections with previous indices are appropriately established (Appendix S1), and the behaviour and meaning of the index are clearly identified (e.g. minimum, maximum values, dependence on species richness).
- (3) *Attributing various weights to species abundances.* Another important point that has been raised in the development of functional and phylogenetic indices of diversity is the relative importance of species abundances *versus* differences among species. In this vein, new indices could incorporate additional information that weights the relative importance of species abundances when measuring functional and phylogenetic diversity (see for instance Ricotta & Szeidl, 2006; Pavoine *et al.*, 2009a).

In the next two subsections we consider these aspects of trait and phylogenetic measures in the traditional taxonomic context and highlight their dependence on scales.

## (2) Trait and phylogenetic diversities find their foundation in species diversity

Historically, biodiversity studies have focused on species-oriented measures, where the diversity of a community depends on the number of species and their relative abundances. Not surprisingly, many measures of trait and phylogenetic diversity now rely on these previous developments. For instance, Faith's (1992) phylogenetic diversity was developed to estimate the number of distinct trait states found in a community, translating the question of measuring biodiversity from species to that of counts of trait types. Two of the most commonly used indices for species diversity are the Simpson and the Shannon indices. The quadratic entropy index is a generalization of the Simpson

index to include distinct (trait or phylogenetic) distances among species, whereas the former version of the Simpson index assumed that species were equidistant. Several novel indices of phylogenetic diversity now rely on the Shannon index of species diversity (Allen *et al.*, 2009; Pavoine *et al.*, 2009a).

Furthermore, regardless of how an index for trait or phylogenetic diversity has been developed, one of the principal properties of a biodiversity measure that is first analyzed is the shape of the relationship between the new index and species richness. Additionally, a core question is does the index always increase when a new species is added to a community? This property which is rooted in the use of species richness as a measure of ecological diversity is considered by many as an absolute requirement for an appropriate index of diversity (e.g. Izsak & Papp, 2000; Ricotta, 2006; Petchey & Gaston, 2007). All these links between novel measures of trait and phylogenetic diversity and traditional species diversity demonstrate the critical, central role that species richness, evenness and abundance still have in studies of biodiversity.

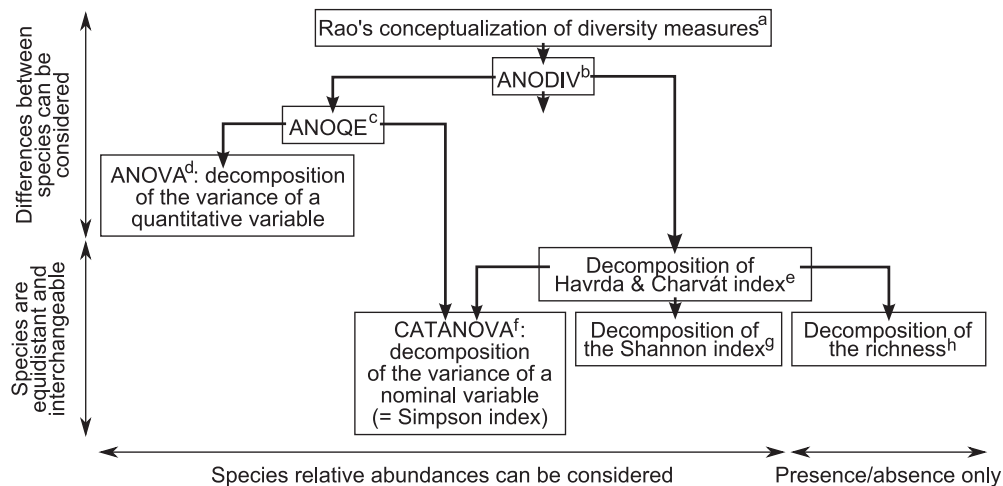
## (3) Towards a spatio-temporal decomposition of biodiversity

It is now well appreciated that species, trait, and phylogenetic diversity need to be integrated across spatial scales. Along this vein, a number of methodological advances have been made such that species, trait or phylogenetic diversity within a region or a metacommunity (set of local communities linked by dispersal,  $\gamma$ ) is divided into a local ( $\alpha$ ) diversity and a component associated with the differences between local communities ( $\beta$  diversity) (Veech *et al.*, 2002; Pavoine & Dolédec, 2005; Bryant *et al.*, 2008; Graham & Fine, 2008; Ricotta & Burrascano, 2008). Regional and local diversities are obviously interconnected. Regional processes drive local community assembly (Ricklefs, 1987) and the size of the regional species pool affects the composition of the local communities. By contrast, any process that leads to the local extinction of a species, to character displacement, or speciation may also influence the composition of the regional species pool.

What is less known is that the additive decomposition of biodiversity measures (where  $\gamma = \alpha + \beta$ ) can be reconciled with a unified framework for species, trait and phylogenetic diversity (Fig. 2; Pavoine, 2005). Graphical analyses of species, trait and phylogenetic diversity within and between assemblages (Pavoine *et al.*, 2004), linked with statistical approaches (Pavoine & Dolédec, 2005; Hardy & Senterre, 2007; Péliissier & Couteron, 2007) can be developed to understand the mechanisms that underlie biodiversity patterns.

The decompositions of biodiversity indices traditionally have been explored across the spatial scales ( $\gamma$ ,  $\beta$  and  $\alpha$  levels) (Whittaker, 1960). However, the mathematical frameworks on which these indices are based also allow other types of decompositions including temporal analyses. Accordingly the numerous approaches that have been developed in the





**Fig. 2.** Connections between additive decompositions of diversity indices. <sup>a</sup> (Rao, 1986); <sup>b</sup> the analysis of diversity (ANODIV) allows the decomposition of diversity indices according to crossed and hierarchical factors (Rao, 1986); <sup>c</sup> the analysis of the quadratic entropy (ANOQ) denotes the decomposition of the quadratic entropy index (see Table 1) according to any set of crossed and/or hierarchical factors (Rao, 1986; Pavoine & Dolédec, 2005); <sup>d</sup> the analysis of variance (ANOVA) corresponds to the decomposition of the variance of a quantitative variable across any set of crossed and/or hierarchical factors (Fisher, 1925); <sup>e</sup> the decomposition of Havrda & Charvát index  $(1 - \sum_i p_i^a)/(1 - a)$ , where  $p_i$  is the relative abundance of species  $i$  and  $a$  denotes a parameter that must be chosen ( $a \geq 0$ ), is possible on any levels of hierarchical factors, and on crossed factors depending on the values of  $a$  (Rao, 1986); the decomposition of Havrda & Charvát index has three special cases: <sup>f</sup> the Simpson index with  $a = 2$  is decomposable over any number of hierarchical and crossed factors (Light & Margolin, 1971; Anderson & Landis, 1980; Rao, 1986; Lande, 1996); <sup>g</sup> the Shannon index with  $a$  tends to 1 is decomposable over any number of hierarchical but only two crossed factors (Lewontin, 1972; Rao, 1986; Lande, 1996); <sup>h</sup> the richness with  $a = 0$  is decomposable over any number of hierarchical but no crossed factors (Rao, 1986; Lande, 1996).

literature to analyse diversity on hierarchical spatial scales (e.g. local communities, regions, continents) could be applied to analyse diversity across a hierarchy of temporal scales (e.g. years, decades, and centuries). New research should focus on these temporal aspects and, more importantly on spatio-temporal analyses. Recently, Pavoine *et al.* (2009a) developed this approach to understand rockfish (genus: *Sebastes*) phylogenetic diversity (as measured by the quadratic entropy, see Table 1) in the Southern California Bight. The global diversity of the rockfish assemblage was measured within the whole period of study (1980–2007; the  $\gamma$ -like component), within each year (the  $\alpha$ -like component) and among years (the  $\beta$ -like component). This approach tests whether differences among years are higher than expected by chance. Pavoine *et al.* (2009a) demonstrated significant temporal changes in the phylogenetic composition of the assemblage driven by a drastic decline in abundance of six lineages. By contrast, an increase in the abundance of other lineages followed La Niña events. Such temporal analyses reveal the impact of global changes (here fishing pressure and sea water warming). The quadratic entropy index used in the Pavoine *et al.* (2009a) study has even more potential. It can, for instance, allow spatio-temporal diversity decomposition where total diversity is divided into a component of diversity within time and space units, a component due to differences between time units, a component due to differences between spatial units and an interaction component due to the combined effects

of time and space (mathematical approaches for these decompositions can be found in Rao, 1986). The quadratic entropy has been adapted to measure species diversity, trait diversity and phylogenetic diversity in a wide range of applications (Pavoine *et al.*, 2004; Botta-Dukát, 2005). Yet, we still find no applications of such spatio-temporal decompositions to understanding biodiversity.

In this Section we have demonstrated that the measures and approaches to species, trait, and phylogenetic diversity could be unified. Unifying semantic differences as described in Section II and unifying appropriate statistical frameworks as argued in this section are essential steps in linking distinct measures of diversity. There remain many unexplored mathematical aspects of biodiversity analyses which could be very promising. This is acutely true where the focus is on the effects of global change on biodiversity. In the subsequent sections of this review we demonstrate why the inclusion of phylogenetic and trait diversity, in addition to species diversity, into community assembly studies will enhance our understanding of the processes that underpin ecological community compositions.

#### IV. EXPLORING A MULTI-DIMENSIONAL APPROACH TO BIODIVERSITY

While most studies of diversity focused on species, traits, or phylogeny, some have tracked patterns associated

with combinations of diversity measures to draw stronger inferences on the potential ecological and evolutionary processes that affect the compositions of communities and regions. For example, within a region, high species- $\beta$ -diversity (species turnover) could occur through deterministic environmental filtering or limited dispersal. To distinguish between these two mechanisms, patterns in trait, phylogenetic and species diversity can be used. Under environmental filtering the differences among habitats in terms of traits (and phylogeny if traits have a phylogenetic signal) are high, because trait values are associated with habitat characteristics. It is thus expected that for a given amount of species turnover among habitats, environmental filtering leads to higher trait turnover than expected if species were distributed randomly across the habitats. In the African rainforest, inselbergs that comprise a range of ecological microhabitats differ in levels of plant diversity. Parmentier & Hardy (2009) found that phylogenetic clustering was significant between plots from different microhabitats and increased with habitat differentiation, suggesting that environmental filtering is the predominant process structuring the assemblage. However, the phylogenetic structure between plots of similar microhabitats was random. Observed species differences between plots of similar microhabitats (which increased with geographic distance), were affected by limited dispersal. As the phylogenetic differences between plots with distinct ecologies were close to the root of the phylogenetic tree, Parmentier & Hardy (2009) hypothesized that the relationships between phylogenetic structure and environmental filtering were primarily due to ancient diversification events in the plant communities followed by phylogenetic conservatism.

If our goal is to seek general principles underlying community assembly then we advocate that these will only emerge by adopting a more pluralistic approach and combining observed patterns for several indices of diversity (Table 2).

### (1) Species richness *versus* trait and phylogenetic diversity

By understanding the link between species diversity, trait diversity and phylogenetic diversity it will be possible to identify the mechanisms that shaped local communities (Table 2). Patterns of phylogenetic richness at large spatial scales are likely to be primarily determined by species richness. However, the spatial patterns of the relative phylogenetic richness (phylogenetic richness divided by species richness) might provide insights into the historical evolutionary processes including the balance between speciation and extinction that affect community assembly. This is likely as the spatial representation of relative phylogenetic richness will allow changes in phylogenetic richness that are not caused by species richness to be realized. Davies *et al.* (2007) for instance explained global variation in parrot (Aves: Psittaciformes) species richness through the correlations between relative phylogenetic diversity and environmental factors (Table 2). Extending measures

of biodiversity to more than two indices is likely to be essential in highlighting the suite of mechanisms affecting species distribution. Understanding the decomposition of trait and phylogenetic diversity into richness, regularity and divergence will be essential to this goal (Mason *et al.*, 2008a).

### (2) Traits might explain phylogenetic diversity...

Understanding how traits change and evolve is necessary for interpreting the patterns of phylogenetic overdispersion *versus* clustering (Table 3). Indeed, both competition associated with traits that have been conserved through evolutionary time (niche conservatism) and environmental filtering processes associated with traits that have converged through evolution can lead to local phylogenetic overdispersion within communities (Kraft *et al.*, 2007). Measuring trait diversity in addition to phylogenetic diversity distinguishes between these alternative mechanisms: in communities that display high phylogenetic diversity, high trait diversity tends to suggest that competition on phylogenetically conserved traits is the main driver, whereas low trait diversity is evidence for environmental filtering on convergent traits. The presence of environmental filtering should be determined by clear associations between environments and traits (see Mayfield & Levine, 2010 for other possible mechanisms).

### (3) ... and phylogeny might explain trait diversity

Variation in trait states may be partitioned into components related to (a) a species' environment, (b) both environment and phylogeny, (c) phylogeny, and (d) an unexplained component (error) (Desclaves *et al.*, 2003). These relative components provide insights into the mechanisms that can determine trait diversity (Diniz-Filho & Bini, 2008). A high value for (a) might indicate that species have responded to environmental changes through adaptations; either by phenotypic plasticity or by evolving adaptations in the traits without geographic range shifts. A high (b) value might indicate that species evolved according to niche conservatism if there is a causal relationship between phylogeny and the environment. Component (c) arises through long-term evolutionary constraints and stabilizing selection.

### (4) Different patterns revealed by different aspects of biodiversity

Most applications of biodiversity indices use a single measure of either trait or phylogenetic diversity. Few studies have compared trait richness, trait regularity and trait divergence or phylogenetic richness, phylogenetic regularity and phylogenetic divergence. Yet, it is expected that trait and/or phylogenetic richness, regularity and divergence are related to distinct mechanisms affecting community assembly. For instance, by using a taxonomy instead of a phylogeny, it has been found that, for fish, zoobenthos and macrophytes, eutrophication in lagoons in southern

Table 2. Overview of potential explanations for the positive or negative correlations between two indices of diversity

Pattern	Explanations	References
Evolutionary pathways of traits		
Positive correlation between trait and phylogenetic diversity	- Phylogenetic signal; phylogenetic niche conservatism	Losos (2008)
No relationships between trait and phylogenetic diversity	- Traits were all labile; mixture of conserved and labile traits	Losos (2008)
Community ecology		
At global scales ( $\gamma$ ):	Biogeographic and historical factors	
High species richness and low relative phylogenetic diversity	- Increase in speciation rates when species richness is driven by topographic variability - Areas where sympatric species occurred by rapid adaptive radiation; areas that are cradle of evolution	Davies <i>et al.</i> (2007) Davies <i>et al.</i> (2007)
High species richness and high relative phylogenetic diversity	- Decrease in extinction rates where driven by productive energy and generally by ambient energy - Areas that were colonized early and had more time for speciation	Davies <i>et al.</i> (2007) Wiens & Donoghue (2004)
At local scales ( $\alpha$ ):	Ecological factors	
Low trait diversity relative to species diversity	- Environmental filtering if associated with specified environmental variables	Holdaway & Sparrow (2006)
High trait diversity relative to species diversity	- Limiting similarity processes (e.g. competition, mutualism, facilitation) at small spatial scales	Holdaway & Sparrow (2006)
High species diversity and high trait diversity	- Heterogeneity and niche complementarity (e.g. following disturbance)	Mayfield <i>et al.</i> (2005); Grime (2006)
No relationships between species diversity and trait diversity	- Balance between environmental filtering and limiting similarity	Hubbell (2006); Mason <i>et al.</i> (2008b)
Low phylogenetic diversity and high trait diversity relative to species diversity	- Negative interactions between related, similar species, leading to character displacement and/or replacement by less similar species	Prinzing <i>et al.</i> (2008)
Turnover ( $\beta$ , linking $\gamma$ with $\alpha$ )	Ecological and historical factors interact	
High species $\beta$ -diversity <sup>1</sup> and low trait $\beta$ -diversity <sup>1</sup>	- Within patches of similar habitat, community assemblage might be historically contingent due to species sequence arrival (stochastic factors) and deterministic due to environmental filtering - Competition within patches of similar habitat	Fukami <i>et al.</i> (2005) Slingsby & Verboom (2006)
High species $\beta$ -diversity <sup>1</sup> , high trait $\beta$ -diversity <sup>1</sup>	- Environmental filtering: $\beta$ -diversity is high between patches of different habitats	Cavender-Bares <i>et al.</i> (2006)
High phylo $\beta$ -diversity <sup>1</sup> and high trait $\beta$ -diversity <sup>1</sup>	- Environmental filtering and niche conservatism	Kraft <i>et al.</i> (2007)
Low phylo $\beta$ -diversity <sup>1</sup> and high trait $\beta$ -diversity <sup>1</sup>	- Environmental filtering and trait convergence	Kraft <i>et al.</i> (2007)
Low or random phylo $\beta$ -diversity <sup>1</sup> and low trait $\beta$ -diversity <sup>1</sup>	- Competition and niche conservatism	Kraft <i>et al.</i> (2007)

<sup>1</sup>Low (*versus* high) species  $\beta$ -diversity means low (*versus* high) turnover between communities and thus higher (*versus* lower)  $\alpha$  species diversity than expected given the regional species pools; low (*versus* high) trait  $\beta$ -diversity means low (*versus* high) differences in trait composition between communities and thus higher (*versus* lower)  $\alpha$  trait diversity than expected given the regional species pools, which corresponds to local trait overdispersion (*versus* clustering); Low (*versus* high) phylo  $\beta$ -diversity means low (*versus* high) differences in the phylogenetic composition between communities and thus higher (*versus* lower)  $\alpha$  phylogenetic diversity than expected given the regional species pools, which corresponds to local phylogenetic overdispersion (*versus* clustering).

France had low impact on species richness and taxonomic divergence but led to taxonomic skewness due to nonrandom loss of species (Mouillot *et al.*, 2005a).

Consequently, combining diversity indices into two-dimensional plots or by using multidimensional statistical techniques could help to tease out the mechanisms that

Table 3. Examples of the connections between trait evolution and trait patterns (linked to ecological processes) with the phylogenetic pattern of a metacommunity. This table is based on Table 1 in Webb *et al.* (2002) and Table 1 in Kraft *et al.* (2007). However it allows traits to follow different evolutionary pathways. We assume that  $\beta$  traits have been selected where environmental filtering acts, and  $\alpha$  traits where limiting similarity acts (Pickett & Bazzaz, 1978; Ackerly *et al.*, 2006; Silvertown *et al.*, 2006)

	Conserved $\alpha$ and $\beta$ traits	Convergent $\alpha$ traits; conserved $\beta$ traits	Convergent $\alpha$ and $\beta$ traits
Environmental filtering (trait clustering)	Phylogenetic clustering	Phylogenetic clustering	Phylogenetic overdispersion
Limiting similarity (trait overdispersion)	Phylogenetic overdispersion	Phylogenetic clustering or randomness	Phylogenetic clustering or randomness
Balance between environmental filtering and limiting similarity <sup>1</sup> (trait randomness)	Phylogenetic randomness	Phylogenetic clustering or randomness	Phylogenetic randomness

<sup>1</sup>Trait diversity is measured on a mix of  $\alpha$  and  $\beta$  traits.

shape communities at several spatial scales. Furthermore considering the differences between trait and phylogenetic diversity is crucial in order to distinguish between local ecological and broad, historical, biogeographic processes.

## V. EMPIRICAL RESULTS: LINKING BIODIVERSITY WITH HISTORY AND BIOGEOGRAPHY

At large scales, the majority of original studies on biodiversity focussed on measures of species richness and ignored evolutionary and functional processes associated with diversity. Trait diversity is still seldom used at large scales, probably as it requires the characterization of carefully selected traits for numerous species and clades. Likewise, phylogenetic methods have been mostly developed to reconstruct the environment, area and date of origin associated with lineages, to identify the evolutionary processes that have led to differences between extant species, to estimate extinction and diversification rates (Ricklefs, 2007), and to search for the phylogenetic identity of invasive and endangered species, but less often to measure phylogenetic diversity. We review below the handful of studies that combined phylogenetic diversity analysis at broad scales with analyses of species diversity or trait diversity. Throughout this part of the review, we demonstrate that comparing phylogenetic diversity with species diversity can reveal historic processes including recent adaptive radiation, high immigration rates, differences in speciation rates, and range expansion among lineages. Furthermore, combining phylogenetic and trait diversity can be used to disentangle hypotheses on historical and biogeographic processes *versus* ecological processes in determining species compositions of communities and regions. Consequently, we advocate that ongoing research should focus on merging phylogenetic analyses with species and trait diversity analyses with the objective of resolving the determinants of community diversity and structures.

### (1) Linking species richness with phylogenetic diversity to reveal assembly formation processes

Correlating species diversity with phylogenetic diversity has helped to illustrate the sequence of speciation and dispersal events in assemblage formation processes. For instance, Cardillo, Gittleman & Purvis (2008) found that, in the majority of island mammal assemblages, phylogenetic patterns were random. This might be explained by a lack of phylogenetic signal in key ecological traits, although trait values were not available to verify this hypothesis. Nevertheless, on land-bridge islands, phylogenetic divergence in some mammal taxa tended to be higher in islands with high species richness, high maximum elevation, greater habitat homogeneity, or small area. Land-bridge islands are likely to have resulted from restricted sets of species isolated by rising sea level at the end of the Pleistocene, that were subsequently affected by selective or random extinction. Accordingly, apart from possible human-induced extinctions and introductions, these patterns of phylogenetic and species diversity can be interpreted by competition for resources and selective extinctions after the islands were isolated. By contrast, phylogenetic divergence on oceanic islands was weakly associated with island attributes and decreased with species richness. For part of the taxa (primates, rodents), this might indicate that oceanic islands were predominantly shaped by colonization and endemic speciation leading to low phylogenetic divergence within an island despite high species richness. More generally, low phylogenetic diversity associated with high species richness and endemism might indicate hotspots of recent adaptive radiation (e.g. Cape floristic region of South Africa and oceanic archipelagos such as Hawaii) that were formed by sympatric species that subsequently diversified extensively (Slingsby & Verboom, 2006).

In the analysis of assembly formation processes, phylogenetic skewness might be used to complement other aspects of phylogenetic diversity including phylogenetic richness and divergence, and phylogenetic overdispersion *versus* clustering. Phylogenetic skewness (imbalance of



the phylogenetic tree shape as opposed to phylogenetic regularity, see Section II) was developed in biodiversity studies by Clarke & Warwick (2001) but is still seldom applied in empirical studies. Yet it might reveal evolutionary and historical processes of diversification and expansion at the origin of assembly formation. Indeed, phylogenetic skewness might arise if radiations are geographically limited, when subclades achieve different diversification success in different areas, and when some lineages are inherently more likely to speciate (or are less vulnerable to extinction). It can also appear when some species extend their ranges further and faster than others (as observed in African primates; Heard & Cox, 2007).

Accordingly, through these studies, we demonstrate that hypotheses on colonization, expansion, diversification, and extinction processes might be drawn by associating studies on species diversity with those of a multi-dimensional approach to phylogenetic diversity. In one subsequent step, the time for speciation hypothesis developed below connects colonization events with the level and direction of speciation and explains species richness patterns with phylogenetic diversity patterns.

## (2) Phylogenetic diversity disentangles large-scale gradients in species richness

A high phylogenetic diversity across a region might be used as evidence to determine the origin of a species group when other arguments have been assembled (e.g. Braby, Trueman & Eastwood, 2005). Indeed, according to the “time-for-speciation” hypothesis, an area colonized early has had more time to diversify (leading to both high species and phylogenetic richness) than areas more recently colonized by a subset of lineages that have had less time to diversify (low species and phylogenetic richness). Nevertheless, high species and phylogenetic richness might arise from other mechanisms including high diversification rates. High species richness in an area can thus be explained by the “time-for-speciation” hypothesis if it can be demonstrated that the area was colonized early (in comparison with specified reference areas with lower species richness), that the area exhibits high phylogenetic richness, and that species within the area did not emerge as a result of a high diversification rate. To date, the “time-for-speciation” hypothesis has been most extensively tested along large-scale geographic gradients (Wiens & Donoghue, 2004).

The question of understanding why assemblages are species-rich or -poor has more recently been extended to why clades have dispersed into some areas but not others (Wiens & Donoghue, 2004). Here, to illustrate this, we explore the use of phylogenetic diversity in understanding one of the most well-studied large-scale patterns in species richness: the latitudinal gradient where species numbers increase from the poles to the equator. The mechanisms invoked to describe this pattern have focussed on a bias in diversification rates due to buffers against extinction and/or an acceleration in speciation due to metabolic activation or a greater climatic zonation on tropical mountain slopes providing opportunities for geographic isolation (Ricklefs,

2006; Kozak & Wiens, 2007; Svenning *et al.*, 2008); see Mittelbach *et al.* (2007) for a review of other potential mechanisms. More recently, climatic niche conservatism controlling dispersal has also been proposed as one of the probable causes of the latitudinal bias in species richness (Wiens & Donoghue, 2004; Pyron & Burbrink, 2009), at least for a large range of groups of organisms. This hypothesis predicts higher phylogenetic diversity (many older clades) in the original climate area (Wiens & Donoghue, 2004) and links the time-for-speciation hypothesis with dispersal mechanisms (e.g. limited dispersal from the original climatic region). It assumes that the traits associated with climatic preferences of species are conserved in the phylogeny, strongly restricting the ability of species to adapt to new climatic environments. The hypothesis is, therefore, contingent on both ecological and evolutionary history.

For example, New World leaf bat (Phyllostomidae) diversity can be described by the climatic conservatism hypothesis (Stevens, 2006). In this study, Stevens (2006) proposed a novel test of the climatic conservatism hypothesis. He not only determined patterns in species and phylogenetic diversity but also tested if the observed phylogenetic diversity could be confounded with species richness. A phylogenetic tree was built from nuclear and mitochondrial genes and several aspects of phylogenetic structure were used. They relate to the amount of independent evolutionary time (mean and variance in species ages, i.e. time from speciation) and to the overall amount of evolutionary time (mean and variance of the distance from a taxon to the root of the phylogenetic tree). All these measures evaluate the mean and variance in species contributions to phylogenetic richness. As specified in Kerr & Currie (1999), the distance of a taxon to the root of the phyllostomid tree was used as a measure of the rate of sequence divergence of that taxon; taxa with long root distances being the product of more diversification than taxa with short root distances. Species average age and the variance in the distance from a taxon to the root of the phylogenetic tree were shown to decrease with latitude. Furthermore, the average distance from a taxon to the root of the phylogenetic tree first decreased and then increased with latitude. By contrast, the variance in species ages was not correlated with latitude. Sampling of species demonstrated that these patterns of phylogenetic diversity could not have been obtained randomly from species richness. Accordingly, as the proportion of the most derived and least variable taxa increased from the centre to the periphery of the geographic range in this family of bats, this suggests that climatic niche conservatism and a continuously expanding geographic range explain the diversity in this group of species.

Phylogenetic diversity patterns have thus helped to identify the processes that underpin the latitudinal gradients in species richness. Nevertheless, the power of phylogenetic diversity to explain species richness patterns is contingent on specific geographic or taxon constraints. For example, climatic and landcover variables but not phylogenetic diversity (measured as mean taxon age) explained variation in species richness

in cicindelids (tiger beetles) and freshwater fish in North America (Kerr & Currie, 1999). In addition, Kerr & Currie (2009) found that, in treefrogs (Hylidae) in the western hemisphere, phylo- $\alpha$ -diversity (within 100 × 100 km equal area quadrats) and phylo- $\beta$ -diversity (among quadrats) were strongly related to minimum annual temperature, indicating conservatism in cold tolerance. However, local species richness was determined solely by precipitation and not by temperature.

### (3) What about trait diversity?

Studies of trait diversity at large scales are scarce (but see, Willig, 2001; Davies *et al.*, 2003; Stevens *et al.*, 2003; Micheli & Halpern, 2005; Beche & Statzner, 2009; Ingram & Shurin, 2009). We found no studies that combined species, trait and phylogenetic diversity at large spatial or temporal scales. Yet trait diversity could also help to disentangle large-scale patterns including latitudinal gradients in species richness. This is why the establishment of large trait databases is crucial (e.g. Kleyer *et al.*, 2008); and we suggest that new research on the mechanisms that determine community structure at large scales should include trait diversity. Indeed, for instance, the increase in species richness towards the equator could occur due to an increase in the number of functional groups within a community as well as the number of species per functional group (Willig, 2001). By comparing species richness with functional diversity measures, Stevens *et al.* (2003) found that trait diversity in New World bat communities generally increased towards the equator at a faster rate than expected given spatial variation in species richness. They found that this pattern in trait diversity is dependent on the composition of species at the regional scale. Furthermore, local communities were characterised by trait clustering (lower trait diversity than expected), a few functional groups dominating species richness by having large numbers of species. The traits included in this analysis were those associated with resource exploitation. This indicated that the increase in trait diversity with decreasing latitude could be due to the combined effects of local variations in the quantity and quality of resources and regional variations in species composition (species- $\beta$ -diversity among regions, especially at the area of transition between temperate and subtropical zones). Combining these results with those given in Stevens (2006) (see Section V.2), these differences in species composition across regions might be due to species expanding their geographic range differently because of climatic niche conservatism.

Another interesting aspect of trait diversity at large scales is that, combined with species (or genus) diversity (Beche & Statzner, 2009) or phylogenetic diversity (Ingram & Shurin, 2009), it can discriminate between local *versus* long-term biogeographic processes in determining the composition of local assemblages. For instance, Ingram & Shurin (2009) analysed 30 published Pacific rockfish (*Sebastes* spp.) assemblages. They analysed diversity in morphology (represented by body size and eye size) and dietary variables (represented by gill raker length and number). They found

overdispersion in gill raker length and number (and to a lower extent in body size) indicating limiting similarity where biotic forces (e.g. competition, mutualism) tend to keep coexisting species from being too similar (leading to high local trait diversity). By contrast, they found clustering in eye size indicating environmental filtering where abiotic forces act to constrain certain traits within limits (leading to low local trait diversity). They also found phylogenetic overdispersion. This could not be explained by the traits included in the analyses because they revealed either clustering or overdispersion and had low phylogenetic signal. Phylogenetic diversity increased in deeper and higher latitude assemblages and decreased in shallow southern assemblages. Again this pattern contrasts with trait diversity as the diversities in body size and gill raker characteristics were insensitive to both depth and latitude, whereas patterns of diversity in eye size with depth and latitude contradicted those of phylogenetic diversity. Ingram & Shurin (2009) concluded that traits were affected by local ecological processes while phylogenetic diversity was affected by the biogeographic history of the *Sebastes* genus in the north-east Pacific. *Sebastes* species originated from the north-west Pacific and expanded southward and inshore followed by repeated speciation. Accordingly, the higher phylogenetic diversity in the ancestral deep and high-latitude habitats might be due to the migration of recent lineages south and inshore.

In this section, we demonstrated that, coupled together, species, trait and phylogenetic diversities have the potential to discriminate ecological and historical processes at large scales. A striking point of these large-scale studies is that the indices used to evaluate phylogenetic structures (e.g. average species age) are often different from those given in Table 1 and primarily used at local scales. As continental processes might affect regional and local processes, we advocate that new studies of phylogenetic diversity at broad scales also include those indices given in Table 1, so that the measurement of phylogenetic diversity at both broad and local scales could be usefully compared. Summarizing the results of this section we can state that low phylogenetic richness and/or divergence associated with high species richness and endemism indicates that communities have been assembled from a recent adaptive radiation; high phylogenetic richness/divergence indicates high immigration rates from larger spatial scales with low geographic and/or climatic barriers, or ancient areas. High phylogenetic regularity might arise if lineages are equally likely to speciate or to expand their range. Finally, the comparison of the level of species or phylogenetic variation across regions to the level of trait change might indicate the relative importance of biogeographic, historical factors (e.g. colonization and endemic speciation events) *versus* local ecological factors that drive assemblage formation. Regarding our main objective, these results demonstrate the necessity to combine several aspects of biodiversity (here species richness, phylogenetic and, if possible, trait richness/regularity/divergence) in the search for community assembly processes.

## VI. DIVERSITY AT THE LOCAL SCALE: EMPIRICAL PATTERNS

At local scales, many evolutionary and ecological processes affect patterns of diversity. These include major components of neutral community models: random speciation and extinction, ecological drift, and also interactions among individuals provided that they are unrelated to fitness differences among species. By contrast, fitness-dependent competition, facilitation, mutualism and environmental filtering are deterministic processes (acting through fitness differences among species according to abiotic or biotic interactions; major components of niche-based models) affecting diversity. An important question is how biodiversity patterns could help to distinguish between stochastic and deterministic forces affecting community structure. Several studies on a variety of taxa have demonstrated that local trait and phylogenetic diversity patterns are associated with environmental factors and species interactions indicating that deterministic ecological processes act within local communities. These studies focused, for example, on yeasts (Anderson, Lachance & Starmer, 2004), grasslands (Fukami *et al.*, 2005; Mayfield *et al.*, 2005), herb-layer plants (Gerhold *et al.*, 2008), trees (Webb, 2000; Cavender-Bares *et al.*, 2006), geographic plant ranges (Chave *et al.*, 2007), fishes (Helmus *et al.*, 2007b; Mason *et al.*, 2008b), birds (Lovette & Hochachka, 2006), and bats (Stevens *et al.*, 2003). Here, we have selected some of those studies that combined several aspects of biodiversity to draw hypotheses on the mechanisms that shape the composition of communities. Fig. 3 summarizes patterns and processes associated with species and trait diversity acting at the local scale. The combined analysis of species diversity and trait diversity (and/or phylogenetic diversity) at the local scale has highlighted that communities that are structured by ecological processes such as competition and environmental filtering are driven more by niche-based than neutral processes. By contrast, neutral processes may be more likely in species-rich communities that are dispersal-limited and where the success of new species (through reproduction and/or immigration) is low (Hubbell, 2006). Neutral processes might also act within groups of species with similar ecological traits, whereas niche-driven processes will act between groups (Bonsall, Jansen & Hassell, 2004; Herault, 2007) to influence community assembly. The addition of phylogenetic diversity with trait diversity still remains to be clarified. Indeed many studies used phylogenetic diversity as a proxy for trait diversity. We advocate that future research studies should highlight the crucial role of phylogenetic data in determining the evolutionary processes that underpin both species and trait diversity.

### (1) Phylogenies or traits

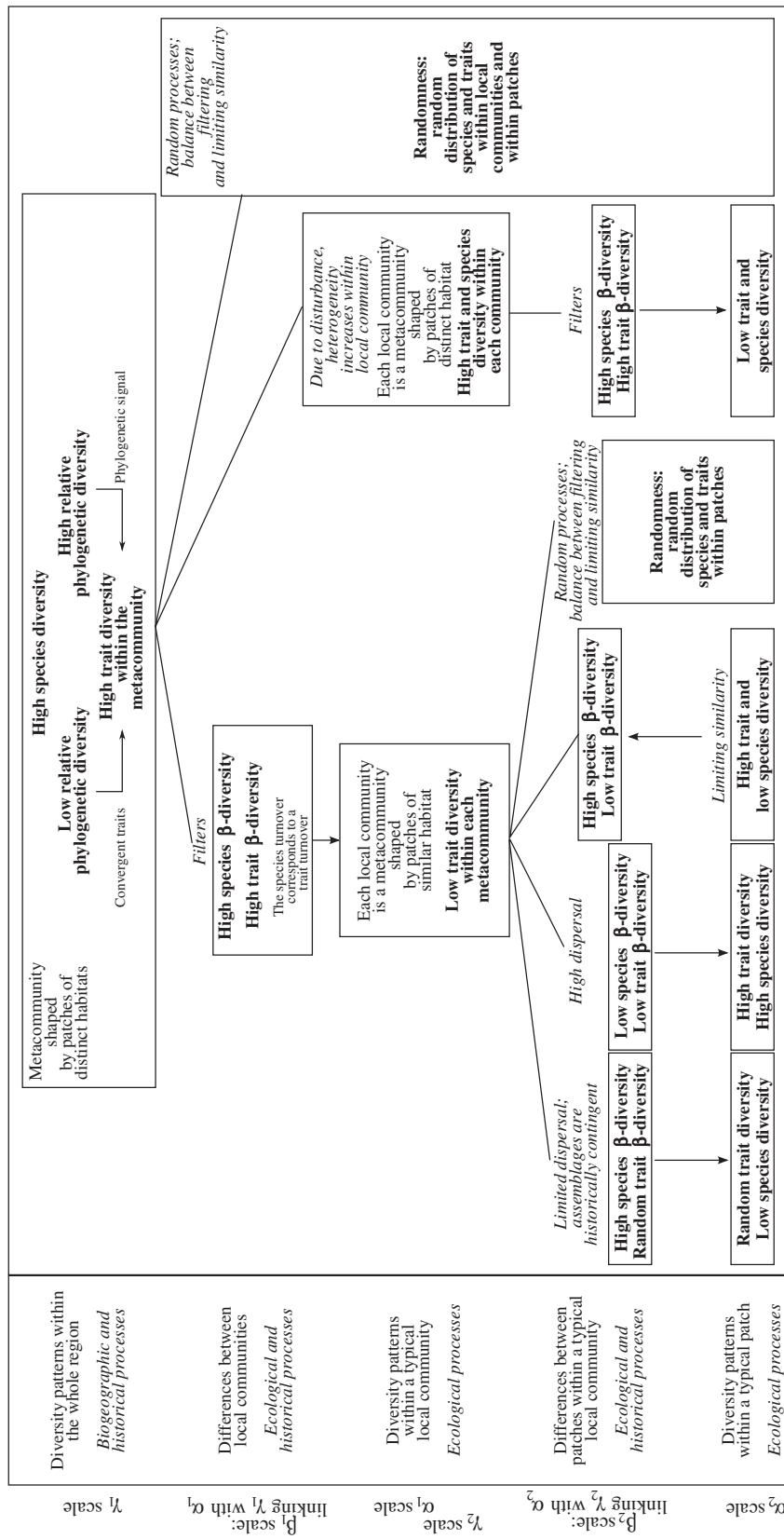
It has been hypothesized that at local scales ecological factors act faster than biogeographic and/or historical factors (Ricklefs, 2004). Consequently, trait diversity is used to explore the ecological mechanisms associated with local community assembly. However, a critical step in the

measurement of trait diversity is the choice of a subset of traits and the measurement of the trait values for a wide range of species (Petchey *et al.*, 2009). Given that phylogenetic details integrate more information on trait diversity than a simple finite set of traits, one possibility is to focus on phylogenetic diversity, even if the goal is to interpret the observed patterns of a (meta)community in terms of traits. Many studies have thus used phylogenetic relatedness as a proxy for trait similarity (Swenson & Enquist, 2009).

However, a problem of conflating phylogenetic diversity with trait diversity in understanding assembly patterns is that the phylogenetic signal of the metacommunity will ultimately depend on the evolutionary pathways that important traits have followed. Recent studies of community assembly have opposed conserved traits against convergent traits (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2006). Conservation here means phylogenetic signal in trait variation across species (more closely related taxa are more similar) rather than higher phylogenetic signal than expected from a Brownian model (which would imply mechanisms that decrease trait evolutionary rates) (Losos, 2008). Convergence here means that related species pairs display, on average, traits more dissimilar than less-related species pairs. The use of phylogenetic diversity as a surrogate for trait diversity is often justified by the fact that, even if some traits affecting community organization are evolutionary labile, most of them are expected to exhibit some phylogenetic signal (through ancestor legacy) (Webb, 2000). However no congruence has been obtained so far on the conserved or convergent status of traits involved in distinct ecological processes (Ackerly, 2003; Ackerly, Schilck & Webb, 2006; Emerson & Gillepsie, 2008; Losos, 2008). This is why we advocate shifting from considering phylogeny as a proxy to considering phylogeny as a complementary source of information for revealing evolutionary and biogeographic processes underpinning diversity.

### (2) Using both phylogenies and traits to disentangle local processes

Phylogenetic diversity studies indeed add an extra dimension to understanding local processes by revealing historically contingent processes. Harrison & Cornell (2007 page S1) stated that “community phylogeny merges the ecologist’s traditional concern with the distribution of traits among coexisting taxa with phylogenetic approaches to understanding where and when those traits evolved”. Accordingly, instead of using phylogenetic diversity as a proxy for trait diversity, we should follow this idea of “community phylogeny” and use phylogeny to evaluate the evolutionary history of key traits involved in ecological processes (e.g. environmental filtering) at local scales. Such an approach has the potential to associate prospective approaches, asking how present-day ecological processes may lead to evolutionary changes, and retrospective approaches, asking how present-day ecological conditions can be understood as the outcome of historical contingent events (Losos, 1994). The connections between prospective and retrospective approaches should be the focus



**Fig. 3.** Overview of the potential connections between indices of diversity in community ecology (under the mechanisms cited in Tables 2 and 3). Observed processes are given in *italics*. Observed patterns are given in **bold type**. We assumed high trait and species diversity at the larger regional scale as this will determine the possibilities of high trait and species diversity at local scales and/or high trait and species turnover between local spatial units. High trait diversity at larger scales is necessary for the occupation of various niches at lower scales. The level of diversity at one scale is given relative to its level at the higher scale. Low diversity at  $\alpha_1$  level means lower diversity within a local community at  $\alpha_1$  level than expected from the diversity at  $\gamma_1$  level in absence of deterministic processes. We consider that trait (species)  $\beta$  and  $\alpha$  diversity are random if traits (species) are distributed randomly within local communities and/or patches as specified.



of ongoing studies. Recently, Prinzing *et al.* (2008) determined that communities of phylogenetically related species might be more prone to trait overdispersion through character displacement or species replacement to limit species competition. In addition, several studies demonstrated that interactions among species can have feedbacks on evolutionary processes causing *in situ* speciation, adaptive radiation (Cavender-Bares *et al.*, 2009) and random or convergent trait evolution (Losos *et al.*, 2003; Elias *et al.*, 2008).

New methodologies are now developed to analyse patterns in trait diversity with an explicitly phylogenetic context. As highlighted in Section IV, to merge evolutionary with ecological approaches, some suggested partitioning the variation in trait values across phylogenetic and ecological (environment and/or space) factors (e.g. Desveiges *et al.*, 2003; Freckleton & Jetz, 2009). This process might be used to evaluate the level of phylogenetic signals in trait variation. It might also be used to evaluate phylogenetic niche conservatism. Traits are under phylogenetic niche conservatism if their variation is explained by environmental factors that are correlated with phylogenetic factors. Recently, Pillar & Duarte (2010) highlighted how to evaluate phylogenetic niche conservatism by combining tests for phylogenetic signals with tests for associations between trait diversity and environmental gradients. They analysed plant diversity along a grazing gradient in natural grasslands in Brazil. They selected seven functional traits and found that four had a significant phylogenetic signal. However only two displayed a significant phylogenetic signal at the metacommunity level: i.e. communities that were more similar in their phylogenetic structure were also more similar in their average trait values. Furthermore, the traits that were associated with environmental filtering across the grazing gradient were those that had no phylogenetic signal. Accordingly, the traits involved in the environmental gradient evolved independently of the phylogeny. Phylogeny and environment thus independently explained the values of distinct traits, which invalidates the assumption of phylogenetic niche conservatism.

Moreover, rather than searching for global patterns of evolutionary and ecological factors across whole communities, future research should ask which traits, which lineages and which environmental variables are responsible for patterns of the composition of communities within a region. Mayfield, Boni & Ackerly (2009) determined environmental filtering effects not across whole communities but from specific clades. In a fragmented southern Costa Rican landscape, they demonstrated associations between rain forest understorey and animal dispersal traits in monocots, rain forest understorey and insect pollination in the Piperaceae, and deforested habitats and wind dispersal in some Asterids. Their approach evaluates whether individual clades are maintained in a habitat because of environmental filtering, which provides a precise indication on the predominance of ecological processes over historical processes in determining phylogenetic diversity patterns. In a similar vein, Pavoine *et al.* (2010) showed how trait diversity might be decomposed across the nodes of a phylogenetic tree

revealing which lineages contribute more to trait diversity. Here trait diversity may incorporate species abundances and the phylogenetic pattern in trait diversity may be compared across spatial scales. This may determine whether the clades that contribute more to trait diversity at a regional scale are those that contribute to trait diversity at a local scale. Ubiquitous clades are likely to affect all scales while clades with limited dispersal will have their highest influence in patterns of trait diversity at the local scale. Applied to butterfly communities of chalk grassland in northern France and southern Belgium, they found that environmental filtering in traits with limited phylogenetic signal determined the co-occurrence of species in local communities. Trait diversity within local communities was mainly due to trait differences among species within three families (Nymphalidae, Satyridae and Pieridae) whereas trait diversity at the metacommunity level was determined by large trait differences both within and among seven families.

Here, we have separated the empirical studies between large scales and local scales. Of course there is a continuum in the scales at which studies are performed and some combine local, regional and large-scale processes. Nevertheless, it should be noted that the use of phylogenetic diversity as an indicator of historical processes is more pronounced in large-scale, biogeographic studies. Most local-scale studies have so far used phylogenetic diversity as a proxy for trait diversity, or to validate the results obtained with a limited number of traits (evaluating whether some important traits could have been omitted from the analysis). Yet, in summary, studying trait diversity in a phylogenetic context has the potential to highlight: (i) whether important traits have been omitted (if structures are found in the phylogenetic relatedness among species but not in their trait states); (ii) whether phylogenetic patterns are due to phylogenetic niche conservatism, implying both phylogenetic signals and environmental filtering in trait values; (iii) whether a particular clade is maintained in a habitat because of environmental filtering; (iv) whether the clades that contribute to regional trait diversity also contribute to local trait diversity; and (v) whether ecological factors such as species interactions might have affected the shape of the phylogeny leading to speciation and radiation. Species diversity should not be excluded from these analyses, and obviously the patterns of trait diversity at local scales can be interpreted more broadly when compared to patterns of species diversity (see Fig. 3). Based on this we advocate studies that compare species diversity, trait diversity and phylogenetic diversity across spatial scales to reveal the patterns of community structure driven by diversity.

## VII. DIRECTIONS FOR FUTURE RESEARCH

Synthesizing findings on patterns of species, trait, and phylogenetic diversity could open up a range of new questions and answering these questions will be essential in order to understand the future of biodiversity in terms of changes in ecosystem function and losses of evolutionary history.

### **(1) Do trait diversity and phylogenetic diversity increase with spatial distances?**

It is well-known that biogeographic patterns and correlations change with distance (Fortin & Dale, 2005). From this, the distance-decay similarity principle assumes that the similarity in species composition between patches is expected to decay with the spatial distance between them; and species richness is expected to increase with area size. Few studies have investigated similar trends in trait and phylogenetic diversity (but see Bryant *et al.*, 2008) and this requires further exploration.

### **(2) Could phylogenetic and trait diversity explain global-scale gradients?**

Across an elevation gradient in Tanzanian tropical rainforest, large tree species richness is random but there is a constant turnover of species composition and an increase in phylogenetic diversity from low to high elevation (Tallents *et al.*, 2005). This pattern reveals restricted elevation ranges at the family level and the occurrence of distinct lineages (notably gymnosperms) at high elevation. The investigation of phylogenetic and trait  $\alpha$  and  $\beta$  diversity across wide regions (or gradients) is rare yet it could help to clarify underlying ecological and historical mechanisms affecting the persistence of the regional species pool and the structure of local species assemblages. However, most analysis of trait diversity at large scale calculated trait diversity within local communities only (but see the local plus watershed scales in Beche & Statzner, 2009). Diversifying the spatial scales at which trait and phylogenetic diversity are measured is a challenging aspect to future research on community assembly rules.

### **(3) Is it possible to integrate the complementary strengths associated with phylogeny and traits?**

Considering phylogenetic diversity as a surrogate for trait diversity is very restrictive. Phylogenetic diversity is a much more inclusive measure that quantifies the combined effects of genetic and phenotypic diversity, and provides historical and evolutionary explanations for patterns in biodiversity. As far as we know only one study has extended traditional analyses by measuring trait diversity with phylogenetically independent contrasts (Tofts & Silvertown, 2000). Another approach integrates trait differences at each level of the phylogenetic tree (Pavoine *et al.*, 2010). More research is needed to exploit both the historical and ecological potential of phylogenetic diversity.

### **(4) Could phylogenetic and trait distinctiveness complement studies on biodiversity?**

In contrast to diversity, distinctiveness is a species-specific measure that evaluates how a focal species is different from all others in a community. Still seldom investigated, distinctiveness is also associated with key mechanisms, especially species extinction (species distinct in their trait states and phylogenetic position might be more vulnerable; Magnuson-Ford *et al.*, 2009) and invasion (phylogenetically

distinct species are more likely to invade an area without extinction or exclusion of native species; Strauss, Webb & Salamin, 2006). Distinctiveness as a complementary measure to diversity requires more detailed exploration and analysis.

### **(5) How much phylogenetic and trait diversity is endangered?**

Numerous studies have now explored the question of conserving phylogenetic diversity as a means of conserving both species traits and maintaining diversity for future evolutionary diversification (Forest *et al.*, 2007; May, 2009). However, the problem of directly conserving trait diversity (Fonseca & Ganade, 2001; Dalerum *et al.*, 2009) and species through the processes and mechanisms that drive community assembly (Smith & Grether, 2008) still requires extensive investigation.

### **(6) What rationale underlies a diversity index?**

The development of diversity indices is still in its infancy. The relationships between measures and processes as described in Table 2 are dependent on the metric used. Contradictory results may appear as a given type of diversity at a given scale could be expressed by various metrics with different statistical behaviours. Consequently, there is a risk of erroneous interpretations especially if simple verbal arguments are followed in a simplistic way. There is a clear and important need for theoretical studies (Pavoine & Bonsall, 2009) and validation against simulated datasets where processes are controlled and clearly defined. Furthermore, the inclusion of additional ecological and evolutionary details (such as intraspecific variation) into trait and phylogenetic diversity indices should be the focus of future studies (e.g. Cianciaruso *et al.*, 2009 for trait diversity).

## **VIII. CONCLUSIONS**

- (1) The myriad of approaches developed to measure biodiversity has enriched our understanding of community organisation. Each approach captures a different aspect of diversity. Phylogenetic diversity offers historical explanation to large-scale processes that impact local communities and to local ecological processes that feedback on species and trait evolution. Trait diversity highlights more directly the ecological processes that affect local communities.
- (2) Merging trait with phylogenetic diversity analyses requires a unifying vocabulary, appropriate mathematical indices and comprehensive approaches. Here, we have suggested a semantic framework, demonstrated similarities among indices, and accordingly advocate that new developments in biodiversity measurements rely on strong biological and mathematical justifications. Furthermore, measures of diversity should encompass species, trait and

phylogenetic diversity, and include differential weights for species abundances across varying spatio-temporal scales.

- (3) Although few studies have compared species diversity, trait diversity and phylogenetic diversity, we know that phylogenetic and trait diversity patterns are likely to be at least partially correlated with species diversity patterns. In addition, phylogenetic diversity patterns cannot be interpreted without inference on trait diversity patterns, and trait diversity patterns depend on ecological, stochastic and historical, phylogenetic processes. Species, trait and phylogenetic diversity are thus connected and complementary.
- (4) At large spatial scales, such comparisons can help to identify numerous patterns such as adaptive radiation events, geographic or climatic barriers, areas of origin of a species lineage, unequal speciation and range expansion rates among lineages, and the relative importance of biogeographic factors versus local ecological factors in assemblage formation. At local scales, comparative studies can determine, for instance, whether the amount of species diversity and the presence of particular lineages is influenced by ecological processes acting on particular traits.
- (5) Accordingly, to find clear generalities in the mechanisms that underpin community assembly, biodiversity patterns need to be studied across spatial and temporal scales. They should account for the multiple forms of variation embodied in the multifaceted concept of biodiversity. Studies should include not only species, trait, phylogenetic diversity and abundance, but also aspects of richness, regularity and divergence associated with trait and phylogenetic diversity. Future studies should also focus on trait and lineage-specific mechanisms; integrating the idea that ecological and historical biogeographic processes act on a subset of the community.

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## XI. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

**Appendix S1.** Bestiary of diversity measures: differences among the multivariate indices of biodiversity.

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