Application of functional distances to diversity indices :
A tool toward more integrated choices about conservation?

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Abstract. Measuring biodiversity is a crucial issue to develop sustainable management schemes. A fundamental question arising from conservation policy is about the type of diversity function to be preserved. Weitzman (1992) proposes a conceptual definition of such a biodiversity function, by considering aggregated pairwise distances between species within the set of the ecosystem. In his application to crane conservation (Weitzman, 1993), he uses some information about of genetic dissimilarities to measure distances between species. Shifting the focus of those measures from the level of species genetic diversity towards the level of functional diversity may be an interesting application of Weitzman's approach to determine an operationally meaningful diversity function that allows for choosing among policy preservation. Functional distance measures are indeed directly related to some more general aspect of ecosystem functioning. They play a crucial role in the maintenance of important ecosystem processes, and put the emphasis on the role of species interactions. Combining Weitzman approach and functional diversity allows diversity assessment methods to move closer to the concept of ecosystem services used by most economists (even if greater validation of measures is required). In this paper, we want to review how the abundant albeit debatable findings in the field of functional diversity research may provide some crucial information to be used in defining an operational value of diversity function. Building on the approach developed by Weitzman on the aggregation of species pairwise dissimilarities, we look at the applicability of functional distance measures in place or in complement of the phylogenetic distances used by Weitzman to determine the most preferable biodiversity set. Operational implications and constraints are discussed.

1. Introduction

Biodiversity preservation constitutes a considerable challenge ahead of us, and probably one of our greatest and most urgent responsibility towards future generations and our own. The vibrant denunciation of the accelerating loss of species in response to human population and economic development pressures was launched by Wilson in his 1988's "Biodiversity" book. The following years saw the emergence of an extensive literature, especially in ecology, on the role of biodiversity in providing livelihoods for humans (e.g. Chapin et al., 2000; Cardinale et al., 2012). A crucial question is how the degradation of all levels of biological diversity may alter the functioning of ecosystems, and consequently their ability to provide society with the goods and services required to for their sustainable social and economic development. The extent to which human-induced modifications of biodiversity components may affect ecosystem functioning is however subject to an intense debate in the ecology community (Hooper et al., 2005).

To offer a clear and exhaustive definition of biodiversity is an extremely difficult task that may even appear unrealistic. The concept reflects indeed the intrinsic variety, variability and complexity of life, leading our definition to be necessarily oriented or partial. However, to some degree, it is possible to gain information about this complexity by decomposing biodiversity in several components reflecting objective hierarchical units. Biologists often use an operational decomposition into the genetic, taxonomic and ecosystemic levels of diversity (Marty, Vivien, Lepart, & Larrere, 2009). But many other classifications may be considered with for example populations, species, family, order, genus, phylum, ecosystem, etc. (Groombridge, 1992). Beyond those operational and theoretical classifications, one level of diversity reaching currently general importance in ecological research is the concept of 'functional diversity'. The concept is used across a wide range of ecosystems and taxa (Petchey & Gaston, 2006) and stands as 'the range and value of those species and organismal traits that influence ecosystem functioning' (Tilman, 2001). A specificity of the functional diversity approach is to focus on what species 'do' in ecosystem rather than on phylogenetic and their evolutionary history.

Several measures of diversity are proposed in the literature. Most are related to the number of species (e.g. Fisher index, Shannon-Weaver index), some include information about species evenness and relative abundances and others add information about species dissimilarity (e.g. Weitzman index, Bervoets and Gravel index, Nehring et Puppe index). The procedure developed by Weitzman (1992) to rank different set of species according to their diversity is the only measures for which we dispose of an axiomatic characterization, and that doesn't violate properties that should be met by a diversity function. Weitzman provided an illustration of his procedure by using information about genetic distances between species (Weitzman, 1993).

The principal contribution of the present paper is to assess whether gaining information about functional distances between species may be of interest to rank different diversity sets. The choice between different configurations would be made on the basis of distances between functional aspects of species rather than their genetic divergence, which may not provide information about the role of species in the ecosystem. This would constitute a rather interesting mix of ecological indices and indices of prioritization, and may help to include the three level of biodiversity into measures (richness, evenness and divergence).

In a first part, we will describe different indicators used in biodiversity measurement and the issues attached to them. Subjectivity implied by choices about 'what' we want to preserve in biodiversity and 'why', is illustrated through differences in the development of biodiversity indicators in ecology and in economics. This will follow with a general overview of different biodiversity indices developed in the literature, leading to identify the three components of biodiversity that should (theoretically) be reflected in species diversity indicators: species richness, evenness, and divergence. We relate this observation to functional diversity, which also present those three different facets: functional richness, evenness, and divergence.

In a second part, we will describe more precisely the idea of Weitzman's criterion, as the only dissimilarity index relying on an axiomatic characterization. We will put forward its advantages and its limitations, especially in terms of the practicality of the use of genetic distances among species. We will discuss the improvements proposed on this basis by Weikard (2005), and show that it could

go further. We suggest that genetic distances may be insufficient to provide information about the role of species within a community, and propose to apply measures of functional diversity (functional trait distances) to this stepwise procedure. We provide a basic example of how this could be done in practise by defining functional traits and how to allocate values.

The third part will be devoted to describe more precisely the functional distances to be used and the way it is traditionally measured, mostly in the ecological literature. We then discuss the practical consequences of applying such a trait-based measure of distances, which is still loaded by many uncertainties related to the status of current knowledge about fundamental ecological processes linking biodiversity, ecosystem functions and services ((Cardinale et al., 2012). We conclude by raising potential implications of such an analysis, which could take benefit of some larger multicriteria evaluation method, implying fuzzy set considerations in order to derive some more operational results (Munda, Nijkamp, & Rietveld, 1995).

2. Biodiversity: Why measure it and what to measure ?

2.1. Need for prioritization in biodiversity conservation

Conservation of biodiversity is facing important budget constraints, associated to reduced availability of public funds to biodiversity issues worldwide (Feger & Pirard, 2011). In such a context, talking about identifying and prioritizing conservation goals is no longer considered an awkward thought. The identification of funding needs, gaps and priorities of biodiversity conservation in every country was indeed one of the most important recommendations of the CBD during the 10th Conference of Parties in 2010 in Nagoya (CBD, 2010); While ecologists have a crucial role to play in identifying the elements of biodiversity that contribute to ecosystem maintenance and functioning as well as potential goals for conservation, economists may contribute in determining what could be the most efficient methods to prioritize and achieve such goals. Among the measures developed by economists, some procedures focused on the prioritization of species and ranking of diversity sets to be preserved. Such procedures belong to cost-effectiveness economic models,

which could therefore contribute to target more efficiently diversity policies ((Eppink & van den Bergh, 2007).

## 2.2. Ecological and economic measures of biodiversity

Different measures of biodiversity have been proposed through the years by ecologists and more recently by economists. Although they differ in their purpose, both approaches provide some fundamental – but quite differentiated – insights to the question: what should we preserve, and why? For economists, biodiversity must be preserved as a social value, valuable to society in two main ways: First, it can provide a larger set of options on natural assets for current and future generations. This allows increased possible choices of agents from this set and consequently freedom of choices. Whether higher diversity is synonymous of freedom is however questionable and to some extent implausible, especially if we consider that access to natural resources is far from equally shared, and need to be regulated for its sustainable use. Second, diversity represents some instrumental value in providing some degree of "well-being" or welfare to society. This welfare is evaluated mainly through the definition of ecosystem services of provisioning, regulating, supporting, and cultural services. Economists therefore developed a rather utilitarian view of biodiversity, which raises several questions about the objectives pursued when measuring such diversity. In each case, measuring biodiversity is about evaluating and ranking the options offered by different biodiversity configurations. The measure must allow a choice among possible options which would be the most valuable to society, or which would preserve the greatest choice set. This quite operational standpoint doesn't account much for ecological dimensions in deciding over sets of biodiversity.

On the other hand, ecologists endorse a more *conservative view* of species diversity and consider e.g. how it guarantees long term functioning of ecosystems. In order to provide more ecologically accurate indices, distribution and relative abundances of species within the set are much more often included into the measures (Baumgärtner, 2007). Measuring biodiversity follow therefore a rather descriptive objective, in an attempt to understand and represent natural processes as accurately as possible. In general, those measures don't tend to decide or discriminate among different set of species. In order to make operational decisions about biodiversity preservation, it may be important to

reconcile those views and use them conjointly in order to provide more sustainable and accurate estimations of diversity.

2.3. Overview of biodiversity measures: from species diversity to functional diversity

Traditionally, measures of biodiversity have focused on species diversity in ecosystems, by focusing on different aspects of this diversity, entailing species **richness, evenness and divergence**. Biodiversity is therefore considered as a set of species, which may be measured in terms of their *number* (or richness of species) and the *evenness* of their distribution within the ecosystem considered, but also the general "*distance*" or "divergence" between species. Measures of biodiversity may consider those three facets to different extent, depending on the type of indicator.
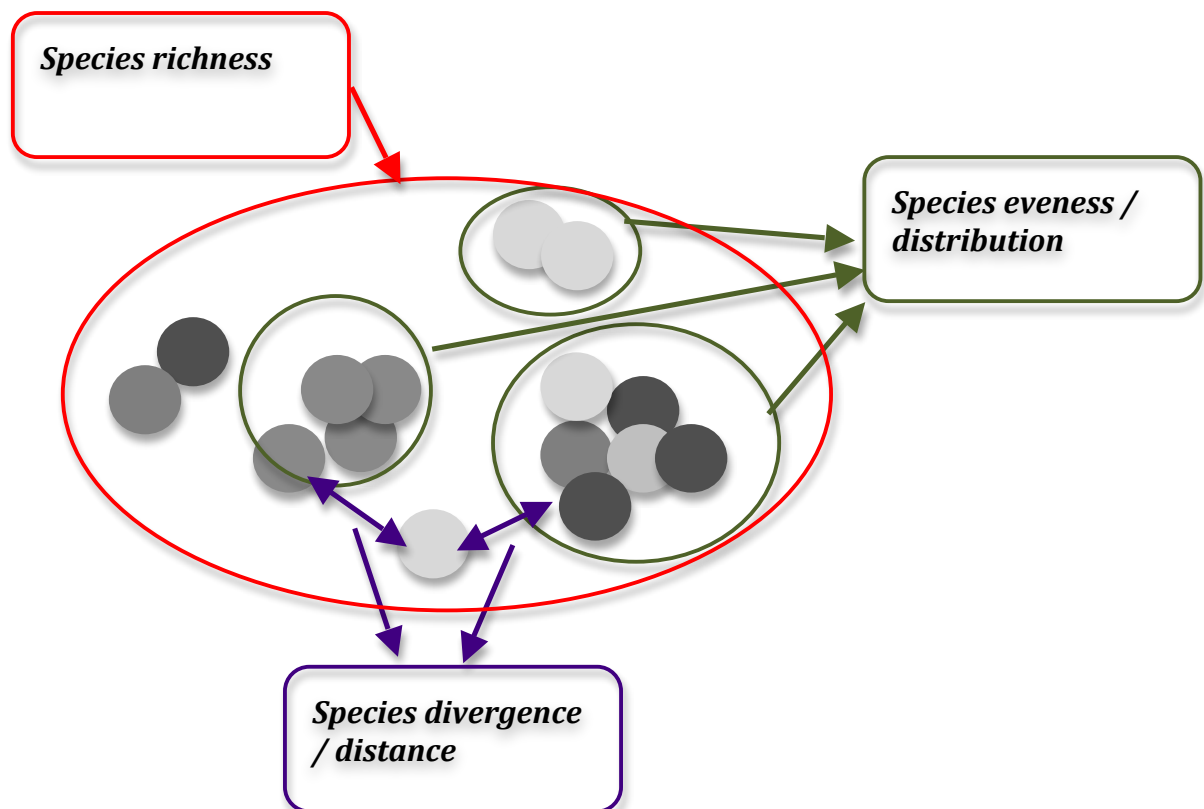
Counting of equivalent species

Traditional biodiversity indices like cardinal criteria didn't account for any distances or differences among species and consider species richness as a way to rank different samples of species. Those measures implicitly considered that (1) all species are considered equal, only pondered by their relative abundances, and (2) all individual are equal, whatever their sizes and shape. Many compound indices incorporating relative proportions of individual species were developed

on this basis, and were used as a main way to quantify biodiversity (Magurran, 2004). The Shannon H or Simpson indices, reflecting both species richness and proportions remain central in many literatures. Species are supposed to coexist and maintain their existence in a system independently of their own particularities or characteristics. One of the main problems with this approach is that species are in fact quite different in shape, size, and functioning, and some measures of the degree of divergence between organisms may be crucial in quantifying biodiversity.

Towards including differences between species in the measure

Firstly, relative abundances may provide information about each species' viability and "efficiency" in the system. Some measure of relative abundance should be included in such measures in order to reflect more accurately the role of diversity. Diversity indices must therefore combine notions of richness and evenness of the species distribution in the ecosystem. In order to determine evenness, we dispose of a bunch of indicators (Berger-Parker, Simpson, Shannon-Wiener), which are non-decreasing functions of richness and evenness, and may be written as a general expression of the relative abundance of a species h and of a positive parameter: $D_E = \left[\sum_h p_h^\alpha \right]^{1/1-\alpha}$. We will further look at a generalization of the Simpson index of diversity, which is the Rao's coefficient.

Secondly, indicators still have to be sensitive to existing dissimilarities among species. There are basically three different approaches that attempt to give an operational content to dissimilarity. The first build on the concept of distance and evaluates the diversity of a sample thanks to a certain cardinal aggregation of dissimilarities. The second is an aggregation of ordinal dissimilarities constructed from a quaternary ordering relationship between pairs of species, by ordering pairs of elements. The last approach rest on a vision of biodiversity as a value of realized attributes. In the remaining of this paper, we will concentrate on the first one, focusing on cardinal aggregation of dissimilarities. Several indicators exist that aggregate cardinal dissimilarities, but the one developed by (Weitzman, 1992) is the only one for which an axiomatic characterization have been defined (Bossert, Pattanaik, & Xu, 2002). Those measures require some characterization of distances between species.

3. Weitzman criterion for preserving biodiversity

3.1. Weitzman's procedure

A criterion as the one developed by Weitzman (1992, 1993, 1998) attempts to provide an answer to an important dilemma in conservation policy: how to determine an operationally meaningful value of a diversity function in order to make rational decisions about how best to preserve biodiversity. The motivation behind Weitzman argument is to establish conservation priorities on the basis of each species' contribution to total biodiversity. When evaluating the diversity of a set of species, this contribution is measured in terms of the incremental distance that each species adds to a set of species. In other words, diversity of a set will be measured by the non-redundant aggregation of all pairwise distance between species of this set.

Formally, a dissimilarity measure is a 'distance function' d measuring the distances between all pair of species inside a set in order to give an approximation of its diversity. The originality of Weitzman's approach to diversity measurement is a stepwise construction of the set assessed. Starting from an arbitrary diversity value D^0 (diversity= 0) of the set, Weitzman progressively adds new species to this initial set and estimates at each step, the incremental distance brought by the new incomer into the set. Formally, Weitzman's criterion to measure the diversity of a set X^j is given in a recursive way by the following general formula:

$$D_W(X^j) = \max_{i \in X^j}\left\{D_W(X^j - i) + \delta\left(i, X^j - \{i\}\right)\right\}$$

In other words, the diversity of the set X^j will increase by adding a species i to the set which distance from its nearest neighbor in the set $(\delta(i, X^j - \{i\}))$ is greater than any other pairwise distances already present in the set $(D_W(X^j - i))$. This avoids potential redundancy in the measure of diversity, which results from adding relatively similar species to the set and adds only the incremental distance provided by the new species.

Weitzman criterion is the only indicator of dissimilarities aggregation which is axiomatically characterized, rigorously demonstrated by Bossert, Pattanaik and Xu (2002). Those authors developed a measure equivalent to the one of Weitzman, but much simpler to calculate in the case of large samples of

species. It also proceeds stepwise and aggregates the distance-dissimilarities between species in its measure of diversity. But instead of "constructing" the set iteratively, this criterion "deconstruct" the set of species: it retains in its measure of diversity the shortest pairwise distance between one species and the others present in the set, and eliminates this species from the set. Iterations go on until no species is left in the set, and the total diversity is characterized by the aggregation of all retained distances. This procedure answers a significant problem about the order in which species have to be eliminated, based on the knowledge of distances already present in the set.

Although less complex, this method yields a similar measure of diversity than the one provided by Weitzman. This equivalence property was rigorously demonstrated by Bossert, Pattanaik and Xu (2003), as well as the bi-univocal relation of their measure (and consequently Weitzman's measure) to a set of three important axioms for a diversity index: 1) the monotonicity to dissimilarities, 2) the restricted independence, and 3) the link species indifference, quite related to Weitzman link property.

* "Monotonicity to dissimilarity" states that the ranking of two different sets of species will be determined by the distances between pairs of species within each set. A sample A will therefore be ranked "higher" than another sample B if the distances between species of the set A are greater than in B. Thanks to this property, it is therefore possible to compare the diversity value of different set of species exclusively from looking at pairwise distances between species within the set. It is therefore unnecessary to compare species across sets.

* The second axiom of restricted independence states that the ranking of two sets is unaffected by the addition of an individual increasing similarly the maximum proximity within this set.

* The last axiom of link indifference states that the elimination of the link species l belonging to a set X reduces diversity by an amount exactly equal to the distance between this species and its closest neighbour. The iteration proceeds by identifying a "link" species to be compared to other species in the set. The nearest neighbor is considered as the "representative" species which remains in the set. Those axioms although quite opaque in their theoretical formulation should guarantee that the procedure used won't affect the final ranking and won't violate basic properties of diversity function (Weitzman, 1992, p. 376).

3.2. The distance measures in Weitzman's framework

This approach thus builds implicitly on the possibility to measure some fundamental information about distance-dissimilarity measures between identified components of biodiversity. He provides examples of those distances focusing on the species level, using the degree of phylogenetic distances between species within a set or a community of species. This measure was inspired from the work by Vane-Wright, Humphries, & Williams (1991), using phylogenetic trees of species evolution, which branches length are proportional to the time elapsed since the separation of one species from its closest ancestor. One property of the set of species under study is a property of ultrametric distances[1] between all three pairs of species. This assumption is made in order to be able to use information about phylogenetic trees, in which the distances between species are represented as the total branch length back to their common and most recent ancestor).

Such an approach based on dissimilarities can be used, in Weitzman own words, at different levels of measurement of biodiversity, be it genes, ecosystem functions or habitats. In other words, any other significant distance measure may be used to qualify diversity value. Our idea is to apply some of the functional diversity indices developed mostly in the field of ecology as a way to provide distance estimates required in Weitzman analysis. Weitzman besides noted cautiously that phylogenetic differences may be loosely related to some phenetic differences, and therefore reflect partially some 'physical and behavioral differences' between species. He acknowledges a potential 'good correlation' between the two approaches. If the candidate measures of functional diversity satisfy to this approach, it may be a subsequent extension of the research to see how those information might be combined to provide other distance estimates.

The genetic approach used by Weitzman is appealing theoretically because of the large amount of already published information, but also because it allows for representation on a phylogenetic tree. However, the complexities of acquiring such information on large scales make it difficult to apply in practice. Building on this critic, Weikard (2002) proposed to extend the analysis up to the ecosystem scale, concluding that counting species inside a given ecosystem would be easier than acquiring genetic information.

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[1] For any three species in a set, the two longest distances between them are equal

3.3. *Suggestions of Weikard and the need to go further*

Weikard (2002) raised the concern that diversity value may have an intrinsic and an instrumental value. However instrumental value of biodiversity may not be attributed to a particular species, but to several species in interaction; furthermore, it is necessary for the author to look at the functional role of different species in this interaction rather than their genetic characteristics. This argument is relayed by (Mainwaring, 2001), criticizing the conclusions by Weitzman about crane conservation. He states that "Without knowing the role each crane plays in its local ecosystem, and the broader value of the services of each system, comparing the species' marginal diversity indices does not tell us how to maximize the value of services per conservation dollar ». Weikard looks at diversity as an option or insurance value for the future, and recognize that genetically similar species may morphologically very different. He introduces in his analysis the notion of "attributes" developed by Nehring & Pupp (2002), and narrows down the concept of "traits" or physical characteristics of species, when talking about attributes identified for an individual species, or the concept of "ecosystem functions" when considering attributes related to the interaction of different organisms. He recognize that a more diverse environment may offer more valuable attributes. In his paper of 2002, Weikard attempt to shift the focus from set of species to set of ecosystems. The operational framework he developed requires an estimation of the number of species in each ecosystem, and information about dissimilarity of ecosystem is generated from randomly drawn sample of species from each ecosystem. The idea raised by Weikard is that preservation shouldn't look at species individually but in interaction within a larger set, which is the ecosystem. However, this vision follows an insurance rational and goes back to a ranking of ecosystem on the basis of counting of species and maximizing their number within any given ecosystem. This approach cannot be sufficient to narrow down and understand the role of specific species or group of species within the ecosystem.

Identifying the functional role of species has been the subject of functional ecology for many years. We acknowledge that research in economy could inspire from those advances to orientate more precisely conservation funds to some specific aspects of the ecosystem. In the next part of this paper, we will

attempt to apply functional distances between species to Weitzman diversity function.

4. Functional diversity applied to Weitzman's framework

### 4.1. Functional diversity and functional traits

Functional diversity appears as one particular element of species diversity, which present some similarities in their components. According to Tilman (2001) and Petchey & Gaston (2002), functional diversity represents "the extent of functional trait variation (or differences) among species in a community".
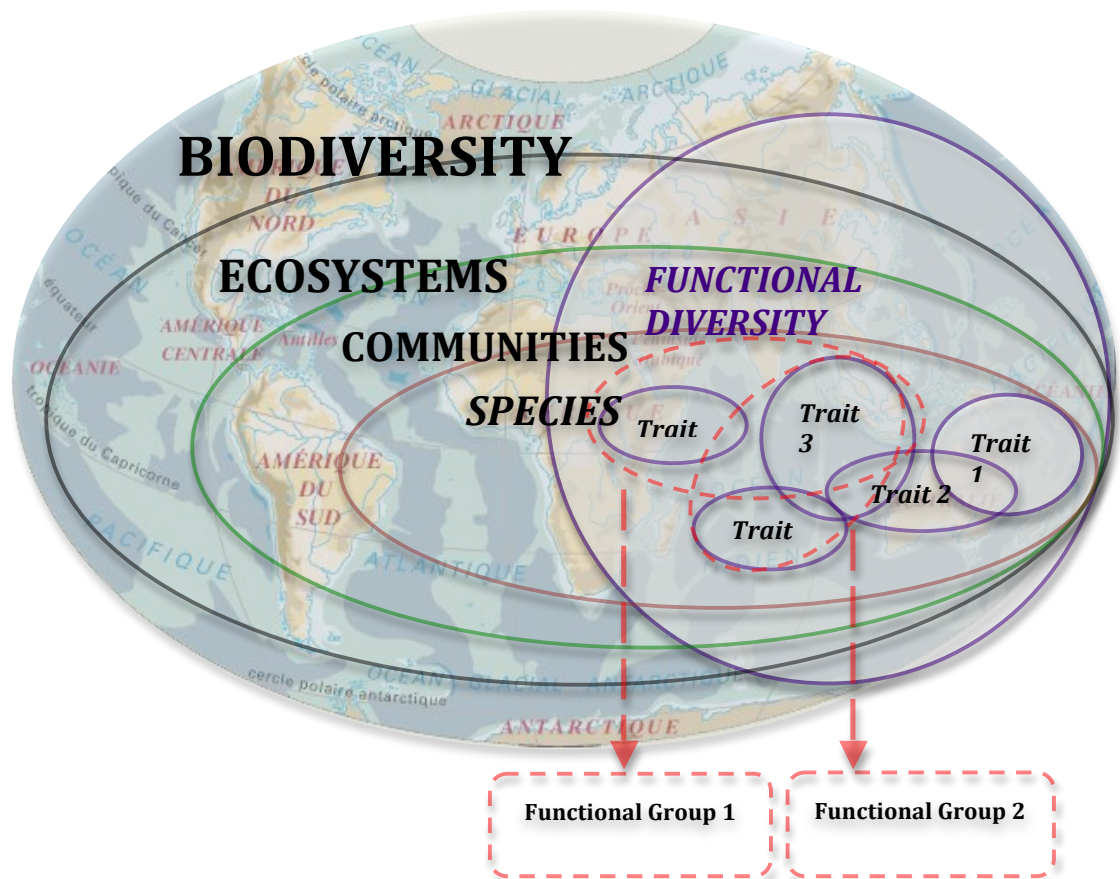
Mason et al (2005) demonstrated that the division of species diversity into species richness, evenness and divergence also applied to the dimension of biodiversity looking at functions. Three facets of functional diversity were consequently identified as functional richness, functional evenness and functional divergence. Measures of functional diversity will therefore have to account for those three facets for a complete characterization of this diversity.

In addition to their genes, species also present various physical, physiological or biological observable characteristics, named "traits". Functional diversity is therefore defined as the value and range of organism traits, or characteristics (Villéger et al 2008). Those traits influence the performance of different organisms living in a community and consequently ecosystem functioning. In order to measure such functions, traits are observed at the individual level (whether morphological, physiological, phenological or behavioural characteristics) and represent intermediary measurement elements. Until now, no consensus exists about how to quantify functional diversity, in spite of the recent development of very different indicators (Petchey et Gaston 2006). Those different measures are subject to several debates about their statistical validity, their properties and what they actually measure ((M. A. Mouchet et al 2010; Petchey & Gaston, 2006; Ricotta, 2005).

Those traits may influence ecosystem processes and functioning in a specific way (effect traits) and imply differentiated responses of species to an environmental perturbation (response traits). They are therefore of crucial importance in their capacity to provide basic ecosystem functions, and among them to provide goods and services that are valuable to society. It has become increasingly obvious to ecologists that some measures of differences among species were crucial to a better understanding of ecosystem functioning (Leps et al (2006), Mouchet et al (2010)). Assessment of functional diversity is thus about measuring the "traits" of species in the community and assigning a value to each of those traits. In the following graph taken from Violle et al. (2007), we can understand how the notion of trait is transversal to several level of organization, from the individual to the ecosystem level.
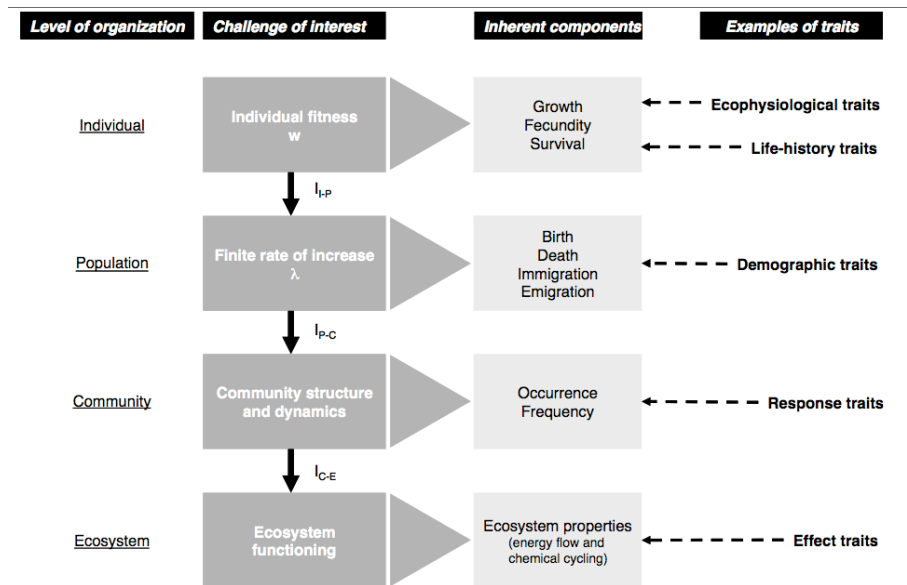
Another illustration taken from the same authors shows how different Morpho-Physio-Phenological (M-P-P) traits (from 1 to k) modulate performance traits (vegetative biomass, reproductive output and plant survival) which determine plant performance and therefore individual fitness (considered as the individual success, survival and capacity to reproduce).
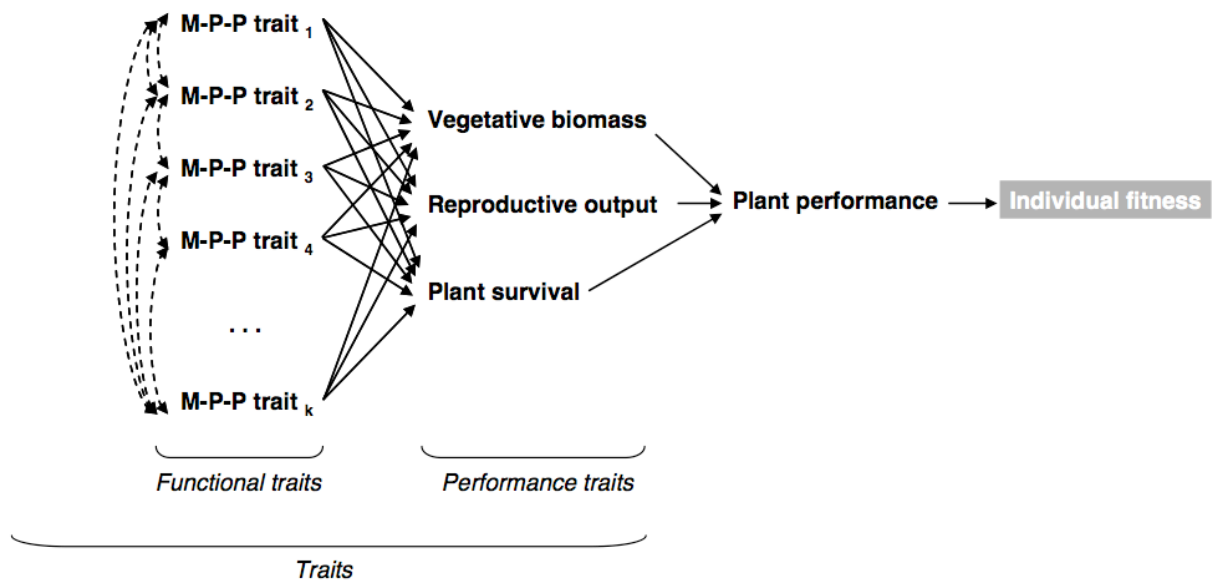
Those different traits are assigned some specific values, depending on the direct observations on the species. Those values are called "attributes" of traits, and may be measured either quantitatively (ml, cm, mm, cm2…), in a binary way (a species is of type *x* or not, taking values 0 or 1), or expressed as a time period (e.g. differences in phonological information, like flowering periods), etc.

The measurement unit doesn't have to be the same among different traits, but it should be the same for a trait measured on different species.

4.2. How to use information about traits to derive distances between species ?

This information about trait values may be obtained through field studies and cooperation with experts in ecology. When applying functional diversity measures to Weitzman's framework, it is necessary to gather two types of information: first, the traits "attributes" or values per species in a specific ecosystem, which will provide a (species x trait) matrix;

	Trait 1	Trait 2	Average value
Species 1			
Species 2			
Species 3			
Species 4			

Second, a measure of species abundances in the different community observed, providing a matrix (species x abundances).

	Plot 1	Plot 2	Plot 3
Species 1			
Species 2			
Species 3			
Species 4			

Those two matrices will be merged into a single (species x species) matrix giving the distances among each pair of species for each community, computed on the basis of the average distances between traits.

	Species 1	Species 2	Species 3	Species 4
Species 1	0	d_{12}	d_{13}	d_{14}
Species 2	d_{12}	0	d_{23}	d_{24}
Species 3	d_{13}	d_{23}	0	d_{34}
Species 4	d_{14}	d_{24}	d_{34}	0

Weitzman's criterion can be computed in the same way than with genetic distances. Here we may ask ourselves what would be the information

given by such an additive indicator: it would provide some general information about the diversity of traits and characteristics of species within an ecosystem. For example, we may see differences in trait values as a proxy for niche differentiation and complementarity, i.e. as a mean of differential way of resource use, a famous concept in community ecology (Mason et al, 2005; Leps et al, 2006)). The more similar the trait values of two species are, the higher the proportion of populations might be expected to overlap in their functions[2]. The interest of using such distance measures is to make use of the extensive work in functional diversity ecology about traits and provide a diversity measure based on the complementarity of species role in the ecosystem.

4.3. Methodological considerations

The usefulness of such an indicator computed through Weitzman procedure should be discussed. Several limitations can be identified in Weitzman's indicator as a mean for measuring accurately "useful" diversity. First, during the iteration process, it doesn't account for abundances of the different species within the set. It ignores therefore how much the distances between species are "weighted" inside the overall ecosystem evaluated. Here, as we are working at the community level, it may be possible to obtain some measure of the relative abundance of the different species composing the community, and include it directly into the distance measure.

For example, it could be possible to calculate the Rao's quadratic coefficient for each pairs of species. Rao's coefficient (also named Rao's Q, and denoted FD_Q) present many desirable properties for describing functional diversity of a community. It is in fact a generalized form of the Simpson Index of Diversity. If proportion of the *i*-th species in a community is p_i and dissimilarity of species *i* and *j* is d_{ij}, the Rao's coefficient is of the form :

$$FD_Q = \sum_{i=1}^{s}\sum_{j=1}^{s} d_{ij} p_i p_j$$ where s is the number of species considered, and

$d_{ii}=0$ (dissimilarity of a species to itself is equal to zero). If $p_{ij} =1$ for any pair of species (each species is completely different), then FD_Q becomes the Simpson index of diversity). (see (Botta-Dukát & Wilson, 2005)). Rao's Q is very flexible

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[2] This overlap could be calculated by probability density functions of two species (see Leps et al 2006)

and may be used with various dissimilarity measures. The only methodological decisions are mainly how to measure species dissimilarity, and how to characterize the proportion of a species in a community.

Having such pondered distances may allow some better consideration of several aspects of diversity, and include some information about relative abundance of species, and therefore of the traits considered. The matrix would be the following:

	Species 1	Species 2	Species 3	Species 4
Species 1	0	$d_{12}p_1p_2$	$d_{13}p_1p_3$	$d_{14}p_1p_4$
Species 2	$d_{12}p_1p_2$	0	$d_{23}p_2p_3$	$d_{24}p_2p_4$
Species 3	$d_{13}p_1p_3$	$d_{23}p_2p_3$	0	$d_{34}p_3p_4$
Species 4	$d_{14}p_1p_4$	$d_{24}p_2p_4$	$d_{34}p_3p_4$	0

The distances would therefore include some information about each species abundances when the distance was measured.

A second major drawback is how to account for traits interactions in providing some specific diversity function. The additive criterion of Weitzman may not be the best way to account for trait combinations to provide some valuable ecosystem functions. It may be necessary to think about other forms of diversity functions that could be additive for some complementary traits, multiplicative for traits that must appear in combination in order to provide a function, or divisive if those traits negatively affect each other. In other words, the interactions induced by an analysis of the traits in an ecosystem may be just too complex to use such a criterion.

What about the link between diversity and ecosystem functioning ?

How to define, measure and assess functional diversity is highly debated (Diaz & Cabido, 2001). Especially, the links between biodiversity loss and ecosystem functioning remains an open question. The review by (Hooper et al., 2005) gives a good deal of the complexity underlying those issues and the many debates that followed on this topic. Consensus arises on many aspects, and notably on the strong influence of species functional characteristics on ecosystem properties. But many uncertainties remain on hypotheses around the exact link between biodiversity and ecosystem functioning on the one hand, on the stability and productivity of ecosystems on the other. Despite uncertainties,

Hooper et al. stress the necessity to incorporate diversity effects into policy and management. In their view, failing to grasp interconnections between diversity and ecosystem would restrict future management options even further.

Methodological difficulties linked to the characterization of functional distances.

Beyond the fact of knowing whether such measure of distance between species is adapted to Weitzman's context, many methodological difficulties and questions arise.

First, which traits must be included into the measure, and for what purpose? In order for this measure of distance to have meaning for biodiversity conservation, it is necessary to select carefully the objective function that is preserved by a higher diversity of traits. For example, if one objective is to maintain soil stability and limit erosion, it could be interesting to look at traits related to length and presence of roots, feeding habits by detritivores or growth forms of plants, etc. This makes it a very interesting characteristics of traits: it is a component of biodiversity that present a (more or less) explicit function, allowing to explain and predict variations in ecosystem level properties. (Loreau, Naeem, & Inchausti, 2001). It follows that a way to select trait is to pick those ones that maximize the explanatory power of functional diversity (Petchey L., Hector, & Gaston, J., 2004). The traits retain is the analysis of functional diversity must be all traits that are important to the particular function of interest, and no traits functionally uninformative. Describe the function to be considered in large detail is therefore of crucial importance in order to choose among which traits must be observed. This is mainly the role of the ecology community to provide such objectives (Hooper et al., 2005). Whatever the means through which this information is acquired (expert knowledge, empirical and theoretical studies), a high degree of uncertainty is attached to the identification of functionally important traits. (Naeem & Wright, 2003).

A second issue is how to weight those traits relatively to the considered ecosystem function or process. Many problem arise from computing diversity from several trait : it is difficult to weight traits according to their role in the function, and to avoid the problem of correlated traits and therefore redundant to describe functional diversity. When several traits are used, the value of average functional trait is computed. The meaningfuless of such a measure may

be questioned, and traits have to be made comparable by standardization, or by log transformation. In addition, the variability of traits within and across species should also be accounted for (if the information is available), with standard deviations for each species' trait.

Third, is it feasible to compare values of diversity when traits are measured in different communities? It may be that traits are not even comparable in different geographical areas. In the same vein, it can be asked whether we should cross information about effect traits (impacting the ecosystem) and response traits (the species adapt to a changing environment. This probably goes back to the choice of the type of ecosystem function that must be preserved.

4.5. Extending to the concept of niche complementarity

In his 1992's paper, Weitzman made reference to "ecological species" (p. 395), each occupying a niche in the ecosystem. This intuition relates to an underlying process of niche complementarity, which translate into complementarity between species relatively to resource use and availability. Weitzman suggested intuitions about complementarity or substitutability between elements of diversity, which should according to him go beyond the mere additivity of differences to characterize diversity.

The correlation between functional diversity and species diversity is extremely context-dependent: according to niche-differentiation, functional characteristics of coexisting species must differ at some level, leading increasing functional diversity to increase with species richness. On the other hand, some strong environmental filters (niche filtering process) may constraint species within a restricted range of functional characteristics ((Loreau, Naeem, & Inchausti, 2001. (Diaz & Cabido, 2001)). If we consider that to each species corresponds a trait, we will stay into the case of measuring species richness rather than measuring functional diversity. It therefore generally admitted in several functional diversity measures that the number of traits must be inferior to the number of species inside the set. The choice of traits must be made in order to describe each functions as well as possible while avoiding redundancy between them ((Villeger, Mason, & Mouillot, 2008).

In any case, those considerations show the limits of Weitzman criterion in choosing among different samples of species. Distances between species in genetic terms may not be sufficient to provide information about the "functionality" of biodiversity. Including some measure of functional distances reveals many aspects and complexities of biodiversity, which mainly relies on complementarity in resource use of the different species in order to provide the most efficiently functioning ecosystem.

5. Discussion & Conclusion

This short review wants to point out the stakes behind ecological and economic cooperation on the issue related to measurement of biodiversity indices. Without more integrated understanding of the ecological processes that link biodiversity, ecosystem functions and services, attempts to forecast the societal consequences of diversity loss and to meet policy objectives are likely to fail. Our proposal of integrating some measure of functional diversity into measures of value of diversity function could be a step toward integrating more ecological research into the definition of policy objectives.

The problem formulated by Weitzman is one of choice about conservation management options. His framework divising a value function of diversity based on genetic distances provides an operational analytical framework that could guide actual conservation policy in a diversity-improving direction. The author admits that an important part of the problem will rely in obtaining the right information about which distances characteristics are considered. We wish to test through rigorous axiomatic analyse, how measures of functional divergence developed by ecologists may be used as a substitute to weitzman's genetic distance, and may provide an incremental amount information available to policy decisions. As we consider to be in the case of "fuzzy evaluations problems" described by Munda et al. (1995), we could refine the precision of our indicators by using Multicriteria evaluation model, considering an impact matrix of the distances between traits which may contain some fuzzy measurement of the performance of such a distance measure with respect to the criterion retained in terms of ecosystem functioning. Furthermore, such a framework could be all the more interesting, as distances

between functions apply to evaluate distances between two sets, and not only between two point measures of diversity, like genetic distances were. One very interesting extension would be to apply some Social Multicriteria Evaluation Method to see how the criterion retained and the choices made about biodiversity conservation matches with the social goals depending on the human context. Another application could be to use the framework of "realized attributes" developed by (Nehring & Pupp, 2002) which matches pretty well with the notions of trait 'attributes' that is affected to a particular set of species.

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