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**Measuring Biodiversity –
an axiomatic evaluation of
measures based on genetic
data**

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Abstract

Biodiversity measurement is necessary to evaluate conservation alternatives and understand how to maximize biodiversity returns on conservation budgets. In the economics literature, most studies focus on species level diversity. Existing measures based on species' pairwise genetic differences do not perform optimally. This paper develops two new biodiversity measures within the same genetic framework. An axiomatic diagnosis for this class of measures is proposed and four biodiversity measures are then compared. Though the axiomatic comparison points towards a single "best" measure, it also indicates that the choice of measure should be dependent on the conservation problem at hand.

Kurzfassung

Biodiversitätsmessung ist notwendig, um alternative Naturschutzstrategien zu bewerten und zu verstehen, auf welche Weise der Beitrag der Biodiversität zum Naturschutz maximiert werden kann. In der Literatur stellen die meisten Berechnungen auf die Ebene der Artendiversität ab, erbringen aber keine optimalen Ergebnisse. Diese Studie entwickelt zwei neue Biodiversitätsmaße innerhalb des gleichen genetischen Rahmens. Sie schlägt eine axiomatische Charakterisierung für diese Gruppe von Maßen vor und vergleicht dann vier Biodiversitätsmaße. Auch wenn der axiomatische Vergleich auf eine einzige „beste“ Maßeinheit hinweist, deutet er auch darauf hin, dass die Wahl des Maßes von der gegebenen Problematik abhängen sollte.

1 Introduction

A foundation to the management of biodiversity, or any other resource, is the development of measures that can be related to its value, be it economic or ecological. Measuring the level of biodiversity is necessary to evaluate alternatives and to understand how to maximize the benefits derived from the use of the (different levels of) the resource.

There have been a few attempts to measure biodiversity, as presented later in this introduction. Yet there are issues, theoretical and computational, with each of the measures offered, as discussed throughout this paper. As a result the measures have not yet been applied in environmental conservation policies. New alternative measures are proposed, in response to some of the issues faced by existing measures. All measures are compared using an axiomatic approach, based on axioms derived from the literature and further axioms developed in this paper.

The remainder of the introduction reviews the literature on biodiversity measurement. The rest of the paper is divided into five more sections. The next section presents specific measures of biodiversity based on genetic distances. Section 3 introduces two new measures of biodiversity, based on genetic dissimilarities, with new properties. A list of axioms is developed and used to compare the diversity measures in Section 4. Finally, Section 5 concludes.

1.1 Biodiversity measurement in the literature

Pearce et al. [17] list three fundamental levels of biological diversity: genetic diversity, species diversity and ecosystem diversity. Genetic diversity refers to the amount of genetic information contained in individual living organisms. Species diversity refers either to the number of species within a certain system or to the dissimilarities between these species, the former is sometimes referred to as species richness. The first framework of diversity measure can be traced back to Shannon et al. [22] who built a diversity index based on species richness. More recent studies using species richness as diversity measures include Scott et al. [21], Eiswerth et al. [7] and Li et al. [13]. Ecosystem diversity refers to the variety of habitats, communities or ecological processes on earth.

The choice of the appropriate level of the analysis is itself matter for debate. Many economic studies focus on the species level, possibly because species have direct values to human consumption.¹ On the other hand, ecosystem processes are not well understood yet, and hence ecosystem diversity can be difficult to define and measure; genetic diversity is also mostly inappropriate for economic studies, as the value of specific genes for human consumption is hardly identifiable (though this is changing with genetically modified agricultural crops).

A prominent diversity measure comes from the work of Weitzman [27],[28],[29]. Weitzman [27] derived the measure of diversity of a set of species from a matrix of genetic distances between each pair of species included in the set. This framework of (genetic) dissimilarity-based diversity measure, Weitzman [27] argues, allows to derive the intrinsic value of diversity. Other early papers

¹Examples of diversity studies focusing, explicitly or not, on species diversity include: Brock et al. [1], Drucker [5], Eiswerth et al. [7], Li et al. [13], Nehring et al. [15],[16], Rowthorn et al. [20], Solow et al. [23] and Weitzman [27].

referring to genetic dissimilarities as measures of diversity include Eiswerth et al. [6] and Solow et al. [23].

Diverging slightly from genetic diversity, Nehring et al. [15],[16] list another type of species-level diversity: phylogenetic diversity, which studies the evolutionary relatedness between organisms. Phylogenetic traits are readily observed and measured and their utility as attributes is either obvious or straightforward to infer. Nonetheless, their genetic basis can be difficult to assess and comparing qualitatively different attributes can prove difficult. However, Nehring et al. [15] successfully derive a measure of species diversity based on the number and relative importance of species' attributes, also with the intention to capture the intrinsic diversity value.

There are merits to both the genetic distance-based and the attributes-based species diversity platforms. A major difference lies in the assumptions of the two frameworks about the relationship between time and evolution. The metrics of the genetic distances approximate the evolutionary process, implicitly assuming evolutionary waves of constant frequency and magnitude. On the contrary, a measure of diversity focusing on the effects of such evolutionary waves (phylogenetic diversity) has the advantage to be independent of any reference to the timing of those waves, only to their sequence. See for instance Massart [14] for a textbook on chemometrics. Goodman et al. [10] compare morphological studies and DNA experimentation for the taxonomy of primates.²

It is not the purpose of this paper to argue in favor of or against either of the phylogenetic or genetic distance diversity platform. It focuses on the genetic diversity framework used in Weitzman ([27],[28],[29]) and others (e.g. Solow et al. [23]), the principal appeal of it being the clarity of the matrix of dissimilarity metrics, which is presented in the next section. New biodiversity measures are presented, within this framework, and are assessed relatively to existing measures using an axiomatic approach.

It must be noted that a problem remains with the genetic (and the phylogenetic) diversity approach: the marginal diversity impact of an extra member of a species already included in the set is nil. However, a group of many individuals of the same species can perform tasks that could not be undertaken by two members of different species. This establishes the importance of the concept of functional diversity³ and the crucial relation between such functionality and the species populations. These links can be examined through the species' interactions within an ecosystem. How to link these interactions to biodiversity measures, other than by using exogenously derived survival probabilities as in Weitzman [28], is out of the scope of this paper.⁴

²Note that the taxonomy derived from the DNA experimentation is generally accepted nowadays and is used in the following chapter.

³Perry [18], in an unpublished work, attempts to model species functional diversity. Fromm [8] and Weikard [26] also discuss and use functional diversity.

⁴For instance, van der Heide et al. [24] have developed dependent (endogenous) survival probabilities in their ranking of conservation priorities. Gerber [9], in Chapters 4 and 5, hints towards the combination of a diversity matrix and a matrix of interaction coefficients between species.

2 Review of Existing Diversity Measures

Species-level diversity reflects differences among species. It is thus necessary to understand how species vary in order to understand biodiversity and to measure it at species level.

2.1 Species evolution and hierarchical trees: overview

Scientists have organized all identified living organisms according to categories, called *taxa*. Starting from the broader of these categories and moving down the ladder to its lowest rung, a summarized list of *taxa* can be described as:

Kingdom, Phylum, Class, Order, Family, Genus, Species

There are more categories within the ones described here, but these are the general taxons.⁵

In this paper, the focus is on measures of biodiversity described as the species level genetic diversity. The genetic distinctiveness between species is measured by the genetic "distance" between each pair of species included in the total set of species considered (i.e. within the ecosystem, or any other geographical or ecological division). Matrices of pairwise genetic distances are produced by DNA-DNA hybridization experiments.⁶

The dissimilarity measures obtained through such experiments provide excellent information about DNA evolution and can be used as approximations to the distances (or time, in terms of evolution) back to the last common knot (i.e. ancestor) that two species shared on the evolutionary tree (Degens et al. [3]).

An example of partial evolutionary tree (also called dendrogram) is given in Figure 1⁷. The distances represented by its branches (though not exactly to scale here) are called ultrametrics and fulfill specific properties (see Degens et al. [3] and Weitzman [27],[28]). These ultrametrics are computed from the raw distance data obtained through the DNA experiments. The raw data used in Weitzman [27] is presented in Table 1 (Appendix).

Other representations that can be constructed from a set of non-ultrametric distances include additive trees and minimum spanning trees (MST). It can be shown that additive trees and minimum spanning trees are actually generalizations of the ultrametrics based dendrograms (see Degens et al. [3]). Given that the raw data is unlikely to be ultrametric, it seems reasonable to focus on other forms of representations than the dendrogram. However, Degens et al. [3] give a list of arguments in favour of the ultrametrics based dendrogram, including the fact that the true phylogenetic history is ultrametric in real time, that the true phylogeny has a root (which does not exist on an additive tree or an MST), as well as further computational problems.

⁵For the taxonomy of all living organisms, together with the extinct branches of the evolutionary tree, the reader can refer to the following website: <http://tolweb.org/tree/>.

⁶Details on experimental procedures can be found in Weitzman [28] for a summary, Krajewski [12] and Caccone et al. [2] for complete descriptions. Wu et al. [30] discuss normalisation techniques that can decrease the variance of the results of hybridization experiments.

⁷This represents the commonly agreed taxonomy of higher order primates.

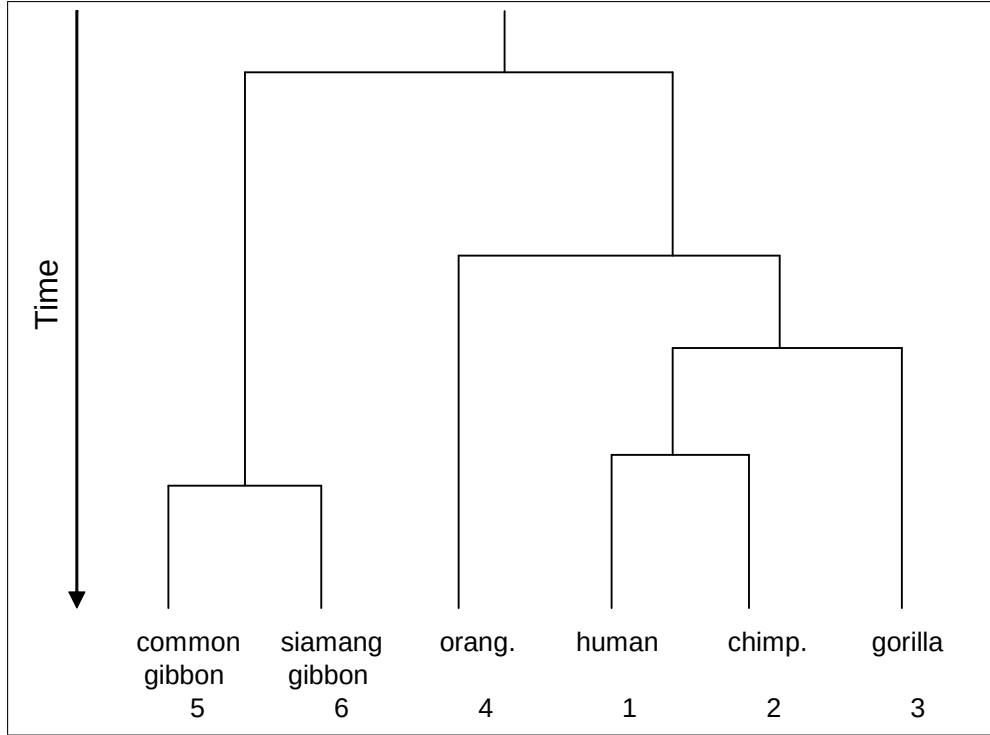


Figure 1: The Taxonomic Tree for Higher Primates

Yet, as the transformation into ultrametrics requires further estimations and statistical errors, the focus in this paper, as in Weitzman [27], is on diversity measures based on raw data of genetic distances.⁸

2.2 Weitzman's measure of diversity

The Weitzman model can be presented as follows. Using Weitzman's [27] notation, let Q be the set of species considered and $V(Q)$ represent the diversity measure of the set Q . Also define $Q \setminus i$ as the set Q without species i and $d(i, j)$ as the distance between species i and j . The distance measure between two species has to satisfy three basic conditions:⁹

$$(i) d(i, i) = 0, (ii) d(i, j) \geq 0, (iii) d(i, j) = d(j, i). \quad (1)$$

It is then necessary to define the distance between one particular species and a given set of species. Weitzman uses the following definition:

$$d(i, Q \setminus i) = \min_{j \in Q \setminus i} d(i, j). \quad (2)$$

This definition ensures that the distance between one species and a set of species is zero if and only if that species is already contained in the set. As Solow et al. [23] point out, other definitions of $d(i, j)$ could fulfil this requirement, but this definition seems to be the most appropriate. It

⁸In Degens et al. [3], keen readers can find descriptions of the different estimation techniques to construct complete taxonomies when they are missing values in the matrix.

⁹Neither condition (i) nor condition (iii) are obvious from the experimentations, as reported in Caccone et al. [2].

further ensures that if a new species enters the set, its incremental contribution to the diversity of the set is equal to its genetic distance with its closest relative within the set.

Weitzman [27] sets that the diversity measure $V(Q)$ of a set of species Q must satisfy the fundamental condition:

$$V(Q) = V(Q \setminus i) + d(i, Q \setminus i), \quad \forall i \in Q. \quad (3)$$

Then the definition of a species' incremental diversity contribution must hold for all species in the set, in other words the dendrogram it represents is "stable". The problem is that the only diversity measure which fulfils Equation 3 for all $i \in Q$ is $V(Q)$ in the particular case of ultrametric distances. A sketch of the proof of this result is presented in Weitzman [27].

The major difficulty with raw (i.e. non-ultrametric) distance data is that the diversity measure $V(Q)$ will be dependent on the order in which the species are included in the set.¹⁰ Weitzman's [27] solution is then a diversity measure of the set Q , denoted hereafter $V_W(Q)$, which is derived from the following minimization problem:

$$\begin{aligned} & \min V(Q) \\ & S.T. : V(Q) \geq V(Q \setminus i) + d(i, Q \setminus i) \end{aligned}$$

for which he shows that the solution is:

$$V_W(Q) = \max_{i \in Q} [V_W(Q \setminus i) + d(i, Q \setminus i)]. \quad (4)$$

The solution is unique when $V(i) \equiv d_0, \forall i$ (d_0 can be zero or any other constant). Assuming that $d_0 = 0$, the results are shown in Table 2 in the Appendix (note that $V_W(1, 2, 3, 4, 5, 6) = 1424$) for the six species of Table 1 (Appendix).

A major problem with Weitzman's algorithm is that it is not stable in the event of species extinction. If a species disappears, the impact on the diversity value of the remaining set is not simply to deduct its branch length from the original diversity value. Further, the associated structure might change as a result of extinction, which is not the case with the true evolutionary tree. This problem will be discussed again in a later section comparing the diversity measures. It is a major fault but Weitzman [27] shows that it cannot be overcome. He also shows that no other algorithm can better ensure than the recursive programming of Equation 4 that, in the absence of ultrametrics, the condition of Equation 3 is satisfied as closely as possible in all cases.

2.3 Alternative biodiversity measures

There have been a few attempts at alternative measures to Weitzman's. Two of these are of particular interest to this paper. The mean diversity measure (Hill [11]) is an average function of Weitzman's measure, whilst the measure of diversity preservation (Solow et al. [23]) focuses on the biodiversity loss of an existing set of species when compared with the initial set.

¹⁰If Equation 3 is then not fulfilled for all $i \in Q$, it is possible (in fact in almost all cases) to observe cases where, with $i, j \in Q$, $V(Q) = V(Q \setminus i) + d(i, Q \setminus i) \neq V(Q \setminus j) + d(j, Q \setminus j) = V(Q)$.

2.3.1 A measure of mean diversity

Hill [11], in an unpublished paper, points out that $V_W(Q)$ systematically overestimates the diversity of a set (due to the $\max$ function), unless the distances are ultrametric (in which case the bias is zero). On the other hand, a measure of mean diversity (MD) on a set of n species, defined as

$$V_{MD}(Q) = \frac{1}{n} \sum_{i=1}^n [V_{MD}(Q \setminus i) + d(i, Q \setminus i)], \quad (5)$$

does not suffer from any systematic bias. The mean diversity value of the full set is $V_{MD}(1, 2, 3, 4, 5, 6) = 1339$ for the distances of Table 1 (Appendix). Hill [11] proposes two criteria to measure the divergence from the condition of Equation 3. The first measures the systematic bias, while the second measures "...the dispersion of changes in biodiversity relative to the changes predicted by [...]" Equation 3. These two measures of bias and dispersion are called S_1 and S_2 and are defined as:

$$S_1 = \frac{1}{n} \sum_{i=1}^n [V(Q) - V(Q \setminus i) - d(i, Q \setminus i)]$$

$$S_2 = \frac{1}{n} \sqrt{\sum_{i=1}^n [V(Q) - V(Q \setminus i) - d(i, Q \setminus i)]^2}.$$

By definition, $V_{MD}(Q)$ does not suffer from any systematic bias and thus $S_1(V_{MD}) = 0$ for all Q . For $Q = \{1, 2, 3, 4, 5, 6\}$, $S_1(V_W) = 19.17$, $S_2(V_{MD}) = 7.92$ and $S_2(V_W) = 10.10$. Both the measure of bias and the measure of dispersion suggest that the mean diversity measure performs better than Equation 4. $V_{MD}(Q)$ will be further tested by the axiomatic approach later on.

2.3.2 A measure of diversity preservation

In an early article contemporaneous to Weitzman's [27], Solow et al. [23] derived another measure of diversity, using a matrix of genetic distances similar to that used in Weitzman [28]. Starting with the same conditions defined in Equations 1 and 2, their measure of diversity reflects the willingness to preserve a set of species as representative as possible of the reference set. Following Solow et al. [23], the measure of diversity preservation $V_P(Q)$ is:

$$V_P(Q) = - \sum_{k \in E} d(k, Q), \quad (6)$$

with Q the set of existing species and E the set of extinct species,¹¹ so that $(Q \cap E) = \emptyset$. This diversity measure is defined on the distances between the extinct species (i.e. k) and the set of preserved species, $d(k, Q)$. The optimal conservation outcome maximizes $V_P(Q)$, with a maximum possible value of zero. By convention, the authors defined that $V_P(Q) = -[n(\max d(k, E \setminus k))]$ when all species disappeared ($Q = \emptyset$), with n the total number of species.

As explained earlier, only ultrametric distances can describe the whole evolutionary tree. Weitzman [27] considers his measure $V_W(Q)$ as the best approximation to measuring the length of the tree formed by the set Q , albeit with a systematic positive bias when applied to non-ultrametric

¹¹These definitions of the sets Q and E will be valid throughout the remainder of the paper.

distances. If the distances are ultrametric, then the total length of the branches snapped off the tree because of extinction can be measured exactly as $V_W(Q \cup E) - V_W(Q)$. The Solow et al. [23] preservation measure is an approximation to the latter difference, based on the set of measured distances (Table 1, Appendix). However, unlike Weitzman [27], the authors do not offer justifications for their choice of preservation measure, $V_P(Q)$, or a diagnosis of its performance. I provide below a few illustrations of the shortcomings of $V_P(Q)$, with further diagnosis offered later in the axiomatic approach.

In Table 3 (Appendix), I present the preservation measure for all the possible subsets drawn from Table 1 (Appendix). $V_P(Q)$ is easily calculated. However, Table 3 (Appendix) reveals some striking facts. Firstly, $V_P(Q)$ cannot differentiate between the diversity benefits of preserving species i or j when $d(i, j) = \min d(i, Q \setminus i) = \min d(j, Q \setminus j)$, e.g. between species 5 and 6. Secondly, $V_P(Q)$ overestimates the biodiversity loss if $d(k, Q) > d(k, E \setminus k)$. For instance, $V_P(1, 2, 3, 4) = -896$ but $V_P(1, 2, 3, 4, 5)$ is only -126 and the difference would clearly overestimate the diversity input of species 5 into the set. This situation arises because $V_P(Q)$ ignores the diversity among the extinct species and focuses entirely on their respective distance to the set Q .

The taxonomic tree representation of species 1 to 6 can help illustrate the shortcomings of $V_P(Q)$. Abstraction made of the actual length of its branches, the preservation measure can be visualized as approximating the branch lengths of all the extinct species as they are added back onto the tree. In some cases $V_P(Q)$ does exactly that. In other cases, $V_P(Q)$ is unable to account for some segments of the tree and double-counts others. Illustrations are provided below. The full lines in Figures 2 to 4 indicate the species that are preserved, the thin lines define branch segments rightfully included in $V_P(Q)$, the dashed lines signal the extinct branches which are not accounted for by $V_P(Q)$ and the multiple lines illustrate segments which are accounted for more than once by $V_P(Q)$.¹²

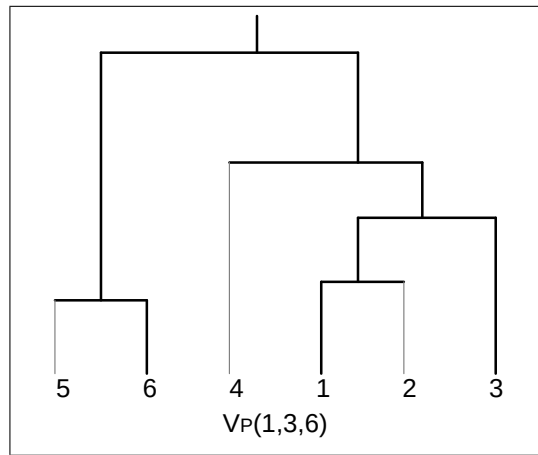
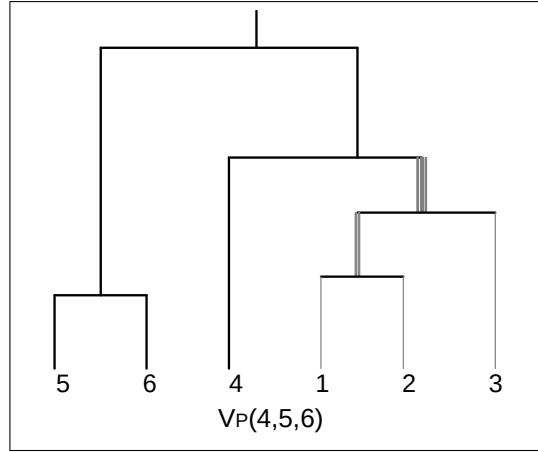
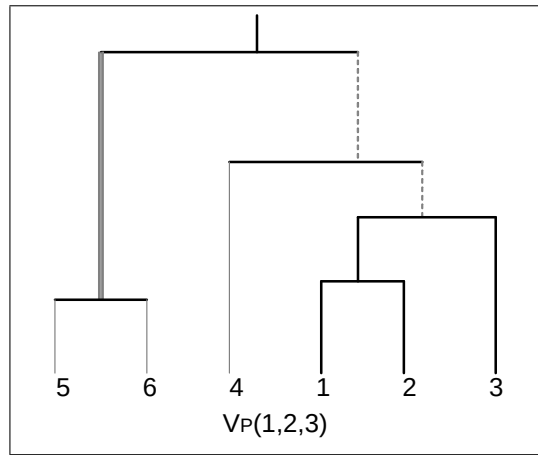


Figure 2: Tree Representation of $V_P(1, 3, 6)$

¹²This is an illustration only and the distances used in $V_P(Q)$ are not equivalent to the ultrametrics of the tree presented earlier. Rather, $V_P(Q)$ is based on the distances $d(k, Q)$, which are all minimum distances.

Figure 3: Tree Representation of $V_P(4, 5, 6)$ Figure 4: Tree Representation of $V_P(1, 2, 3)$

The lesson from the three figures is that the identification of the structure of the group of extinct species E is crucial, though ignored by $V_P(Q)$. Figures 2 to 4 illustrate the three critical cases encountered when "re-creating" the evolutionary tree: the extinct set includes all the species from either of the two clades resulting from the first node (Figure 4), the extinct set contains all the species of a terminal multi-species clade (Figure 3), or neither of these two cases (Figure 2). In the latter case, all branches are accounted for, $V_P(1, 3, 6)$ can be considered a good approximation of the actual loss of diversity incurred when species 2, 4 and 6 disappear. $V_P(4, 5, 6)$ on the other hand overestimates the loss of genetic diversity, as Figure 3 shows. $V_P(1, 2, 3)$ overestimates the diversity loss, but the accuracy of the estimated loss depends on the relative lengths of the dashed and double lines (Figure 4). This last case is in a sense the worst scenario, as the sign of the bias of $V_P(1, 2, 3)$ is not known *a priori*.

3 New Biodiversity Measures

Drawing on the lessons of the previous section, I develop here a new measure of the diversity loss and an index of relative diversity.

3.1 A measure of biodiversity loss

The measure of diversity loss, which I name $V_L(Q)$, should approximate as precisely as possible the actual loss of biodiversity incurred when (groups of) species cannot be preserved. The intuition behind measuring diversity loss is that the distances forming $V_L(Q)$ should, when "added back" onto the incomplete tree, recreate the original taxonomy as closely as possible.

Since $V_W(Q \cup E) - V_W(E) \neq V_W(Q)$, it is impractical to use $V_W(E)$ to measure the biodiversity loss. The inequality is partly due to the fact that $V_W(E)$ would only account for the distances within the set of extinct species, without considering the distances between the species of E and the species of Q . Furthermore, $V_W(E)$ can either over- or underestimate the biodiversity loss, depending on the extinct species.

No specific formula for $V_L(Q)$ could be found to fully satisfy the three general cases mentioned in Section 2.3.2; nonetheless, one of them performed well. The following formula for $V_L(Q)$ leads to the same result as $V_P(Q)$ in cases similar to Figure 2. In the other configurations, $V_L(Q)$ has a strictly negative bias and can thus serve as a lower bound for biodiversity loss. The formula is as follows:

$$V_L(Q) = -\max d(k, Q \cup E \setminus k) + V_L(Q \cup k). \quad (7)$$

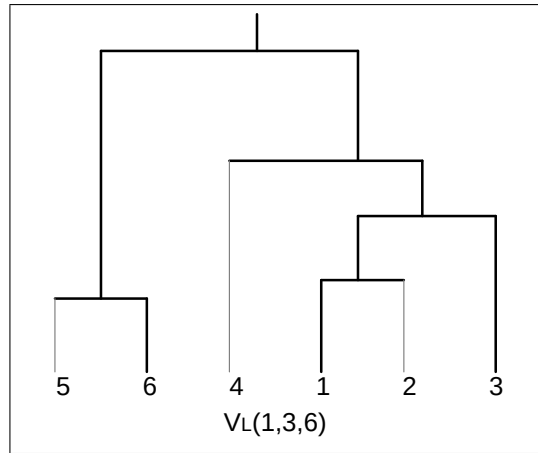
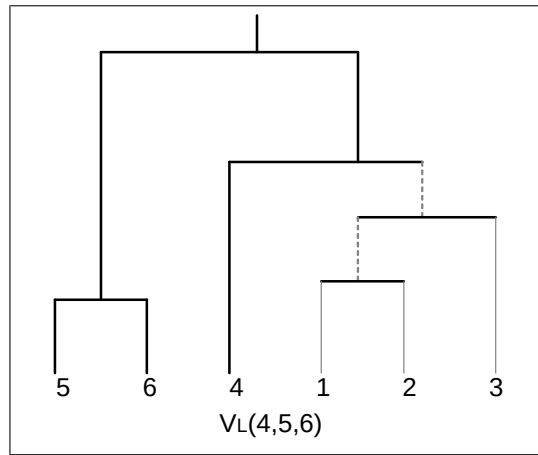
Equation 7 is a recursion, operating similarly to Equation 4.¹³ At each stage of the recursion, one branch is added back onto the tree and that species leaves the set E and joins the set Q . The process is over when all the species of E have been added back into Q . If at one stage of the recursion, two species both share the maximum distances as defined above, then either one of the two species can be chosen, without affecting the final result. By definition if $E = \emptyset$, then $V_L(Q) = 0$ and if $E = \{k\}$, then the formula simplifies to $V_L(Q) = d(k, Q \cup E \setminus k)$.

Figures 5 to 7 illustrate the fit of $V_L(Q)$: none of the distances are double-counted and $V_L(Q)$ offers the certainty that it either accurately represents the loss of diversity or that it can serve as its minimum bound.

Moreover, neither $V_P(Q)$ nor $V_L(Q)$ can be justified on the grounds of their absolute deviation from the actual total length of lost branches. For instance, in Figures 3 and 6, the overestimation of the diversity loss from $V_P(4, 5, 6)$ is clearly larger than the underestimation resulting from $V_L(4, 5, 6)$. Conversely, Figures 4 and 7 show that the overestimation of $V_P(1, 2, 3)$ is smaller than the underestimation of $V_L(1, 2, 3)$. Both results are independent of the relative lengths of the branches. Table 4 (Appendix) presents a complete account of $V_L(Q)$ for all subsets of $[1, 2, 3, 4, 5, 6]$.¹⁴

¹³The computational requirements necessary for the calculation of Equation 7 should be lower than for Equation 4, as the $\max$ function is not applied directly to the recursive term.

¹⁴As there is no uncertainty about the nature of the misrepresentation in Equation 7, my intuition has been that it

Figure 5: Tree Representation of $V_L(1, 3, 6)$ Figure 6: Tree Representation of $V_L(4, 5, 6)$

3.2 An index of relative diversity

The different measures of diversity and diversity loss presented above cannot be compared if the units in which they are provided are not the same or cannot be derived from each other. Genetic distances can be measured in different units, even from similar procedures, and can be derived from different experimentations. Furthermore, in a situation where species get extinct and others can be re-introduced within an ecosystem,¹⁵ it might be useful to consider a measure of diversity comparing the new level of diversity to a baseline level. Such a measure could also be applied to

should be possible to modify it in order to account for some of the missing links. I believe that the misrepresentations occur because of the inability of Equation 7 to recreate the entire structure of the tree when the set E contains all the species of either one of the terminal clades (i.e. $[1, 2]$ and $[5, 6]$ in this example). In such cases, Equation 7 fails to account for the linking segments between any extinct clade (terminal or not) and both the previous and the next node on the tree. A plethora of alternative formulas were tested, but at this stage my conclusion is that there potentially exists no universal formula deriving a tighter lower bound for the actual diversity loss.

¹⁵Re-introductions of extinct species have recently become quite common in some places, although yet mostly restricted to emblematic species, such as bears and wolves in western Europe.

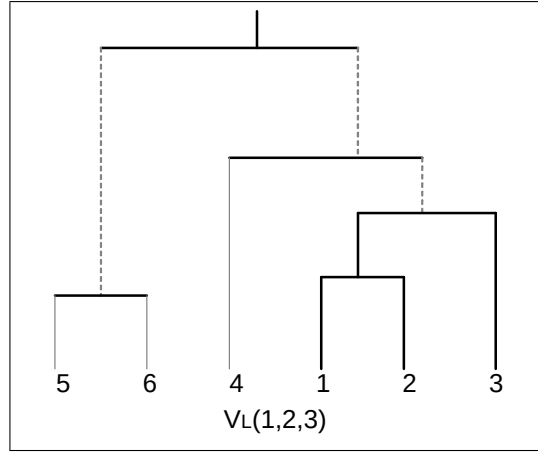


Figure 7: Tree Representation of $V_L(1, 2, 3)$

compare how pristine two ecosystems with very different levels of biodiversity are, by computing the current level of diversity as a ratio of the initial level of diversity. The following index of relative diversity can do that:

$$V_R(Q) = \frac{\max [V_W(Q \setminus i) + d(i, Q \setminus i)]}{\max [V_W(Q \setminus i) + d(i, Q \setminus i)] + (\max d(k, Q \cup E \setminus k) - V_L(Q \cup k))}. \quad (8)$$

Again, Q is defined as the existing set of species and E is defined as the set of extinct species.¹⁶ If the set of extinct species is an empty set, $V_R(Q)$ is equal to one. Conservation would then aim at keeping $V_R(Q)$ as close as possible to one. Note that in fact:

$$V_R(Q) = \frac{V_W(Q)}{V_W(Q) - V_L(Q)}. \quad (9)$$

Table 5 (Appendix) gives the values of $V_R(Q)$ for all subsets of $[1, 2, 3, 4, 5, 6]$. Table 6 (Appendix) gives a comparison and ranking of different subsets of size 3 when Equations 4 and 8 are applied on Table 1 (Appendix). The subsets are ranked in increasing order according to their biodiversity value and show substantial differences in the rankings. The choice of measure would then strongly impact on conservation decisions.

¹⁶If species are added to the set Q through re-introduction programs, the above formula can be modified by substituting $\max [V(T \setminus h) + d(h, T \setminus h)]$ as the numerator, with $T = Q \cup Y$, Y the set of re-introduced species and $h \in T$.

4 Axiomatic Evaluation

This section, first, presents a number of axioms that a measure of diversity should comply with. New axioms are developed, for a tighter evaluation of diversity measures. Secondly, the measures presented earlier are evaluated against all axioms.

4.1 Axioms

Weitzman [27] developed properties with which to evaluate his measure of biodiversity. In this section I extend Weitzman's list by an additional 4 axioms. The axioms that I have added to Weitzman's list of properties are numbered 7, 11, 12 and 13. The formulation of Weitzman's properties, hereafter referred to as axioms, are available in Weitzman [27]; these axioms are only presented shortly here. The new axioms are presented in more detail.

Axiom 1 defines the *monotonicity in species* of the measure, ensuring that diversity increases if a new species is added to the set. **Axiom 2** formulates the existence of at least one *link species*, restricting Equation 3 to hold for at least one species instead of all species, a case which was shown to happen only with ultrametric distances. **Axiom 3**, the *twin property*, states that diversity should not increase if the added species is identical to one of the species already included in the set. **Axiom 4** formalizes the *continuity in distances* of the diversity measure. **Axiom 5** postulates the *monotonicity in distances* of the diversity measure (i.e. the diversity value increases if all distances are subjected to the same "augmenting" function). **Axiom 6** fixes an *upper bound in the diversity increment caused by adding one species* equal to the maximum distance between the new species and any species already in the set.

Axiom 7: *Lower bound in diversity change caused by adding one species*

For the lower bound in the increment of $V(Q)$, it must be true that:

$$V(Q \cup j) \geq V(Q) + d(j, Q), \quad \forall Q \text{ and } \forall j \notin Q$$

with

$$d(j, Q) \equiv \min_{i \in Q} d(j, i).$$

In other words, the lowest increment in biodiversity when adding a species to the set Q is at least equal to the minimum distance between the added species and the set.

Axiom 8 favours the *most distantly related species* by stating that if one species of the set is consistently more distant to the rest of the set than another, it should systematically be preserved over the other, *ceteris paribus*. **Axiom 9** defines the *irrelevance of equally distant relatives* and ensures that if one species is equally related to all species, whether this species is present or not does not affect decisions regarding the preservation of any subset of Q . **Axiom 10**, named *Min-Loss extinction*, ensures that if one species can't be preserved, it should be one of the two species with the smallest pairwise distance.

Axiom 11: *Consistency in group disaggregation*

Consider two groups of species, Q_1 and Q_2 , each defining their complement E_1 and E_2 such that $Q_1 \cup E_1 = S = Q_2 \cup E_2$, with S the total reference catalogue of species. Further, $Q_1 \cap Q_2 = I$

with $I \neq \emptyset$. A desirable property is that if

$$V(Q_1) \geq V(Q_2)$$

then it should also be true that

$$V(Q_1 \setminus i) \geq V(Q_2 \setminus i)$$

for all $i \in I$. This axiom implicitly links the structure of the set Q to its diversity value. It ensures that a set with one single species dominating its total diversity value cannot exceed in diversity value another set containing the same species but displaying a more "balanced" structure.

Axiom 12: *Null diversity of a single species*

Diversity is a comparative concept, which can only be assessed by comparing at least two species. The notion of distance is thus appealing to measure how different two items are, while that notion of difference can serve as a measure of diversity. If the set is reduced to a single species, it is hence normal that

$$V(i) = 0 \forall i.$$

Even in the case of the rooted tree, it is the diversity within the set that $V(Q)$ measures, not the diversity between Q and other sets.

Axiom 13: *Homogeneity in distances*

Genetic distances are given in many different units. It is thus desirable to have a diversity measure which is unaffected by the choice of the units. Such a measure should therefore be homogenous of degree zero, at the very least of degree one:

$$\begin{aligned} V(Q_1) &= V(Q_2) \text{ where } d(i, j) \text{ in } Q_1 = \lambda d(i, j) \text{ in } Q_2, \forall i, j; \\ \text{if } V(Q_1) &\neq V(Q_2) \text{ then it should be true that } V(Q_1) = \lambda V(Q_2). \end{aligned}$$

4.2 Comparing diversity measures

Weitzman [27] proved that $V_W(Q)$ complies with Axioms 1 to 6, 8, 9 and 10. $V_W(Q)$ complies with Axiom 7 by construction and the minimum bound is $d(j, Q)$. $V_W(Q)$ fails to comply with Axiom 11, for instance: $V_W(3, 5, 6) = 658$ is larger than $V_W(2, 3, 4) = 591$, but $V_W(5, 6) = 126$ is less than $V_W(2, 4) = 328$. $V_W(Q)$ can comply with Axiom 12 as a matter of definition and it fulfills Axiom 13 because it fulfills Axiom 5.

The proof of the compliance of $V_P(Q)$ and $V_L(Q)$ to the different axioms often flows from their construction (i.e. a summation formula rather than a max or min operator as in Weitzman's measure) or can be imputed from Weitzman's results. The behavior of $V_R(Q)$ can in most cases be inferred from the compliance status of $V_W(Q)$ and $V_L(Q)$. As $V_{MD}(Q)$ fails to fulfil the Axiom 1, which is also the most fundamental, it is not assessed any further.¹⁷ The performance of the four main diversity measures presented in Sections 2.2, 2.3 and 3 is summarized in Table 7 (Appendix).

The axiomatic approach offers the following insights:

¹⁷The proofs for $V_P(Q)$, $V_L(Q)$ and $V_R(Q)$ were not included as a matter of space but can be requested by contacting the author. They are often either a matter of definition or can be derived from the proofs presented in Weitzman [27]. The proof of the compliance of $V_L(Q)$ with the new Axiom 11 is presented in the Appendix.

- Weitzman's measure of diversity $V_W(Q)$ complies with the most axioms, fulfilling 12 of the 13 axioms;
- however, the index of relative diversity $V_R(Q)$ offers a good alternative. Its compliance with a less general version of Axiom 5 (monotonicity in distances) can be solved for defined classes of the augmenting function. The only axiomatic "failure" of $V_R(Q)$ as compared to $V_W(Q)$ is Axiom 10 (Min-Loss extinction). And finally,
- a dry look at Table 7 (Appendix) is not sufficient to choose between $V_P(Q)$ and $V_L(Q)$. I believe that the measure of biodiversity loss $V_L(Q)$ offers a better alternative than $V_P(Q)$, for the following reasons. Firstly, the compliance to Axiom 6 (upper bound in diversity increase) is more important than Axiom 7 (lower bound on diversity increase) in that it ensures a consistently conservative estimate of the actual biodiversity loss. This synthesizes one of the points raised in Section 3.1. Secondly, both measures fail with respect to Axiom 8 (favour distant species), but both comply to a looser version of the axiom. Thirdly, Axiom 10 (Min-Loss extinction) is not necessarily obvious in its application to a measure of biodiversity loss, due to the question of the appropriate set of reference, whereas Axiom 11 can be viewed as one of the most important axioms in a "dynamic" setting where conservation options are not guaranteed to be successful.

Ultimately, the choice between $V_W(Q)$, $V_R(Q)$ and $V_L(Q)$ probably should be dictated by the context in which the diversity measure is used. As a first example, I consider two candidate sites for conservation. If the two sites are similar, $V_W(Q)$ is probably the best measure to rank the sites in terms of biodiversity content. If the two sites are assessed against a reference set of species, $V_L(Q)$ provides the best alternative in measuring the difference between the existing and the reference sets of species. If the two sites contain vastly different sets of species, a measure of genetic diversity is less appropriate and $V_R(Q)$ is undoubtedly the best option. The index of relative diversity serves well as an indicator of the "pristine-ness" of the genetic pool: both sites are assessed against their respective initial state, not directly against each other.

For the second example, I consider the case of a set of species whose individual conservation status needs to be assessed, either separately or within a subset of species. The diversity and loss measures are both consistent measures: $V_W(Q)$ consistently overestimates the diversity value of the preserved set of species, whilst $V_L(Q)$ consistently underestimates the diversity loss. The choice between the diversity and the loss measure is then simply dictated by the emphasis placed on either evaluating the existing diversity or the loss of diversity. In this example the index of relative diversity is less consistent, given that the bias of its numerator is positive but the bias of its denominator is unknown.

5 Conclusion

This paper presented and developed various techniques to measure biodiversity at the species level from a set of pairwise genetic distances. The four main biodiversity measures were then compared by mean of an axiomatic approach. The axiomatic approach showed the superiority of $V_W(Q)$ compared to the other three candidates. However, Weitzman's measure is not consistent in the event of species disappearance (because $V(Q) \neq V(Q \setminus i) + d(i, Q \setminus i)$ for all i) and thus fails with respect to the axiom of consistency in group disaggregation (Axiom 11). When comparing the diversity of two sets, the fact that $V_W(Q)$ ignores the structure of the sets whose diversity value it is comparing can be a significant drawback. This is especially true if extinction is likely to occur. Only the measure of biodiversity loss $V_L(Q)$ fulfils this axiom. It seems natural that a measure focusing on the value of the genetic information that has been lost should account for the structure of the preserved set. $V_L(Q)$ also complies with the most crucial of Weitzman's axioms. Consequently, $V_L(Q)$ is viewed as a superior measure to its most direct competitor $V_P(Q)$, the measure of diversity preservation proposed by Solow et al. [23]. Generally though, all the measures of genetic diversity presented here perform reasonably well and ought to be considered according to their contextual application. Criteria such as the importance placed on a reference set of species, or whether the biodiversity measurement will be used to choose between two conservation projects far apart in terms of the species they target, should play a significant role in the choice of diversity measure.

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Appendix

Definition. $V_L(Q) = -\max d(k, Q \cup E \setminus k) + V_L(Q \cup k)$, with E the set of extinct species, Q the set of living species and $k \in E$.

Axiom 11. Consider two groups of species Q_1 and Q_2 , such that $S - Q_1 = E_1$ and $S - Q_2 = E_2$. Further, $Q_1 \cap Q_2 = \{I\}$, with $I \neq \emptyset$. If

$$V_L(Q_1) \geq V_L(Q_2) \quad (\text{A1})$$

then it should also be true that

$$V_L(Q_1 \setminus i) \geq V_L(Q_2 \setminus i), \quad (\text{A2})$$

with $i \in I$.

Proof. By definition of $V_L(Q)$, the impact of a single species on the diversity of the set Q , whether that species is added to or subtracted from the set, is its distance to its nearest relative in the entire catalogue of species $Q \cup E = S$. In other words, the impact of a single species (added or subtracted) on the diversity of the set Q is independent of which other species belong to Q or not. Hence, $\forall i$

$$V_L(Q) - V_L(Q \setminus i) = d(i, S \setminus i). \quad (\text{A3})$$

This is true by extension for Q_1 and Q_2 . So, reordering A3 and substituting in A1 we obtain A2. ■

Note: $V_L(Q)$ is the only diversity measure presented in this paper for which Equation A3 is true, for all i .

Table 1: A Matrix of Measured Genetic Distances

species	1	2	3	4	5	6	common name
1	0	159	250	349	495	513	human
2	159	0	234	328	448	448	common chimpanzee
3	250	234	0	357	532	498	gorilla
4	349	328	357	0	477	488	orangutan
5	495	448	532	477	0	126	common gibbon
6	513	448	498	488	126	0	siamang gibbon

Table 2: Weitzman's Measure of Diversity for all Subsets

2 species	3 species	4 species	5 species
$V_W(1, 2)=159$	$V_W(1, 2, 3)=409$	$V_W(1, 2, 3, 4)=766$	$V_W(1, 2, 3, 4, 5)=1298$
$V_W(1, 3)=250$	$V_W(1, 2, 4)=508$	$V_W(1, 2, 3, 5)=941$	$V_W(1, 2, 3, 4, 6)=1271$
$V_W(1, 4)=349$	$V_W(1, 2, 5)=654$	$V_W(1, 2, 3, 6)=922$	$V_W(1, 2, 3, 5, 6)=1067$
$V_W(1, 5)=495$	$V_W(1, 2, 6)=672$	$V_W(1, 2, 4, 5)=1003$	$V_W(1, 2, 4, 5, 6)=1147$
$V_W(1, 6)=513$	$V_W(1, 3, 4)=607$	$V_W(1, 2, 4, 6)=1021$	$V_W(1, 3, 4, 5, 6)=1265$
$V_W(2, 3)=234$	$V_W(1, 3, 5)=782$	$V_W(1, 2, 5, 6)=798$	$V_W(2, 3, 4, 5, 6)=1249$
$V_W(2, 4)=328$	$V_W(1, 3, 6)=763$	$V_W(1, 3, 4, 5)=1139$	
$V_W(2, 5)=448$	$V_W(1, 4, 5)=844$	$V_W(1, 3, 4, 6)=1112$	
$V_W(2, 6)=448$	$V_W(1, 4, 6)=862$	$V_W(1, 3, 5, 6)=908$	
$V_W(3, 4)=357$	$V_W(1, 5, 6)=639$	$V_W(1, 4, 5, 6)=988$	
$V_W(3, 5)=532$	$V_W(2, 3, 4)=591$	$V_W(2, 3, 4, 5)=1123$	
$V_W(3, 6)=498$	$V_W(2, 3, 5)=766$	$V_W(2, 3, 4, 6)=1089$	
$V_W(4, 5)=477$	$V_W(2, 3, 6)=732$	$V_W(2, 3, 5, 6)=892$	
$V_W(4, 6)=488$	$V_W(2, 4, 5)=805$	$V_W(2, 4, 5, 6)=942$	
$V_W(5, 6)=126$	$V_W(2, 4, 6)=816$	$V_W(3, 4, 5, 6)=1015$	
	$V_W(2, 5, 6)=574$		
	$V_W(3, 4, 5)=889$		
	$V_W(3, 4, 6)=855$		
	$V_W(3, 5, 6)=658$		
	$V_W(4, 5, 6)=614$		

Table 3: The Measure of Diversity Preservation for all Subsets

1 species	2 species	3 species	4 species
$V_P(1)=-1766$	$V_P(1,2)=-1458$	$V_P(1,2,3)=-1224$	$V_P(1,2,3,4)=-896$
$V_P(2)=-1617$	$V_P(1,3)=-1501$	$V_P(1,2,4)=-1130$	$V_P(1,2,3,5)=-454$
$V_P(3)=-1871$	$V_P(1,4)=-1374$	$V_P(1,2,5)=-688$	$V_P(1,2,3,6)=-454$
$V_P(4)=-1999$	$V_P(1,5)=-884$	$V_P(1,2,6)=-688$	$V_P(1,2,4,5)=-360$
$V_P(5)=-2078$	$V_P(1,6)=-884$	$V_P(1,3,4)=-1124$	$V_P(1,2,4,6)=-360$
$V_P(6)=-2073$	$V_P(2,3)=-1383$	$V_P(1,3,5)=-634$	$V_P(1,2,5,6)=-562$
	$V_P(2,4)=-1289$	$V_P(1,3,6)=-634$	$V_P(1,3,4,5)=-285$
	$V_P(2,5)=-847$	$V_P(1,4,5)=-535$	$V_P(1,3,4,6)=-285$
	$V_P(2,6)=-847$	$V_P(1,4,6)=-535$	$V_P(1,3,5,6)=-508$
	$V_P(3,4)=-1449$	$V_P(1,5,6)=-758$	$V_P(1,4,5,6)=-409$
	$V_P(3,5)=-967$	$V_P(2,3,4)=-1055$	$V_P(2,3,4,5)=-285$
	$V_P(3,6)=-967$	$V_P(2,3,5)=-613$	$V_P(2,3,4,6)=-285$
	$V_P(4,5)=-1160$	$V_P(2,3,6)=-613$	$V_P(2,3,5,6)=-487$
	$V_P(4,6)=-1160$	$V_P(2,4,5)=-519$	$V_P(2,4,5,6)=-393$
5 species	$V_P(5,6)=-1918$	$V_P(2,4,6)=-519$	$V_P(3,4,5,6)=-484$
$V_P(1,2,3,4,5)=-126$		$V_P(2,5,6)=-721$	
$V_P(1,2,3,4,6)=-126$		$V_P(3,4,5)=-610$	
$V_P(1,2,3,5,6)=-328$		$V_P(3,4,6)=-610$	
$V_P(1,2,4,5,6)=-234$		$V_P(3,5,6)=-841$	
$V_P(1,3,4,5,6)=-159$		$V_P(4,5,6)=-1034$	
$V_P(2,3,4,5,6)=-159$			

Table 4: The Measure of Diversity Loss for all Subsets

1 species	2 species	3 species	4 species
$V_L(1)=-973$	$V_L(1,2)=-814$	$V_L(1,2,3)=-580$	$V_L(1,2,3,4)=-252$
$V_L(2)=-973$	$V_L(1,3)=-739$	$V_L(1,2,4)=-486$	$V_L(1,2,3,5)=-454$
$V_L(3)=-898$	$V_L(1,4)=-645$	$V_L(1,2,5)=-688$	$V_L(1,2,3,6)=-454$
$V_L(4)=-804$	$V_L(1,5)=-847$	$V_L(1,2,6)=-688$	$V_L(1,2,4,5)=-360$
$V_L(5)=-1006$	$V_L(1,6)=-847$	$V_L(1,3,4)=-411$	$V_L(1,2,4,6)=-360$
$V_L(6)=-1006$	$V_L(2,3)=-739$	$V_L(1,3,5)=-613$	$V_L(1,2,5,6)=-562$
	$V_L(2,4)=-645$	$V_L(1,3,6)=-613$	$V_L(1,3,4,5)=-285$
	$V_L(2,5)=-847$	$V_L(1,4,5)=-519$	$V_L(1,3,4,6)=-285$
	$V_L(2,6)=-847$	$V_L(1,4,6)=-519$	$V_L(1,3,5,6)=-487$
	$V_L(3,4)=-570$	$V_L(1,5,6)=-721$	$V_L(1,4,5,6)=-393$
	$V_L(3,5)=-772$	$V_L(2,3,4)=-411$	$V_L(2,3,4,5)=-285$
	$V_L(3,6)=-772$	$V_L(2,3,5)=-613$	$V_L(2,3,4,6)=-285$
	$V_L(4,5)=-678$	$V_L(2,3,6)=-613$	$V_L(2,3,5,6)=-487$
	$V_L(4,6)=-678$	$V_L(2,4,5)=-519$	$V_L(2,4,5,6)=-393$
5 species	$V_L(5,6)=-880$	$V_L(2,4,6)=-519$	$V_L(3,4,5,6)=-318$
$V_L(1,2,3,4,5)=-126$		$V_L(2,5,6)=-721$	
$V_L(1,2,3,4,6)=-126$		$V_L(3,4,5)=-444$	
$V_L(1,2,3,5,6)=-328$		$V_L(3,4,6)=-444$	
$V_L(1,2,4,5,6)=-234$		$V_L(3,5,6)=-646$	
$V_L(1,3,4,5,6)=-159$		$V_L(4,5,6)=-552$	
$V_L(2,3,4,5,6)=-159$			

Table 5: The Relative Measure of Diversity for all Subsets

2 species	3 species	4 species	5 species
$V_R(1,2)=0.1634$	$V_R(1,2,3)=0.4160$	$V_R(1,2,3,4)=0.7525$	$V_R(1,2,3,4,5)=0.9115$
$V_R(1,3)=0.2528$	$V_R(1,2,4)=0.5111$	$V_R(1,2,3,5)=0.6746$	$V_R(1,2,3,4,6)=0.9098$
$V_R(1,4)=0.3511$	$V_R(1,2,5)=0.4873$	$V_R(1,2,3,6)=0.6701$	$V_R(1,2,3,5,6)=0.7649$
$V_R(1,5)=0.3689$	$V_R(1,2,6)=0.4941$	$V_R(1,2,4,5)=0.7359$	$V_R(1,2,4,5,6)=0.8306$
$V_R(1,6)=0.3772$	$V_R(1,3,4)=0.5963$	$V_R(1,2,4,6)=0.7393$	$V_R(1,3,4,5,6)=0.8883$
$V_R(2,3)=0.2405$	$V_R(1,3,5)=0.5606$	$V_R(1,2,5,6)=0.5868$	$V_R(2,3,4,5,6)=0.8871$
$V_R(2,4)=0.3371$	$V_R(1,3,6)=0.5545$	$V_R(1,3,4,5)=0.7999$	
$V_R(2,5)=0.3460$	$V_R(1,4,5)=0.6192$	$V_R(1,3,4,6)=0.7960$	
$V_R(2,6)=0.3460$	$V_R(1,4,6)=0.6242$	$V_R(1,3,5,6)=0.6509$	
$V_R(3,4)=0.3851$	$V_R(1,5,6)=0.4670$	$V_R(1,4,5,6)=0.7154$	
$V_R(3,5)=0.4080$	$V_R(2,3,4)=0.5898$	$V_R(2,3,4,5)=0.7980$	
$V_R(3,6)=0.3921$	$V_R(2,3,5)=0.5555$	$V_R(2,3,4,6)=0.7929$	
$V_R(4,5)=0.4130$	$V_R(2,3,6)=0.5442$	$V_R(2,3,5,6)=0.6470$	
$V_R(4,6)=0.4185$	$V_R(2,4,5)=0.6080$	$V_R(2,4,5,6)=0.7056$	
$V_R(5,6)=0.1553$	$V_R(2,4,6)=0.6112$	$V_R(3,4,5,6)=0.7614$	
	$V_R(2,5,6)=0.4432$		
	$V_R(3,4,5)=0.6669$		
	$V_R(3,4,6)=0.6582$		
	$V_R(3,5,6)=0.5046$		
	$V_R(4,5,6)=0.5267$		

Table 6: Examples of Biodiversity Rankings

Subset Q	$V_W(Q)$	Rank	$V_R(Q)$	Rank
(1,3,4)	607	16	0.5963	7
(1,4,5)	844	4	0.6192	4
(1,4,6)	862	2	0.6242	3
(2,3,4)	591	17	0.5898	8
(2,4,5)	805	6	0.6080	6
(2,4,6)	816	5	0.6112	5
(3,4,5)	889	1	0.6669	1
(3,4,6)	855	3	0.6582	2

Table 7: Axiomatic Comparison of the Diversity Measures

Axioms	$V_W(Q)$	$V_P(Q)$	$V_L(Q)$	$V_R(Q)$
1: monotonicity in species	YES	YES	YES	YES
2: existence of link species	YES	YES	YES	n.a.
3: twin property	YES	YES	YES	YES
4: continuity in distances	YES	YES	YES	YES
5: monotonicity in distances	YES	YES	YES	NO
6: upper bound in species' diversity increase	YES	NO	YES	YES
7: lower bound in species' diversity change	YES	YES	NO	YES
8: favour the most distant species	YES	NO	NO	YES
9: irrelevance of equally distant species	YES	YES	YES	n.a.
10: Min-Loss extinction	YES	YES	NO	NO
11: consistency in group disaggregation	NO	NO	YES	NO
12: null diversity of single species	YES	n.a.	n.a.	YES
13: homogeneity in distances	YES	YES	YES	YES

n.a. = the axiom does not apply for this measure

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