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A Tale of Two Diversities

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A Tale of Two Diversities[*]

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Abstract

Efficient management of biodiversity aims at allocating conservation efforts in order to maximize diversity. Defining a diversity criterion is however far to be trivial; there is not one but several indices that can be used as biodiversity measures. This paper elicits and compares two *in situ* criterions for biodiversity conservation, based on two biodiversity indices stemming from different disciplines: Weitzman's index in economics and Rao's index in ecology. Both indices combines differently pieces of information about (1) species survival probability, and (2) measures of dissimilarity between species. In order to truly have *in situ* protection criterions, we add another layer of information about (3) the ecological interactions between species. Considering a simple three species ecosystem, we show that choosing one criterion or the other has policy implications, for they sometimes deliver diverging protection recommendations. We unravel the role played by the elements (1), (2) and (3) in the ranking, which allows us to highlight some specificities of the *in situ* criterions. For example, other things equal, Weitzman's *in situ* ranking tends to favor "robust" species, while Rao's *in situ* ranking gives priority to "fragile" species.

Keywords: conservation priorities, ecological interactions, biodiversity indices.

JEL Classification: C6, Q5.

1 Introduction

The science of biodiversity conservation has grown rapidly in recent decades. Important progress has been made on two interconnected fronts. On the one

hand, reflection has advanced on definitions and measures of biodiversity to produce what could be called a "biodiversity index theory" (for general overviews, see Mangurran, 2004, Baumgartner, 2004, Aulong, Figuières and Erdlenbruch, 2005, 2008). On the other hand - and building on this first front - progress has been made on how to maximize a biodiversity measure, or more generally a biodiversity-related goal, subject to a number of constraints. The challenge here is to understand the nature of a "solution" (*e.g.* the *extreme* policy in Weitzman's *Noah's ark metaphor*, 1998) and, more recently, to better take into account ecological interactions for real *in situ* policies (Baumgartner, 2004, Simanier, 2008, van der Heide, van den Bergh and van Ierland, 2005, Courtois, Figuières and Mulier, 2014). As a result, at least at the conceptual level, we are not without means to rationalize *in situ* protection efforts. Actually, the problem we still have to face is rather one of a plethora of means, for the biodiversity index theory does not advocate a unique "superior" index of biodiversity. Rather it offers a range of meaningful indices, and one may expect that using different indices as objective functions in optimization problems will lead to different solutions. Which index to choose, then?

From a consequentialist point of view, answering this question requires to compare the outcomes of different *in situ* optimization exercises, that differ from one another with respect to the biodiversity index retained as the objective function to be maximized. An important sub-class of indices, advocated in Wood (2000), is based on data about pairwise dissimilarities between species (Rao, 1986, Weitzman, 1992, Solow, Polasky and Broadus, 1993, Hill, 2001, Gerber, 2011)[1]. Gerber (2011) provides a comparison of the last four indices, though not in a context of *in situ* protection plans. And Rao's index has been ignored, despite its importance in ecology and biology.

Using the framework developed by Courtois et al. (2014) with ecological interactions for *in situ* cost-benefit analysis, the originality of the present paper is to scrutinize the consequences of using two diversity indices: Weitzman (1992)' s index, which is popular in several literatures including economics, and Rao (1982)' s index, mostly used in ecology and biology, but largely ignored by economists. Will both indices lead to the same policy? They both account simultaneously for survival probabilities and dissimilarity measures. Rao's index is defined as the expected dissimilarity between two entities randomly drawn from a collection, whereas Weitzman's index, in the specific context we will analyze, is the expected length of the evolutionary tree associated to the collection. The axiomatic properties of both indices have been elicited (Rao, 1986, Bossert, Pattanaik and Xu, 2002), which gives them some transparency as measures of diversity.

Since our goal is to unravel and understand basic issues, we will simplify the study whenever possible. Attention is restricted to a three-species ecosystem[2] with ecological interactions. Weitzman's and Rao's indices are used for

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[1]This is a range of other important and related papers, among which Vane-Wright, Humphries and Williams (1991), Crozier (1992), Faith (1992), Bossert, Pattanaik and Xu (2003).

[2]As explained later, a two-species ecosystem would be even simpler, but would not allow

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the comparison of particularly simple preservation policies, where the manager of a natural park has enough budget to care about at most one single species. Which one should he choose, given the advantages it provides either for its own sake or, indirectly, *via* ecological interactions?

The sketch of the paper is the following. In section 2 we model our *in situ* prioritization criterions. After describing the characteristics of our three species ecosystem, we define how both indices generally combine pieces of information and how they may be used for ranking species for in situ conservation. Section 3 aims at disentangling the role of the different aspects that compose the criterions, namely (i) the autonomous survival probabilities, (ii) the dissimilarities, (iii) the coefficients of ecological interactions. We end the paper with a discussion on the limits and perspectives of this approach.

2   A class of *in situ* prioritization problems

Consider an ecosystem with three species. To each species i, $i = 1, 2, 3$, is attached a survival probability P_i that, because of ecological interactions[3], partly depends on the survival probabilities of the two other species P_j, with $j \neq i$, and partly on the protection effort it receives, $x_i \in \{0, \overline{x}\}$. The efforts considered in this paper are as simple as possible, of a binary nature, *i.e.* a species is protected ($x_i = \overline{x}$) or not ($x_i = 0$); and the entire available budget is just enough to cover the protection of one species, no more, no less. Protection plans for two or three species at the same time are not affordable. Without being too specific for the moment - more details will be given in the following sections - if $\mathbf{X}$ stands for a 3-dimensional vector of efforts, with components x_i, and $\mathbf{P}$ is the vector of linearly interdependent survival probabilities, with components P_i, then the link between efforts and probabilities is a 3-dimensional vector of functions $\mathbf{P}(\mathbf{X})$.

We compare conservation effort plans regarding to how well they perform from the perspective of indices of expected biodiversity. We shall invoke alternatively two different indices of expected biodiversity: Weitzman's index, noted $W(\mathbf{P})$, and Rao's index, $R(\mathbf{P})$. Both belong to the family of expected diversity measures aggregating dissimilarities between species. Both combine in different ways: *i*) species survival probability, and *ii*) some measure of dissimilarities between species. Given the link between interdependent probabilities and efforts, $\mathbf{P}(\mathbf{X})$, we can then express *in situ* expected diversity indices, $\mathcal{W}(\mathbf{X}) \equiv W(\mathbf{P}(\mathbf{X}))$, and $\mathcal{R}(\mathbf{X}) \equiv R(\mathbf{P}(\mathbf{X}))$. Under this background, the originality of the present paper is to explore and compare optimal *in situ* protection plans. Put differently, we solve the programs $\max_{\mathbf{X}} \mathcal{W}(\mathbf{X})$ and $\max_{\mathbf{X}} \mathcal{R}(\mathbf{X})$ and compare their respective outcomes.

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to study the role of dissimilarities on the results. At least three species are needed for that purpose.

[3]The present paper belongs to a recent trend in the literature that tries to take into account ecological interactions, via the modelling of interdependent probabilities (Baumgartner, 2004, van der Heide, van den Bergh and van Ierland, 2005, Simanier 2008).

Now let us enter deeper into details about $\mathbf{P}, W, R$ and $\mathbf{X}$.

2.1 Interdependent survival probabilities of species

In the absence of ecological interactions and protection policies, each species i has an *autonomous survival probability* $q_i \in [0,1]$, $i = 1, 2, 3$. In order to take into account the ecological interactions and the protection efforts put in place, those raw data have to be modified to arrive at *interdependent survival probabilities,* denoted $P_i \in [\underline{P}_i, \overline{P}_i]$, $i = 1, 2, 3$. We assume these probabilities are linear functions of the protection efforts x_i, $i = 1, 2, 3$, measured in terms of probability variations, and of numbers $r_{ij} \equiv \partial P_i / \partial P_j, i \neq j$ representing the marginal ecological impact of species j on the survival probability of species i. We assume $|r_{ij}| < 1$, *i.e.* a variation in probability P_j has a less than proportional impact on P_i. Overall, the system of interdependent probabilities of survival for three species is as follows:

$$
\begin{cases}
P_1 = q_1 + x_1 + r_{12}P_2 + r_{13}P_3 \\
P_2 = q_2 + x_2 + r_{21}P_1 + r_{23}P_3 \\
P_3 = q_3 + x_3 + r_{31}P_1 + r_{32}P_2
\end{cases} . \tag{1}
$$

For practicality, let us define the following vectors and matrices, denoted in bold characters:

$$
\mathbf{Q} \equiv \begin{bmatrix} q_1 \\ q_2 \\ q_3 \end{bmatrix}, \ \mathbf{R} \equiv \begin{bmatrix} 0 & r_{12} & r_{13} \\ r_{21} & 0 & r_{23} \\ r_{31} & r_{32} & 0 \end{bmatrix}, \ \mathbf{I} \equiv \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix},
$$

$$
\mathbf{P} \equiv \begin{bmatrix} P_1 \\ P_2 \\ P_3 \end{bmatrix}, \ \overline{\mathbf{P}} \equiv \begin{bmatrix} \overline{P}_1 \\ \overline{P}_2 \\ \overline{P}_3 \end{bmatrix}, \ \underline{\mathbf{P}} \equiv \begin{bmatrix} \underline{P}_1 \\ \underline{P}_2 \\ \underline{P}_3 \end{bmatrix}, \ \mathbf{X} \equiv \begin{bmatrix} x_1 \\ x_2 \\ x_3 \end{bmatrix} .
$$

In matrix form, the system (1) of probabilities reads as:

$$
\mathbf{P} = \mathbf{Q} + \mathbf{X} + \mathbf{R} * \mathbf{P}. \tag{2}
$$

Under the following assumption :

$$
r_{23}r_{32} + r_{12}r_{21} + r_{13}r_{31} + r_{12}r_{31}r_{23} + r_{21}r_{13}r_{32} < 1 \ ,
$$

the system (2) can be solved[4] to give:

$$
\mathbf{P} = [\mathbf{I} - \mathbf{R}]^{-1} * (\mathbf{Q} + \mathbf{X}) \ . \tag{3}
$$

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[4]This is a sufficent condition for solvability. The necessary condition is:

$$
r_{23}r_{32} + r_{12}r_{21} + r_{13}r_{31} + r_{12}r_{31}r_{23} + r_{21}r_{13}r_{32} \neq 1 \ .
$$

We use the sufficient condition instead of the necessary condition because it leads to a more natural dependence of probabilities with regards to the model parameters. See in Appendix A the expressions for $P_1(\mathbf{X}), P_2(\mathbf{X})$ and $P_3(\mathbf{X})$.

Besides, one must ensure that the result is between 0 and 1. Two positions are possible on this issue: 1) to assume that, in applications the estimates one can make of the model parameters naturally guarantee this condition, 2) identify an upper bound for conservation efforts that guarantees this property. An algorithm exists for this purpose. It is available from the authors on request.

Thus, a particular protection plan $\mathbf{X}$ induces a particular vector of survival probabilities. Let $\mathcal{P}(\mathbf{X}) \equiv [\mathbf{I} - \mathbf{R}]^{-1} * (\mathbf{Q} + \mathbf{X})$ refers to the affine mapping from efforts into probabilities, *i.e.* the expression of the survival probability system as a function of efforts. $\mathcal{P}(\mathbf{X})$ is a vector, each element of which can be given explicitly (see Appendix A). Survival probabilities without protection policies are therefore:

$$\underline{\mathbf{P}} = \mathcal{P}(0 * \iota) \ , \tag{4}$$

where ι is a three-dimensional vector with all components equal to 1, and therefore $0 * \iota$ is a vector made of 3 zeroes. In the absence of ecological interactions, $[\mathbf{I} - \mathbf{R}]^{-1}$ is the identity matrix, and the bounds on probabilities are $\underline{\mathbf{P}} = \mathbf{Q}$ and $\overline{\mathbf{P}} = \underline{\mathbf{P}} + \overline{x} * \iota = \mathbf{Q} + \overline{x} * \iota$.

2.2 Species dissimilarities

Species are also characterized by their *dissimilarities*, which at a general level can be described as pairwise distances between any two species. Those distances can be given different contents. They can measure genetic distances by means of DNA-DNA hybridization (as in Krajewski, 1989, Caccone and Powell, 1989). Another possibility, used in phylogenetics, is to conceive species as terminal nodes in a tree structure. Pairwise dissimilarities are then given by adequate branch lengths (Faith, 1992, 1994). All these dissimilarity metrics have in common to capture and measure the intuitive notion of "differences among biological entities" (Wood, 2000). In order to fix ideas, it is here useful to refer to the library metaphor as in Weitzman (1998), under which each species is understood as a library, that is a collection of books. And a book itself is a valuable piece of information. Hence, the dissimilarity or distance between species i and j is measured by the number of books present in i but not in j. Dissimilarities, or differences in books, do not influence directly each species survival probabilities, but enters in a different way in the measure provided by biodiversity indices.

We will assume that distances among species are ultrametric[5], meaning that the two greatest pairwise distances in our group of three species are equal. The

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[5]There are two reasons to focus on the ultrametric case.

Firstly, when applied to a non ultrametric framework Rao's index may lead to unpalatable diversity rankings, where only few species are retained for conservation. In an extreme example, with one variable measured as source of distinctiveness among species, quadratic entropy is equal to the variance and retains species showing the extreme values of this variable (Pavoine et al., 2004, 2005). By contrast, in the ultrametric case Rao's index reaches its maximum value when all species are granted some protection.

Secondly, Weitzman (1992) constructed his diversity function using a complex iterative process. But this calculation boils down to the simple computation of the expected length of the evolutionary tree when distances are ultrametric. In addition, Solow and Polasky (1994) shows that apart from ultrametric distances, Weitzman's index is not strictly monotone relatively to distances used. Indeed, in a three species case (which is the case developed in this paper), Weitzman's measure of diversity is equivalent to the sum of the largest and the smallest distance. It is thus insensitive to any modification of the intermediary distance.

ultrametric property is possessed by all dissimilarities which can be directly associated with rooted trees in which all the end nodes are equidistant from the root of the tree (Van de Peer, 2003). Ultrametric distances provides an interesting framework for comparing both indices outcomes while keeping matters as simple as possible, especially as we introduce potential interactions among species of this tree.

In the three species case, ultrametric dissimilarities translate into a phylogenetic tree representation with proportional branches as shown in Figure 1 below, and where:

Figure 1: An ultrametric tree with three species
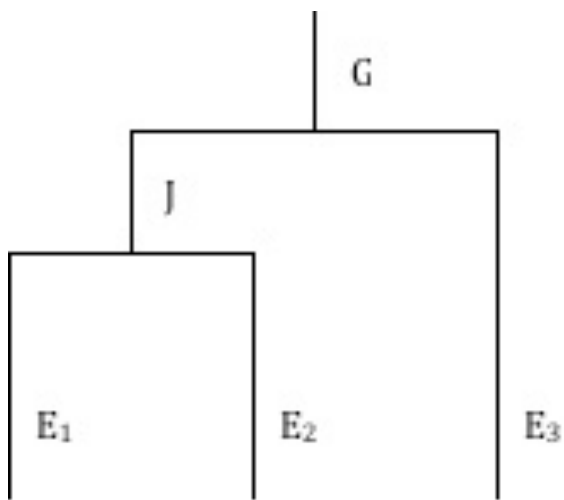
- E_i, is the number of "books" specific to species (library) i and only species i (with $i = 1, 2, 3$),

- J, is the number of "books" species 1 and 2 have in common,

- G, is the number of "books" common to 1, 2 and 3 (later we set G arbitrarily close to zero, and thus species 3 has no common books with species 1 and 2).

The number of "books" contained in libraries 1, 2 and 3 are:

$$M_1 = E_1 + J + G \ ,$$
$$M_2 = E_2 + J \ + G,$$
$$M_3 = E_3 + G.$$

Denoting d_{ij} the distance between species i and j, we obtain the following values for our distances between species 1, 2 and 3 in the ultrametric case :

$$d_{12} = d_{21} = E_1 = E_2 = E,$$
$$d_{13} = d_{31} = d_{23} = d_{32} = E_2 + J = E_1 + J = E_3$$

Notice that those distances are symmetric, $d_{ij} = d_{ji}$, $\forall i, j$. And distances between three species i, k, l are ultrametric if and only if for all i, k, l we can verify :

$$d_{kl} \leq \max\left(d_{ki}, d_{il}\right) \ .$$

When $J = 0$ there are no common genes between species 1 and 2. Thus we get back to a case very similar to the two-species case, in which the tree representation is as in Figure 2.

Figure 2: An ultrametric tree with three species and $J = 0$
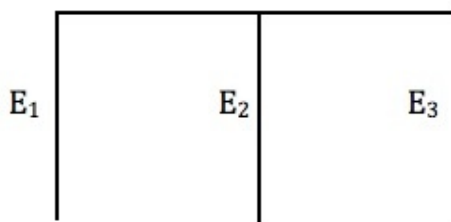
In this setting where $J = 0$, ecological interactions and survival probabilities are the only parameters discriminating the three species. Indeed, the three

species are here perfectly substitutable from the point of view of their dissimilarities. As J raises away from 0, we are able to represent the role of dissimilarity among species for both indicators since $E_1 = E_2 \neq E_3$.

2.3 Definitions of *in situ* indices for biodiversity

The indices used in this paper are built on the space of ecological and dissimilarity parameters presented so far. Denote Ω this space, and

$$e = (\mathbf{Q}, \mathbf{R}, \overline{x}, E, J, G) \in \Omega \ ,$$

a particular element of this parameters space.

Weitzman's index for *in situ* protection When applied in our three-species ecosystem with ultrametric distances, Weitzman's expected diversity index is the expected length of the evolutionary tree depicted earlier. More precisely:

- If no species disappears, an event that occurs with probability $P_1 P_2 P_3$, the length of the total tree, or the total number of different books if the three libraries are available, is $E_1 + E_2 + J + E_3 + G$,

- if only species 1 survives, an event occurring with probability $(1 - P_2)(1 - P_3) P_1$, the length of the tree is $E_1 + J + G$,

- if only species 1 and 2 survives, an event with probability $P_1 P_2 (1 - P_3)$, the length of the tree is $E_1 + E_2 + J + G$,

- and so on...

Therefore, the expected length of the tree is:

$$
\begin{aligned}
W(\mathbf{P}) = {} & P_1 P_2 P_3 \left(E_1 + E_2 + J + E_3 + G \right) + (1 - P_2)(1 - P_3) P_1 \left(E_1 + J + G \right) \\
& + (1 - P_1)(1 - P_3) P_2 \left(E_2 + J + G \right) + (1 - P_1)(1 - P_2) P_3 \left(E_3 + G \right) \\
& + P_1 P_2 (1 - P_3) \left(E_1 + E_2 + J + G \right) + P_1 P_3 (1 - P_2) \left(E_1 + J + E_3 + G \right) \\
& + P_2 P_3 (1 - P_1) \left(E_2 + J + E_3 + G \right) \ .
\end{aligned}
$$

Given that G is arbitrarily close to zero and can be neglected, after tedious algebra Weitzman's expected diversity boils down to a simple expression:

$$
\begin{aligned}
W(\mathbf{P}) &= P_1 \left(E_1 + J \right) + P_2 \left(E_2 + J \right) + P_3 E_3 - P_1 P_2 J \\
&= \left(P_1 + P_2 + P_3 \right) \left(E + J \right) - P_1 P_2 J.
\end{aligned}
$$

Since the goal is to rank protection priorities while taking into account ecological interactions, the above index has to be modified in order to incorporate

the later information. We obtain the desired qualification by plugging the relation $\mathcal{P}(\mathbf{X})$ between efforts and probabilities into $W(\mathbf{P})$. This results in what may be further called *Weitzman's in situ biodiversity index*:

$$
\begin{aligned}
\mathcal{W}(\mathbf{X}) &\equiv W \circ \mathcal{P}(\mathbf{X}) , \\
&= [P_1(\mathbf{X}) + P_2(\mathbf{X}) + P_3(\mathbf{X})](E+J) - P_1(\mathbf{X}) P_2(\mathbf{X}) J .
\end{aligned} \tag{5}
$$

As shown in Appendix B, we can rewrite more synthetically this expression under a matrix form:

$$
\mathcal{W}_e(\mathbf{X}) = \mathbf{X}^T * \mathbf{A}_e^W * \mathbf{X} + \mathbf{X}^T * \mathbf{B}_e^W + c^W , \tag{6}
$$

where $\mathbf{X}^T$ is the transposed vector of $\mathbf{X}$.

In this formula, $\mathbf{A}_e^w$ and $\mathbf{B}_e^w$ are, respectively, a matrix and a vector whose components are complex combinations of parameters included in the element $e \in \Omega$. Details are given in Appendix B. Note that if the vector e changes, so does expression (6). Hence we explicitly mention this dependence *via* subscripts, as in the notations $\mathcal{W}_e, \mathbf{A}_e^W, \mathbf{B}_e^W$.

Rao's index for *in situ* protection   Rao's index is the expected distance

between any two species randomly drawn from a given set of species. In our three-species ecosystem it is:

$$
\begin{aligned}
R(\mathbf{P}) &= P_1 P_2 (E_1 + E_2) + P_1 P_3 (E_1 + E_3 + J) + P_2 P_3 (E_2 + E_3 + J) , \\
&= 2 P_1 P_2 E + 2 P_1 P_3 (E+J) + 2 P_2 P_3 (E+J) , \\
&= 2 [(P_1 P_2 + P_1 P_3 + P_2 P_3) E + (P_1 + P_2) P_3 J] .
\end{aligned}
$$

Considering again the relation $\mathcal{P}(\mathbf{X})$ between efforts and probabilities, *Rao's in situ biodiversity index* is:

$$
\mathcal{R}(\mathbf{X}) \equiv R(\mathcal{P}(\mathbf{X})) = 2 \left[\begin{array}{c} (P_1(\mathbf{X}) P_2(\mathbf{X}) + P_1(\mathbf{X}) P_3(\mathbf{X}) + P_2(\mathbf{X}) P_3(\mathbf{X})) E \\ + (P_1(\mathbf{X}) + P_2(\mathbf{X})) P_3(\mathbf{X}) J \end{array} \right] . \tag{7}
$$

In Appendix C it is shown that this index boils down to a simple matrix expression:

$$
\mathcal{R}_e(\mathbf{X}) = \mathbf{X}^T * \mathbf{A}_e^R * \mathbf{X} + \mathbf{X}^T * \mathbf{B}_e^R + c^R , \tag{8}
$$

where $\mathbf{A}_e^R$ and $\mathbf{B}_e^R$ are, respectively, a matrix and a vector made of combinations of parameters. The notation emphasizes again a dependence with respect to the vector e of parameters.

2.4 Simple *in situ* protection projects: necessary and sufficient conditions for optimality

Our purpose is to compare three different extremely simple policies: preserving either species 1, or 2 or 3, referred to as

- Project 1:
$$\mathbf{X}_1^T = [\overline{x}, 0, 0] \ ,$$

- Project 2:
$$\mathbf{X}_2^T = [0, \overline{x}, 0] \ ,$$

- Project 3:
$$\mathbf{X}_3^T = [0, 0, \overline{x}] \ .$$

Ranking of projects according to Weitzman's index: For a given vector e of parameters, project 1 is preferred over project 2 and project 3, according to Weitzman's *in situ* index for protection iff:

$$\mathcal{W}_e\left(\mathbf{X}_1\right) \geq \max\left\{\mathcal{W}_e\left(\mathbf{X}_2\right), \mathcal{W}_e\left(\mathbf{X}_3\right)\right\} \ . \tag{9}$$

The formal framework developed so far allows to express the necessary and sufficient condition on parameters for this ranking to hold:

$$[\overline{x},0,0]*\mathbf{A}_e^W*\begin{bmatrix}\overline{x}\\0\\0\end{bmatrix}+[\overline{x},0,0]*\mathbf{B}_e^W \geq \max\left\{\begin{array}{c}[0,\overline{x},0]*\mathbf{A}_e^W*\begin{bmatrix}0\\\overline{x}\\0\end{bmatrix}+[0,\overline{x},0]*\mathbf{B}_e^W;\\[0,0,\overline{x}]*\mathbf{A}_e^W*\begin{bmatrix}0\\0\\\overline{x}\end{bmatrix}+[0,0,\overline{x}]*\mathbf{B}_e^W\end{array}\right\}.$$

Ranking of projects according to Rao's index: If Rao's criterion is used to rank priorities, then project 1 is favored iff the value of Rao's *in situ* index is higher than its value when preserving species 2 or species 3.:

$$\mathcal{R}_e\left(\mathbf{X}_1\right) \geq \max\left\{\mathcal{R}_e\left(\mathbf{X}_2\right), \mathcal{R}_e\left(\mathbf{X}_3\right)\right\} \ , \tag{10}$$

or equivalently:

$$[\overline{x},0,0]*\mathbf{A}_e^R*\begin{bmatrix}\overline{x}\\0\\0\end{bmatrix}+[\overline{x},0,0]*\mathbf{B}_e^R > \max\left\{\begin{array}{c}[0,\overline{x},0]*\mathbf{A}_e^R*\begin{bmatrix}0\\\overline{x}\\0\end{bmatrix}+[0,\overline{x},0]*\mathbf{B}_e^R;\\[0,0,\overline{x}]*\mathbf{A}_e^R*\begin{bmatrix}0\\0\\\overline{x}\end{bmatrix}+[0,0,\overline{x}]*\mathbf{B}_e^R\end{array}\right\}.$$

Mutatis mutandis, the same kind of formal statements can indicate the necessary and sufficient conditions on parameters for project 2 or 3 to be selected by each criterion. And we are also in position to study more in depth special cases, for the particular interest they convey and/or because their simplicity is helpful to grasp the logic of the two *in situ* rankings.

3 Disentangling the underlying logics of in-situ priorities

If a species is favored, of course this is because it differs from the other ones in some way. *Heterogeneity* is the key that explains rankings. This section ranks the policies under several configurations of parameters e_j, chosen in order to isolate the role played by heterogeneity in particular factors. It turns out that the two indices deliver opposite conservation recommendations when heterogeneity comes from autonomous survival probabilities, whereas they largely agree when heterogeneity comes from dissimilarities and ecological interactions.

From a technical point of view, for a given vector of parameters e_j, the entire difficulty boils down to the computation of differences such as:

$$\mathcal{W}_{e_j}\left(\mathbf{X}_k\right) - \mathcal{W}_{e_j}\left(\mathbf{X}_l\right) \ ,$$
$$\mathcal{R}_{e_j}\left(\mathbf{X}_k\right) - \mathcal{R}_{e_j}\left(\mathbf{X}_l\right) \ ,$$

for $k, l = 1, 2, 3$. Then, to achieve the desired conclusions, it remains to analyze the sign of these differences. Although their calculus presents no conceptual difficulties, and always ends up in closed-form expressions, the computational steps are tedious. They have been performed by a software for symbolic calculations (Xcas). Our Xcas spreadsheets are available on request, and an example is given in Appendix D.

3.1 When the indices disagree

3.1.1 The influence of autonomous survival probabilities (Q)

Let us first examine the case in which autonomous survival probabilities are the unique source of heterogeneity among species, and look at the ranking established by both indicators in this specific situation.

Consider a class of conservation problems summarized by the list of parameters e_q, in which $J \geq 0$, $r_{12} = r_{21} = r$, $r_{13} = r_{31} = r_{23} = r_{32} = 0$, and $q_1 \neq q_2$. The vector $\mathbf{Q}$ and the matrix $\mathbf{R}$ become:

$$\mathbf{Q}_{e_q} \equiv \begin{bmatrix} q_1 \\ q_2 \\ 0 \end{bmatrix}, \ \mathbf{R}_{e_q} \equiv \begin{bmatrix} 0 & r & 0 \\ r & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} \ .$$

Actually, if we focus on the ranking between species 1 and 2, the model boils down to a two-species ultrametric case. Tedious computations arrive at:

$$\mathcal{W}_{e_q}\left(\mathbf{X}_1\right) - \mathcal{W}_{e_q}\left(\mathbf{X}_2\right) \quad = \quad \frac{J\overline{x}}{\left(1+r\right)^2}\left(q_1 - q_2\right) , \qquad (11)$$

$$\mathcal{R}_{e_q}\left(\mathbf{X}_1\right) - \mathcal{R}_{e_q}\left(\mathbf{X}_2\right) \quad = \quad \frac{2E\overline{x}}{\left(1+r\right)^2}\left(q_2 - q_1\right) . \qquad (12)$$

So, Weitzman's ranking of the two policies is sensitive to J − featuring indifference when $J = 0$ − whereas Rao's ranking is not. Assuming $J > 0$, from (11) and (12) we can deduce:

Proposition 1 *Let the class of conservation problems be given by the list of parameters e_q and let $J > 0$. In this case, the two diversity indices deliver opposite rankings:*

- *Weitzman's in-situ ranking preserves the "strongest" species, i.e.*

$$\mathcal{W}_{e_q}\left(\mathbf{X}_1\right) \gtreqless \mathcal{W}_{e_q}\left(\mathbf{X}_2\right) \quad \Leftrightarrow \quad q_1 \gtreqless q_2 ,$$

- *whereas Rao's in situ ranking preserves the "weakest" species, i.e.*

$$\mathcal{R}_{e_q}\left(\mathbf{X}_1\right) \gtreqless \mathcal{R}_{e_q}\left(\mathbf{X}_2\right) \quad \Leftrightarrow \quad q_2 \gtreqless q_1 .$$

Ecological interactions have little importance in this first example, since both species are placed in an identical ecological role. Results are simply consistent with the logics embodied in the indicators alone. Weitzman' seeks the longest expected tree and only one species can be protected. If either species 1 or species 2 goes extinct, E "books" are lost but $E + J$ are safe. It is wise then to affect protection resources on the species which is initially the most safe, unless $J = 0$ because in this case, clearly, Weitzman's criterion is indifferent regarding which species should be afforded protection efforts. For Rao, however, the question is: how to choose the combination of probabilities leading to the highest expected dissimilarity? Put more precisely, in this two-species problem Rao seeks the largest product $P_1\left(\mathbf{X}\right)P_2\left(\mathbf{X}\right)$. This is best achieved when the policy helps the weakest species.

3.1.2 Robustness: three species

Those results are somehow robust to the introduction of a third and similar species into the framework, provided that the only source of heterogeneity among species is still their autonomous survival probability. To achieve this, we must keep the same distances between species 1, 2 and 3, and thus $J = 0$ (otherwise, heterogeneity also goes through dissimilarities) and $G = 0$, and where q_3 can take any arbitrary value. That is, we have to consider a slightly

different list of parameters e'_q, and perform again all the computations. It turns out that:

$$\mathcal{W}_{e'_q}\left(\mathbf{X}_1\right) - \mathcal{W}_{e'_q}\left(\mathbf{X}_2\right) = \mathcal{W}_{e'_q}\left(\mathbf{X}_1\right) - \mathcal{W}_{e'_q}\left(\mathbf{X}_3\right) = 0 \ ,$$

in other words, Weitzman's criterion proves to be indifferent between the three conservation policies. As for Rao's index, one finds:

$$\mathcal{R}_{e'_q}\left(\mathbf{X}_1\right) - \mathcal{R}_{e'_q}\left(\mathbf{X}_2\right) = \frac{2E\overline{x}}{\left(r+1\right)^2}\left(q_2 - q_1\right) \ ,$$

$$\mathcal{R}_{e'_q}\left(\mathbf{X}_1\right) - \mathcal{R}_{e'_q}\left(\mathbf{X}_3\right) = \frac{2E\overline{x}}{\left(r+1\right)^2}\left(q_3 - q_1\right) \ ,$$

$$\mathcal{R}_{e'_q}\left(\mathbf{X}_2\right) - \mathcal{R}_{e'_q}\left(\mathbf{X}_3\right) = \frac{2E\overline{x}}{\left(r+1\right)^2}\left(q_3 - q_2\right) \ ,$$

from which one directly deduces that the weakest species is the highest in the ranking.

In a next step, we will examine the role of dissimilarity, discarding any heterogeneity in terms of autonomous survival probabilities and species interactions.

3.2 When the indices agree

3.2.1 The influence of dissimilarity $\left(E_3 \neq E_1 = E_2\right)$

Dissimilarities between species play a different role depending on the indicators. In a two-species and ultrametric framework, such dissimilarities are necessarily identical $(E_1 = E_2 = E)$ and cannot lead by themselves to differences in rankings (species are perfectly substitutable from the point of view of their dissimilarity). The role of dissimilarity only appears as a third species is added into the framework, and provided that the number of common genes between species 1 and 2 gets away from zero $(J > 0)$ (figure 1). Indeed in this case, $E_1 = E_2 = E$ and $E_3 \neq E$ since $E_3 = E + J$.

Consider the parameter vector e_J in which $q_1 = q_2 = q_3 = q > 0$ and $r_{ij} = 0, \forall i \neq j$. In the absence of ecological interactions and in the ultrametric case where $E_1 = E_2 = E, E_3 = E + J$, the matrices $\mathbf{Q}$ and $\mathbf{R}$ become:

$$\mathbf{Q}_{e_J} \equiv \begin{bmatrix} q \\ q \\ q \end{bmatrix}, \ \mathbf{R}_{e_J} \equiv \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} \ .$$

Key pieces of information are:

$$\mathcal{W}_{e_J}\left(\mathbf{X}_1\right) - \mathcal{W}_{e_J}\left(\mathbf{X}_2\right) = 0 \ ,$$

$$\mathcal{W}_{e_J}\left(\mathbf{X}_3\right) - \mathcal{W}_{e_J}\left(\mathbf{X}_1\right) = \mathcal{W}_{e_J}\left(\mathbf{X}_3\right) - \mathcal{W}_{e_J}\left(\mathbf{X}_2\right) = Jq\overline{x} > 0 \ , \ (\text{since } J > 0, x > 0),$$

$$\mathcal{R}_{e_J}\left(\mathbf{X}_1\right) - \mathcal{R}_{e_J}\left(\mathbf{X}_2\right) = 0 \ ,$$

$$\mathcal{R}_{e_J}\left(\mathbf{X}_3\right) - \mathcal{R}_{e_J}\left(\mathbf{X}_1\right) = \mathcal{R}_{e_J}\left(\mathbf{X}_3\right) - \mathcal{R}_{e_J}\left(\mathbf{X}_2\right) = 2Jq\overline{x} > 0.$$

And a conclusion immediately appears:

Proposition 2 *Let the class of conservation problems be given by the list of parameters e_J. In this three-species ecosystem where dissimilarities are the only source of heterogeneity among species, the two diversity indices deliver the same rankings:*

- *They are indifferent between preserving the two least (and equivalently) dissimilar species (species 1 or 2).*

- *They recommend to preserve the most dissimilar species (species 3).*

This result is intuitive. If only species 1 (or 2) disappears, there remains $2(E+J)$ "books". But if species 3 only disappears, the number of safe "books" falls down to a lower $2E + J$. However, in Section 4.1 it is proved that the property emphasized in Proposition 2 is fragile, more precisely it holds only when ecological interactions are not too strong (even if all those ecological interactions are not a source of heterogeneity).

3.2.2 The influence of ecological interactions

This dimension carries with it all the complexity of the web of life. For instance, the interactions between two species can be considered as unilateral, *e.g.* species 1 impacts species 2 but not vice versa, or bilateral, *e.g.* species 1 impacts species 2 and species 2 impacts species 1. There are $2^2 = 4$ possibilities to consider. But as soon as one contemplates a three-species ecosystem, there are $3^3 = 27$ potential pairwise interactions between species (not even speaking of the additional difficulty linked to the intensity of the ecological interactions). The number of possibilities quickly explodes with the number of species. In face of this complexity, our strategy will be to focus on two illustrative cases of particular interest. And, to simplify matters, we assume away any role for dissimilarities, *i.e.* $G = 0$ and $J = 0$.

Ecological interactions in a two-species ecosystem Consider a situation with two interacting species, 1 and 2 (the third species doesn't interact, neither with species 1 nor with species 2). Consider a parameter vector e_{R2} where $r_{12} \neq r_{21}$, all the other r_{ij} being equal to zero, and $q_1 = q_2 = q, q_3 = 0$. The matrices $\mathbf{Q}$ and $\mathbf{R}$ become :

$$\mathbf{Q}_{e_{R2}} \equiv \begin{bmatrix} q \\ q \\ 0 \end{bmatrix}, \ \mathbf{R}_{e_{R2}} \equiv \begin{bmatrix} 0 & r_{12} & 0 \\ r_{21} & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}.$$

The computation of the biodiversity criterions reveals:

$$\mathcal{W}_{e_{R2}}(\mathbf{X}_1) - \mathcal{W}_{e_{R2}}(\mathbf{X}_2) = \frac{E\overline{x}}{1 - r_{12}r_{21}}(r_{21} - r_{12}) ,$$

$$\mathcal{R}_{e_{R2}}(\mathbf{X}_1) - \mathcal{R}_{e_{R2}}(\mathbf{X}_2) = \frac{2E\overline{x}(2q+x)}{(1 - r_{12}r_{21})^2}(r_{21} - r_{12}) .$$

Thus, we can establish:

Proposition 3 *Let the class of conservation problems be given by the list of parameters e_{R2}. The two criteria deliver the same ranking of policies $\mathbf{X}_1$ and $\mathbf{X}_2$. They recommend to preserve the species with the largest marginal benefit on the survival of the other species:*

$$\mathcal{W}_{e_{R2}}\left(\mathbf{X}_1\right) \underset{<}{\overset{>}{\gtreqqless}} \mathcal{W}_{e_{R2}}\left(\mathbf{X}_2\right) \quad \Leftrightarrow \quad r_{21} \underset{<}{\overset{>}{\gtreqqless}} r_{12}\ ,$$

$$\mathcal{R}_{e_{R2}}\left(\mathbf{X}_1\right) \underset{<}{\overset{>}{\gtreqqless}} \mathcal{R}_{e_{R2}}\left(\mathbf{X}_2\right) \quad \Leftrightarrow \quad r_{21} \underset{<}{\overset{>}{\gtreqqless}} r_{12}\ .$$

The two criteria recommend to preserve the species with the largest marginal benefit on the survival probability of the other species. In fact, this is as if the criteria aimed at maximizing the survival probability of the ecosystem as a whole. This result can be illustrated using the principal categories of interactions between our two species.

i) *Predation*: species 2, a predator, feeds on species 1, its prey. By definition we have $r_{21} > 0$ and $r_{12} < 0$. Both criteria recommend to preserve the prey - here species 1 - since its interaction coefficient is larger ($r_{21} > 0 > r_{12}$).

ii) *Mutualism*: species 1 and 2 impact positively on each other. By definition we have $r_{12} > 0$ and $r_{21} > 0$. Both criteria recommend to preserve the species with the largest marginal benefit on the survival probability of the other species.

iii) *Competition*: species 1 and 2 have to share a common resource in the same living area that cannot fully support both populations. By definition we have $r_{12} < 0$ and $r_{21} < 0$. Both criteria recommend to preserve the species with the lowest negative impact on the other species.

Ecological interactions in a three-species ecosystem   As a third species

is introduced, the impact of interactions on criteria recommendations is more tricky to study as there is an interplay of effects due to combinations of inter-relations. In order to illustrate this complexity we consider a simple ecosystem made of three interacting species characterized by unilateral interactions. We assume a single species, say species 1, impacts the two other ones but these two impact neither each other nor species 1. A possible illustration of this configuration is a predator-prey in which species 1 a predator negatively impacts two preys, species 2 and 3, but does not need them to survive, because other foods are available to him.

Define a vector e_{R3} such that $E_1 = E_2 = E_3 = E$, $J = 0$, $q_1 = q_2 = q_3 = q$ and all interaction coefficients beside r_{21} and r_{31} are null. The only distinction between the three species is how they interact. Matrices $\mathbf{Q}$ and $\mathbf{R}$ become :

$$\mathbf{Q}_{e_{R3}} \equiv \begin{bmatrix} q \\ q \\ q \end{bmatrix}\ , \quad \mathbf{R}_{e_{R3}} \equiv \begin{bmatrix} 0 & 0 & 0 \\ r_{21} & 0 & 0 \\ r_{31} & 0 & 0 \end{bmatrix}\ .$$

And relative performances of policies are measured by:

$$\mathcal{W}_{e_{R3}}(\mathbf{X}_1) - \mathcal{W}_{e_{R3}}(\mathbf{X}_2) = E\overline{x}(r_{21} + r_{31}) , \tag{13}$$

$$\mathcal{W}_{e_{R3}}(\mathbf{X}_1) - \mathcal{W}_{e_{R3}}(\mathbf{X}_3) = E\overline{x}(r_{21} + r_{31}) , \tag{14}$$

$$\mathcal{W}_{e_{R3}}(\mathbf{X}_2) - \mathcal{W}_{e_{R3}}(\mathbf{X}_3) = 0 , \tag{15}$$

$$\mathcal{R}_{e_{R3}}(\mathbf{X}_1) - \mathcal{R}_{e_{R3}}(\mathbf{X}_2) = 2E\overline{x}\left[\begin{array}{c} r_{21}r_{31}(2q+x) + r_{21}(3q+x) \\ +r_{31}(2q+x) \end{array}\right] , \tag{16}$$

$$\mathcal{R}_{e_{R3}}(\mathbf{X}_1) - \mathcal{R}_{e_{R3}}(\mathbf{X}_3) = 2E\overline{x}\left[\begin{array}{c} r_{21}r_{31}(2q+x) + r_{21}(2q+x) \\ +r_{31}(3q+x) \end{array}\right] , \tag{17}$$

$$\mathcal{R}_{e_{R3}}(\mathbf{X}_2) - \mathcal{R}_{e_{R3}}(\mathbf{X}_3) = 2E\overline{x}q(r_{31} - r_{21}) . \tag{18}$$

Weitzman's criterion recommends to preserve species 1 rather than species 2 and 3 iff:

$$\mathcal{W}_{e_{R3}}(\mathbf{X}_1) > \max(\mathcal{W}_{e_{R3}}(\mathbf{X}_2), \mathcal{W}_{e_{R3}}(\mathbf{X}_3)).$$

The above expressions (13) and (14) show that this is true iff $r_{21} + r_{31} > 0$, that is if the cumulated impact of species 1 on the survival probability of the two other species is larger than the cumulated impact of these species on all other species (which is null here as we assume $r_{12} = r_{13} = r_{23} = r_{32} = 0$). This result somehow confirms Proposition 3 as it recommends to put conservation efforts on the species which is the more beneficial (or the less detrimental) to the survival of the species composing the ecosystem.

Similarly, Rao's criterion recommends to preserve species 1 rather than species 2 and 3 when:

$$\mathcal{R}_{e_{R3}}(\mathbf{X}_1) > \max(\mathcal{R}_{e_{R3}}(\mathbf{X}_2), \mathcal{R}_{e_{R3}}(\mathbf{X}_3)).$$

From expressions (16) and (17), this is true iff $r_{21}r_{31}(2q+x) + r_{31}(2q+x) + r_{21}(3q+x) > 0$ and $r_{21}r_{31}(2q+x) + r_{21}(2q+x) + r_{31}(3q+x) > 0$. In case species 1 impacts positively species 2 and 3, preservation effort is put on species 1. Otherwise, interpreting the criterion is more tricky as one of the above inequality may not hold. In such a case, effort is then put on the species which is the more (negatively) impacted by species 1. We find again a confirmation of the result forwarded by Proposition 3. However, the decision rule depicted here is not anymore a simple additive formula but a combination of additive and multiplicative components ($r_{21}r_{31}$) making interpretation fastidious. Adding interrelations or species in the analysis increases complexity as it increases complementarities and multiplicative effects.

4 Interactions between effects

4.1 Autonomous survival probabilities and dissimilarities

Now let us have a look at the combination of autonomous survival probabilities and dissimilarity. Consider a slight departure of parameters configuration e_q

of Section 3.1.1. In the new list of parameters e_{qJ}, the unique difference comes from parameter J which is not null anymore, $J > 0$, and $r_{ij} = r$, when $i \neq j$. The vector $\mathbf{Q}$ and the matrix $\mathbf{R}$ are:

$$\mathbf{Q}_{e_{qJ}} \equiv \begin{bmatrix} q_1 \\ q_2 \\ q_3 \end{bmatrix} , \; \mathbf{R}_{e_{qJ}} \equiv \begin{bmatrix} 0 & r & r \\ r & 0 & r \\ r & r & 0 \end{bmatrix} .$$

And the relative performance of policies can be deduced from:

$$\mathcal{W}_{e_{qJ}}(\mathbf{X}_1) - \mathcal{W}_{e_{qJ}}(\mathbf{X}_2) = \frac{J\bar{x}}{(1+r)^2}(q_1 - q_2) , \tag{19}$$

$$\mathcal{W}_{e_{qJ}}(\mathbf{X}_1) - \mathcal{W}_{e_{qJ}}(\mathbf{X}_3) = \frac{J\bar{x}\left[r(q_1 + q_3 + x) + q_2(1 - r)\right]}{(1+r)^2(2r-1)} , \tag{20}$$

$$\mathcal{W}_{e_{qJ}}(\mathbf{X}_2) - \mathcal{W}_{e_{qJ}}(\mathbf{X}_3) = \frac{J\bar{x}\left[r(q_2 + q_3 + x) + q_1(1 - r)\right]}{(1+r)^2(2r-1)} , \tag{21}$$

$$\mathcal{R}_{e_{qJ}}(\mathbf{X}_1) - \mathcal{R}_{e_{qJ}}(\mathbf{X}_2) = \frac{2E\bar{x}}{(1+r)^2}(q_2 - q_1) , \tag{22}$$

$$\mathcal{R}_{e_{qJ}}(\mathbf{X}_1) - \mathcal{R}_{e_{qJ}}(\mathbf{X}_3) = \frac{2J\bar{x}\left[r(3q_3 - q_1 - q_2) + rx - (q_3 - q_1 - q_2)\right]}{(1+r)^2(2r-1)}$$
$$+ \frac{2E\bar{x}}{(1+r)^2}(q_3 - q_1) , \tag{23}$$

$$\mathcal{R}_{e_{qJ}}(\mathbf{X}_2) - \mathcal{R}_{e_{qJ}}(\mathbf{X}_3) = \frac{2J\bar{x}\left[r(3q_3 - q_1 - q_2) + rx - (q_3 - q_1 - q_2)\right]}{(r+1)^2(2r-1)}$$
$$+ \frac{2E\bar{x}}{(1+r)^2}(q_3 - q_2) . \tag{24}$$

When the choice is between species 1 and 2, one finds again the properties that Weitzman's logic promotes robustness, whereas Rao's index opts for weakness.

The conclusions are more subtle when the third species is at stake, and they depend on the importance of ecological interactions: Weitzman prefers species 3 only if $r < 1/2^6$. In other words, dissimilarity prevails when ecological interactions are not too strong. And the conclusion is even more complex when it comes to Rao's index. Whatever the choice, it is reversed when r crosses the value $1/2$.

Now, as a particular case let the autonomous probabilities of survival be all

---

[6]The value $r = 1/2$ is forbidden. For this paricular value, the system of interdependent probabilities (2) cannot be solved.

identical. The relative performances of policies (19) to (24) simplify to:

$$
\mathcal{W}_{e'_{qJ}}\left(\mathbf{X}_1\right) - \mathcal{W}_{e'_{qJ}}\left(\mathbf{X}_2\right) = 0 , \tag{25}
$$

$$
\mathcal{W}_{e'_{qJ}}\left(\mathbf{X}_1\right) - \mathcal{W}_{e'_{qJ}}\left(\mathbf{X}_3\right) = \frac{J\overline{x}\left[r\left(q+x\right)+q\right]}{\left(1+r\right)^2\left(2r-1\right)} , \tag{26}
$$

$$
\mathcal{W}_{e'_{qJ}}\left(\mathbf{X}_2\right) - \mathcal{W}_{e'_{qJ}}\left(\mathbf{X}_3\right) = \frac{J\overline{x}\left[r\left(q+x\right)+q\right]}{\left(1+r\right)^2\left(2r-1\right)} , \tag{27}
$$

$$
\mathcal{R}_{e'_{qJ}}\left(\mathbf{X}_1\right) - \mathcal{R}_{e'_{qJ}}\left(\mathbf{X}_2\right) = 0 , \tag{28}
$$

$$
\mathcal{R}_{e'_{qJ}}\left(\mathbf{X}_1\right) - \mathcal{R}_{e'_{qJ}}\left(\mathbf{X}_3\right) = \frac{2J\overline{x}\left[r\left(q+x\right)+q\right]}{\left(1+r\right)^2\left(2r-1\right)} , \tag{29}
$$

$$
\mathcal{R}_{e'_{qJ}}\left(\mathbf{X}_2\right) - \mathcal{R}_{e'_{qJ}}\left(\mathbf{X}_3\right) = \frac{2J\overline{x}\left[r\left(q+x\right)+q\right]}{\left(1+r\right)^2\left(2r-1\right)} . \tag{30}
$$

There is indifference between policies 1 and 2, whatever the index used as an objective function. And the most dissimilar species, species 3, is always granted priority when $r < 1/2$, for both indices. But rankings are reversed if ecological interactions are too strong ($r > 1/2$).

4.2   Ecological interactions and dissimilarities

Now, combine the heterogeneity of ecological interactions and dissimilarities. Consider a parameters configuration e_{RJ} in which $J > 0$, and $r_{ij} = 0$, except for r_{12} and r_{21} that can be arbitrarily chosen. The vector $\mathbf{Q}$ and the matrix $\mathbf{R}$ are:

$$
\mathbf{Q}_{e_{RJ}} \equiv \left[\begin{array}{c} q \\ q \\ 0 \end{array}\right] , \quad \mathbf{R}_{e_{RJ}} \equiv \left[\begin{array}{ccc} 0 & r_{12} & 0 \\ r_{21} & 0 & 0 \\ 0 & 0 & 0 \end{array}\right] .
$$

And the relative performance of policies can be deduced from:

$$\mathcal{W}_{e_{RJ}}\left(\mathbf{X}_1\right) - \mathcal{W}_{e_{RJ}}\left(\mathbf{X}_2\right) = \overline{x}\frac{\left(E+J\right)\left(1-r_{12}r_{21}\right)-J\left(2q+x\right)}{\left(1-r_{12}r_{21}\right)^2}\left(r_{21}-r_{12}\right) , \quad (31)$$

$$\mathcal{W}_{e_{RJ}}\left(\mathbf{X}_1\right) - \mathcal{W}_{e_{RJ}}\left(\mathbf{X}_3\right) = \overline{x}\left(E+J\right)\frac{\left(1+r_{12}-r_{12}r_{21}-r_{12}^2r_{21}\right)r_{21}}{\left(1-r_{12}r_{21}\right)^2} \quad (32)$$

$$-\overline{x}J\frac{\left(r_{12}q+2q+x\right)r_{21}+q}{\left(1-r_{12}r_{21}\right)^2} , \quad (33)$$

$$\mathcal{W}_{e_{RJ}}\left(\mathbf{X}_2\right) - \mathcal{W}_{e_{RJ}}\left(\mathbf{X}_3\right) = \overline{x}\left(E+J\right)\frac{\left(1+r_{21}-r_{12}r_{21}-r_{12}r_{21}^2\right)r_{12}}{\left(1-r_{12}r_{21}\right)^2} \quad (34)$$

$$-\overline{x}J\frac{\left(r_{21}q+2q+x\right)r_{12}+q}{\left(1-r_{12}r_{21}\right)^2} , \quad (35)$$

$$\mathcal{R}_{e_{RJ}}\left(\mathbf{X}_1\right) - \mathcal{R}_{e_{RJ}}\left(\mathbf{X}_2\right) = \frac{2E\overline{x}(2q+\overline{x})}{\left(1-r_{12}r_{21}\right)^2}\left(r_{21}-r_{12}\right) , \quad (36)$$

$$\mathcal{R}_{e_{RJ}}\left(\mathbf{X}_1\right) - \mathcal{R}_{e_{RJ}}\left(\mathbf{X}_3\right) = 2\overline{x}\left(E+J\right)\frac{q\left(r_{12}r_{21}{}^2+r_{12}{}^2r_{21}+2r_{12}r_{21}-r_{12}-1\right)}{\left(1-r_{12}r_{21}\right)^2} \quad (37)$$

$$+2\overline{x}\frac{Er_{21}\left(qr_{12}+q+\overline{x}\right)-Jq\left(1+r_{21}\right)}{\left(1-r_{12}r_{21}\right)^2} , \quad (38)$$

$$\mathcal{R}_{e_{RJ}}\left(\mathbf{X}_2\right) - \mathcal{R}_{e_{RJ}}\left(\mathbf{X}_3\right) = 2\overline{x}\left(E+J\right)\frac{q\left[r_{12}r_{21}{}^2+r_{12}{}^2r_{21}+2r_{12}r_{21}-r_{21}-1\right]}{\left(1-r_{12}r_{21}\right)^2} \quad (39)$$

$$+2\overline{x}\frac{Er_{12}\left(qr_{21}+q+\overline{x}\right)-Jq\left(1+r_{12}\right)}{\left(1-r_{12}r_{21}\right)^2} . \quad (40)$$

When the comparison only involves species 1 and 2, that are perfectly substitutable from the point of view of their dissimilarities, and for low values of J the conclusion is clear-cut: both indices favor the species with the largest ecological impact. When species 3 is at stake, conclusions are ambiguous. In order to fix ideas, assume that all ecological impacts are non-negative ($r_{12} \geq 0, r_{21} \geq 0$). Then, for example, Both Weitzman and Rao prefer species 3 over species 1 (or species 2) when the ecological impact of the latter is sufficiently weak. But indices may also diverge. For instance, when the autonomous survival probability q is sufficiently close to 0, Rao clearly drops species 3 in favor of any of the other two. A conclusion that cannot be drawn from Weitzman's index under the same condition on q.

4.3 Autonomous survival probabilities and ecological interactions

Finally, combine the heterogeneity of autonomous survival probabilities with heterogenous ecological interactions. Consider a parameters configuration e_{qR} in which $J \geq 0$, r_{12} and r_{21} can take any values, and all the other r_{ij} are null.

The vector $\mathbf{Q}$ and the matrix $\mathbf{R}$ are:

$$\mathbf{Q}_{e_{qR}} \equiv \begin{bmatrix} q_1 \\ q_2 \\ 0 \end{bmatrix}, \quad \mathbf{R}_{e_{qR}} \equiv \begin{bmatrix} 0 & r_{12} & 0 \\ r_{21} & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}.$$

Computations for rankings of species 1 and 2 arrive at:

$$
\begin{aligned}
\mathcal{W}_{e_{qR}}(\mathbf{X}_1) - \mathcal{W}_{e_{qR}}(\mathbf{X}_2) = & \; J\frac{\overline{x}\left(1 + r_{12}r_{21}\right)}{\left(1 - r_{12}r_{21}\right)^2}(q_1 - q_2) \\
& + J\frac{2\overline{x}}{\left(1 - r_{12}r_{21}\right)^2}(q_2 r_{12} - q_1 r_{21}) \qquad (41) \\
& + \frac{\overline{x}\left[(E + J)\left(1 - r_{12}r_{21}\right) - Jx\right]}{\left(1 - r_{12}r_{21}\right)^2}(r_{21} - r_{12}) \; , \\
\mathcal{R}_{e_{qR}}(\mathbf{X}_1) - \mathcal{R}_{e_{qR}}(\mathbf{X}_2) = & \; \frac{2E\overline{x}\left(1 + r_{12}r_{21}\right)}{\left(1 - r_{12}r_{21}\right)^2}(q_2 - q_1) \\
& - \frac{4E\overline{x}}{\left(1 - r_{12}r_{21}\right)^2}(q_2 r_{12} - q_1 r_{21}) \qquad (42) \\
& + \frac{2E\overline{x}^2}{\left(1 - r_{12}r_{21}\right)^2}(r_{21} - r_{12}).
\end{aligned}
$$

Of course, when $r_{21} = r_{12} = r$, one finds again the results of Section 3.1.1. Recall that Weitzman selects the strongest species - with the largest q_i - for protection, whereas Rao prefers the weakest species (Proposition 1).

As soon as $r_{21} \neq r_{12}$, these results have to be qualified. They are now more complex functions of, not only the $q_i s$, but also the $r_{ij}s$. In order to grasp these qualifications, pretend that species 1 is the strongest $(q_1 > q_2)$. We know from Proposition 1 that, when $r_{21} = r_{12} = r$, Weitzman (respectively Rao) suggests species 1 (resp. species 2) should be protected. Now, imagine that $r_{21} = 0 < r_{12}$. On this basis alone, if q_1 and q_2 were identical, both Weitzman and Rao would prefer species 2 (see Proposition 3). But if $q_1 > q_2$, from expressions (41) and (42) Rao clearly prefers species 2, whereas Weitzman's conclusion is ambiguous. Eventually its answer reveals a trade-off between two opposite effects, and this trade-off depends, among other things, on the importance of J, the number of common "genes" between species 1 and 2.

Under different circumstances, Rao's ranking can also be ambiguous. Assume that $r_{21} = 0 < r_{12}$ and $q_1 < q_2$. Then Weitzman clearly prefers species 2. But Rao's ranking embodies two opposite logics, one in favor of species 2 (the more ecologically beneficial), and the other in favor of species 1 (the weakest species).The final choice will reveal Rao's trade-off between those two opposite forces. And, as can be deduced from expression (42), contrary to Weitzman's trade-off it does not depend on J.

5   Conclusion

This paper modifies Weitzman's and Rao's biodiversity indices in order to incorporate information about ecological interactions, so that they are more suitable for *in situ* protection plans. Using alternatively the qualified Weitzman's and Rao's indices, a simple framework allows us to analyze and compare the corresponding best conservation plans. And we can disentangle, for each *in situ* index of biodiversity, the role played by three drivers: *i*) autonomous survival probabilities $\mathbf{Q}$, *ii*) ecological interaction $\mathbf{R}$ and, *iii*) dissimilarity J, each being considered in strict isolation or in combinations.

There are three important outcomes:

1. the two indices, stemming from different academic backgrounds, clearly combine the pieces of information $\mathbf{Q}$, $\mathbf{R}$ and J in different ways to measure biodiversity. As a consequence, the two indices do not systematically deliver the same conservation recommendations. They disagree when the difference between species comes from autonomous survival probabilities, whereas they largely agree when heterogeneity comes from dissimilarities and/or ecological interactions.

2. When ecological interactions matters for the ranking, the favored species is the one that sustains the best ecological chain. In general, the introduction of ecological interactions among more than two species can lead to complex conclusions.

3. When the three drivers are combined, the policy advocated by each index reveals a specific trade-off between $\mathbf{Q}$, $\mathbf{R}$ and J.

From a practical point of view, an interesting follow-up to this research would be to consider any number of species, among which only a subset can be offered protection. The analytical understanding of the rankings will be lost, but this step does not seem to pose any computer problems.

At a more fundamental level, a reflection should be initiated on the objective of conservation policies. Given its inherent construction, each biodiversity index is a measure of a certain vision of biodiversity. It is interesting to know that, other things equal, there is a tendency for Weitzman's index to favor robust species, whereas Rao's index cares more about fragile species. What is needed now in order to arrive at a unique solution is a criterion to select among indices. The present paper shows that such a criterion will decide upon which trade-off should be made between robust and fragile species.

Appendix

A   The system of interdependent probabilities

Solving the system (2) of ecological interactions for P_1, P_2 and P_3 as functions of $\mathbf{X} = (x_1, x_2, x_3)^T$ gives :

$$P_1(\mathbf{X}) = \frac{(q_1 + x_1)(1 - r_{23}r_{32}) + (q_2 + x_2)(r_{12} + r_{13}r_{32}) + (q_3 + x_3)(r_{12}r_{23} + r_{13})}{1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}}$$

$$(43)$$

$$P_2(\mathbf{X}) = \frac{(q_2 + x_2)(1 - r_{13}r_{31}) + (q_1 + x_1)(r_{21} + r_{31}r_{23}) + (q_3 + x_3)(r_{21}r_{13} + r_{23})}{1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}}$$

$$(44)$$

$$P_3(\mathbf{X}) = \frac{(q_1 + x_1)(r_{31} + r_{32}r_{21}) + (q_2 + x_2)(r_{12}r_{31} + r_{32}) + (q_3 + x_3)(1 - r_{12}r_{21})}{1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}}$$

$$(45)$$

Probability of species 1 can be described as a combination of each species intrinsic survival probability augmented by protection effort, articulated through direct and indirect interactions among species.

In vector notations, probabilities as functions of efforts are:

$$\mathcal{P}(\mathbf{X}) \equiv \begin{bmatrix} P_1(\mathbf{X}) \\ P_2(\mathbf{X}) \\ P_3(\mathbf{X}) \end{bmatrix} = \mathbf{\Lambda} * (\mathbf{Q} + \mathbf{X}) \ .$$

B Weitzman's criterion for in situ protection

In our three-species model, the expected diversity of the ecosystem according to Weitzman's criterion is:

$$\begin{aligned} W(\mathbf{P}) = {} & P_1 P_2 P_3 (E_1 + E_2 + J + E_3 + G) + (1 - P_2)(1 - P_3) P_1 (E_1 + J + G) \\ & + (1 - P_1)(1 - P_3) P_2 (E_2 + J + G) + (1 - P_1)(1 - P_2) P_3 (E_3 + G) \\ & + P_1 P_2 (1 - P_3)(E_1 + E_2 + J + G) + P_1 P_3 (1 - P_2)(E_1 + J + E_3 + G) \\ & + P_2 P_3 (1 - P_1)(E_2 + J + E_3 + G) \ . \end{aligned}$$

Since G is close to zero, this expression simplifies to

$$\begin{aligned} W = {} & P_1 P_2 P_3 (E_1 + E_2 + J + E_3) + (1 - P_2)(1 - P_3) P_1 (E_1 + J) \\ & + (1 - P_1)(1 - P_3) P_2 (E_2 + J) + (1 - P_1)(1 - P_2) P_3 E_3 \\ & + P_1 P_2 (1 - P_3)(E_1 + E_2 + J) + P_1 P_3 (1 - P_2)(E_1 + J + E_3) \\ & + P_2 P_3 (1 - P_1)(E_2 + J + E_3) \ . \end{aligned}$$

Developing and simplifying, Weitzman's expected diversity boils down to:

$$W(\mathbf{P}) = P_1 (E_1 + J) + P_2 (E_2 + J) + P_3 E_3 - P_1 P_2 J \ .$$

Now remember that probabilities are functions of efforts, $\mathcal{P}(\mathbf{X})$. Therefore, Weitzman's expected diversity as a function of efforts is:

$$
\begin{aligned}
\mathcal{W}(\mathbf{X}) &\equiv W(\mathcal{P}(\mathbf{X})) \ , \\
&= P_1(\mathbf{X})(E_1 + J) + P_2(\mathbf{X})(E_2 + J) + P_3(\mathbf{X})E_3 - P_1(\mathbf{X})P_2(\mathbf{X})J \ .
\end{aligned}
$$

Recall finally that, because distances are ultrametric, $E_1 = E_2 = E$ and $E_3 = E + J$. Therefore:

$$
\mathcal{W}(\mathbf{X}) = [P_1(\mathbf{X}) + P_2(\mathbf{X}) + P_3(\mathbf{X})](E + J) - P_1(\mathbf{X})P_2(\mathbf{X})J \ .
$$

More precisely, using (43), (44) and (45):

$$
\mathcal{W}(\mathbf{X}) = \frac{1}{\phi}\left[
\begin{array}{l}
(E + J)\left(
\begin{array}{l}
(q_1 + x_1)(1 - r_{23}r_{32}) + (q_2 + x_2)(r_{12} + r_{13}r_{32}) + (q_3 + x_3)(r_{12}r_{23} + r_{13}) \\
+ (q_2 + x_2)(1 - r_{13}r_{31}) + (q_1 + x_1)(r_{21} + r_{31}r_{23}) + (q_3 + x_3)(r_{21}r_{13} + r_{23}) \\
+ (q_1 + x_1)(r_{31} + r_{32}r_{21}) + (q_2 + x_2)(r_{12}r_{31} + r_{32}) + (q_3 + x_3)(1 - r_{12}r_{21})
\end{array}
\right) \\
- \frac{J}{\phi}\left[
\begin{array}{l}
(q_1 + x_1)(1 - r_{23}r_{32}) \\
+ (q_2 + x_2)(r_{12} + r_{13}r_{32}) \\
+ (q_3 + x_3)(r_{12}r_{23} + r_{13})
\end{array}
\right] * \left[
\begin{array}{l}
(q_2 + x_2)(1 - r_{13}r_{31}) \\
+ (q_1 + x_1)(r_{21} + r_{31}r_{23}) \\
+ (q_3 + x_3)(r_{21}r_{13} + r_{23})
\end{array}
\right]
\end{array}
\right]
$$

$$(46)$$

with $\phi = (1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32})^2$.

We can rewrite this general form as follows:

$$
\mathcal{W}(\mathbf{X}) = \left\{
\begin{array}{c}
a_{11}^W x_1^2 + a_{22}^W x_2^2 + a_{33}^W x_3^2 + a_{12}^W x_1 x_2 + a_{13}^W x_1 x_3 + a_{23}^W x_2 x_3 \\
+ b_1^W x_1 + b_2^W x_2 + b_3^W x_3 + c^W
\end{array}
\right.
\tag{47}
$$

where

$$a_{11}^w = -\frac{J}{\phi^2}\left(1 - r_{23}r_{32}\right)\left(r_{21} + r_{31}r_{23}\right) \ , \ a_{22}^W = -\frac{J}{\phi^2}\left(r_{12} + r_{13}r_{32}\right)\left(1 - r_{13}r_{31}\right)$$

$$a_{33}^W = -\frac{J}{\phi^2}\left(r_{12}r_{23} + r_{13}\right)\left(r_{21}r_{13} + r_{23}\right)$$

$$a_{12}^w = \frac{-J}{\phi^2}\left[\left(1 - r_{23}r_{32}\right)\left(1 - r_{13}r_{31}\right) + \left(r_{12} + r_{13}r_{32}\right)\left(r_{21} + r_{31}r_{23}\right)\right]$$

$$a_{13}^W = \frac{-J}{\phi^2}\left[\left(1 - r_{23}r_{32}\right)\left(r_{21}r_{13} + r_{23}\right) + \left(r_{12}r_{23} + r_{13}\right)\left(r_{21} + r_{31}r_{23}\right)\right]$$

$$a_{23}^W = -\frac{J}{\phi^2}\left[\left(r_{12} + r_{13}r_{32}\right)\left(r_{21}r_{13} + r_{23}\right) + \left(r_{12}r_{23} + r_{13}\right)\left(1 - r_{13}r_{31}\right)\right]$$

$$b_1^w = \left[\begin{array}{c} (E+J)\frac{1}{\phi}\left[\left(1 - r_{23}r_{32}\right) + \left(r_{21} + r_{31}r_{23}\right) + \left(r_{31} + r_{32}r_{21}\right)\right] \\ -\frac{J}{\phi^2}\left(\begin{array}{c} 2q_1\left(1 - r_{23}r_{32}\right)\left(r_{21} + r_{31}r_{23}\right) \\ +q_2\left(\left(1 - r_{23}r_{32}\right)\left(1 - r_{13}r_{31}\right) + \left(r_{12} + r_{13}r_{32}\right)\left(r_{21} + r_{31}r_{23}\right)\right) \\ +q_3\left(\left(1 - r_{23}r_{32}\right)\left(r_{21}r_{13} + r_{23}\right) + \left(r_{12}r_{23} + r_{13}\right)\left(r_{21} + r_{31}r_{23}\right)\right) \end{array}\right) \end{array}\right]$$

$$b_2^W = \left[\begin{array}{c} (E+J)\frac{1}{\phi}\left[\left(r_{12} + r_{13}r_{32}\right) + \left(1 - r_{13}r_{31}\right) + \left(r_{12}r_{31} + r_{32}\right)\right] \\ -\frac{J}{\phi^2}\left[\begin{array}{c} q_1\left(\left(1 - r_{23}r_{32}\right)\left(1 - r_{13}r_{31}\right) + \left(r_{12} + r_{13}r_{32}\right)\left(r_{21} + r_{31}r_{23}\right)\right) \\ +2q_2\left(r_{12} + r_{13}r_{32}\right)\left(1 - r_{13}r_{31}\right) \\ +q_3\left(\left(r_{12} + r_{13}r_{32}\right)\left(r_{21}r_{13} + r_{23}\right) + \left(r_{12}r_{23} + r_{13}\right)\left(1 - r_{13}r_{31}\right)\right) \end{array}\right] \end{array}\right]$$

$$b_3^W = \left[\begin{array}{c} (E+J)\frac{1}{\phi}\left[\left(r_{12}r_{23} + r_{13}\right) + \left(r_{21}r_{13} + r_{23}\right) + \left(1 - r_{12}r_{21}\right)\right] \\ -\frac{J}{\phi^2}\left[q_1\left(\begin{array}{c} \left(1 - r_{23}r_{32}\right)\left(r_{21}r_{13} + r_{23}\right) \\ +\left(r_{12}r_{23} + r_{13}\right)\left(r_{21} + r_{31}r_{23}\right) \end{array}\right) + q_2\left(\begin{array}{c} \left(r_{12} + r_{13}r_{32}\right)\left(r_{21}r_{13} + r_{23}\right) \\ +\left(r_{12}r_{23} + r_{13}\right)\left(1 - r_{13}r_{31}\right) \end{array}\right)\right] \\ +2q_3\left(r_{12}r_{23} + r_{13}\right)\left(r_{21}r_{13} + r_{23}\right) \end{array}\right]$$

$$c^W = \left[\begin{array}{c} (E+J)\frac{1}{\phi}\left[\begin{array}{c} q_1\left(1 - r_{23}r_{32}\right) + q_2\left(r_{12} + r_{13}r_{32}\right) + q_3\left(r_{12}r_{23} + r_{13}\right) \\ +q_1\left(r_{21} + r_{31}r_{23}\right) + q_2\left(1 - r_{13}r_{31}\right) + q_3\left(r_{21}r_{13} + r_{23}\right) \\ +q_1\left(r_{31} + r_{32}r_{21}\right) + q_2\left(r_{12}r_{31} + r_{32}\right) + q_3\left(1 - r_{12}r_{21}\right) \end{array}\right] \\ -\frac{J}{\phi^2}\left[\begin{array}{c} q_1^2\left(1 - r_{23}r_{32}\right)\left(r_{21} + r_{31}r_{23}\right) \\ +q_2^2\left(r_{12} + r_{13}r_{32}\right)\left(1 - r_{13}r_{31}\right) + q_3^2\left(r_{12}r_{23} + r_{13}\right)\left(r_{21}r_{13} + r_{23}\right) \\ +q_1q_2\left(\left(1 - r_{23}r_{32}\right)\left(1 - r_{13}r_{31}\right) + \left(r_{12} + r_{13}r_{32}\right)\left(r_{21} + r_{31}r_{23}\right)\right) \\ +q_1q_3\left(\left(1 - r_{23}r_{32}\right)\left(r_{21}r_{13} + r_{23}\right) + \left(r_{12}r_{23} + r_{13}\right)\left(r_{21} + r_{31}r_{23}\right)\right) \\ +q_2q_3\left(\left(r_{12} + r_{13}r_{32}\right)\left(r_{21}r_{13} + r_{23}\right) + \left(r_{12}r_{23} + r_{13}\right)\left(1 - r_{13}r_{31}\right)\right) \end{array}\right] \end{array}\right]$$

Finally, a matrix form expression would be more compact than (47). Let us define :

$$\mathbf{A}_e^W = \left[\begin{array}{ccc} a_{11}^W & \frac{1}{2}a_{12}^W & \frac{1}{2}a_{13}^W \\ \frac{1}{2}a_{21}^W & a_{22}^W & \frac{1}{2}a_{23}^W \\ \frac{1}{2}a_{31}^W & \frac{1}{2}a_{32}^W & a_{33}^W \end{array}\right] , \ \mathbf{B}_e^W = \left[\begin{array}{c} b_1^W \\ b_2^W \\ b_3^W \end{array}\right] .$$

Then Weitzman's criterion for *in situ* conservation is:

$$\mathcal{W}_e\left(\mathbf{X}\right) = \mathbf{X}^T * \mathbf{A}_e^W * \mathbf{X} + \mathbf{X}^T * \mathbf{B}_e^W + c^W .$$

C Rao's criterion for in situ protection

As explained in the text, given the relation $\mathcal{P}\left(\mathbf{X}\right) \equiv \mathbf{\Lambda}*\left(\mathbf{Q} + \mathbf{X}\right)$ between efforts and probabilities, Rao's index for *in situ* protection is:

$$\begin{aligned}
\mathcal{R}\left(\mathbf{X}\right) &= P_1\left(\mathbf{X}\right) P_2\left(\mathbf{X}\right)\left(E_1 + E_2\right) + P_1\left(\mathbf{X}\right) P_3\left(\mathbf{X}\right)\left(E_1 + E_3 + J\right) + P_2\left(\mathbf{X}\right) P_3\left(\mathbf{X}\right)\left(E_2 + E_3 + J\right) , \\
&= 2\left[\left(P_1\left(\mathbf{X}\right) P_2\left(\mathbf{X}\right) + P_1\left(\mathbf{X}\right) P_3\left(\mathbf{X}\right) + P_2\left(\mathbf{X}\right) P_3\left(\mathbf{X}\right)\right) E + \left(P_1\left(\mathbf{X}\right) + P_2\left(\mathbf{X}\right)\right) P_3\left(\mathbf{X}\right) J\right]
\end{aligned}$$

and using the relation between ultrametric distances, $E_1 = E_2 = E$ and $E_3 = E + J$:

$$\mathcal{R}\left(\mathbf{X}\right) = 2\left[\left(P_1\left(\mathbf{X}\right) P_2\left(\mathbf{X}\right) + P_1\left(\mathbf{X}\right) P_3\left(\mathbf{X}\right) + P_2\left(\mathbf{X}\right) P_3\left(\mathbf{X}\right)\right) E + \left(P_1\left(\mathbf{X}\right) + P_2\left(\mathbf{X}\right)\right) P_3\left(\mathbf{X}\right) J\right] .$$

Using the survival probability system (43), (44), and (45), we obtain the following form for Rao's index:

$$\mathcal{R}\left(\mathbf{X}\right) = \frac{1}{\phi}\left[\begin{array}{c}
E_1\left(\begin{array}{c}\left(q_1 + x_1\right)\left(1 - r_{23}r_{32}\right) \\ + \left(q_2 + x_2\right)\left(r_{12} + r_{13}r_{32}\right) \\ + \left(q_3 + x_3\right)\left(r_{12}r_{23} + r_{13}\right)\end{array}\right)\left(\begin{array}{c}\left(q_1 + x_1\right)\left(r_{21} + r_{31}r_{23} + r_{31} + r_{21}r_{32}\right) \\ + \left(q_2 + x_2\right)\left(1 - r_{13}r_{31} + r_{32} + r_{31}r_{12}\right) \\ + \left(q_3 + x_3\right)\left(r_{23} + r_{21}r_{13} + 1 - r_{21}r_{12}\right)\end{array}\right) \\
+ E_2\left(\begin{array}{c}\left(q_1 + x_1\right)\left(r_{21} + r_{31}r_{23}\right) \\ + \left(q_2 + x_2\right)\left(1 - r_{13}r_{31}\right) \\ + \left(q_3 + x_3\right)\left(r_{23} + r_{21}r_{13}\right)\end{array}\right)\left(\begin{array}{c}\left(q_1 + x_1\right)\left(1 - r_{23}r_{32} + r_{31} + r_{21}r_{32}\right) \\ + \left(q_2 + x_2\right)\left(r_{12} + r_{13}r_{32} + r_{32} + r_{31}r_{12}\right) \\ + \left(q_3 + x_3\right)\left(r_{12}r_{23} + r_{13} + 1 - r_{21}r_{12}\right)\end{array}\right) \\
+ \left(E_3 + J\right)\left(\begin{array}{c}\left(q_1 + x_1\right)\left(r_{31} + r_{21}r_{32}\right) \\ + \left(q_2 + x_2\right)\left(r_{32} + r_{31}r_{12}\right) \\ + \left(q_3 + x_3\right)\left(1 - r_{21}r_{12}\right)\end{array}\right)\left(\begin{array}{c}\left(q_1 + x_1\right)\left(1 - r_{23}r_{32} + r_{21} + r_{31}r_{23}\right) \\ + \left(q_2 + x_2\right)\left(r_{12} + r_{13}r_{32} + 1 - r_{13}r_{31}\right) \\ + \left(q_3 + x_3\right)\left(r_{12}r_{23} + r_{13} + r_{23} + r_{21}r_{13}\right)\end{array}\right)
\end{array}\right]$$

This form can be rewritten as :

$$\mathcal{R}\left(x_1; x_2; x_3\right) = \left\{\begin{array}{c}a_{11}^R x_1^2 + a_{22}^R x_2^2 + a_{33}^R x_3^2 + a_{12}^R x_1 x_2 + a_{13}^R x_1 x_3 + a_{23}^R x_2 x_3 \\ + b_1^R x_1 + b_2^R x_2 + b_3^R x_3 + c^R.\end{array}\right. \tag{48}$$

where

$$\phi = \left(1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}\right)^2$$

$$a_{11}^R = \left[\begin{array}{c} E_1\left(1 - r_{23}r_{32}\right)\left(r_{21} + r_{31}r_{23} + r_{31} + r_{21}r_{32}\right) + E_2\left(r_{21} + r_{31}r_{23}\right)\left(1 - r_{23}r_{32} + r_{31} + r_{21}r_{32}\right) \\ + \left(E_3 + J\right)\left(r_{31} + r_{21}r_{32}\right)\left(1 - r_{23}r_{32} + r_{21} + r_{31}r_{23}\right) \end{array}\right]$$

$$a_{22}^R = \left[\begin{array}{c} E_1\left(r_{12} + r_{13}r_{32}\right)\left(1 - r_{13}r_{31} + r_{32} + r_{31}r_{12}\right) + E_2\left(1 - r_{13}r_{31}\right)\left(r_{12} + r_{13}r_{32} + r_{32} + r_{31}r_{12}\right) \\ + \left(E_3 + J\right)\left(r_{32} + r_{31}r_{12}\right)\left(r_{12} + r_{13}r_{32} + 1 - r_{13}r_{31}\right) \end{array}\right]$$

$$a_{33}^R = \left[\begin{array}{c} E_1\left(r_{12}r_{23} + r_{13}\right)\left(r_{23} + r_{21}r_{13} + 1 - r_{21}r_{12}\right) + E_2\left(r_{23} + r_{21}r_{13}\right)\left(r_{23} + r_{21}r_{13}\right) \\ + \left(E_3 + J\right)\left(1 - r_{21}r_{12}\right)\left(r_{12}r_{23} + r_{13} + r_{23} + r_{21}r_{13}\right) \end{array}\right]$$

$$a_{12}^R = \left[\begin{array}{c} E_1\left[\left(1 - r_{23}r_{32}\right)\left(1 - r_{13}r_{31} + r_{32} + r_{31}r_{12}\right) + \left(r_{12} + r_{13}r_{32}\right)\left(r_{21} + r_{31}r_{23} + r_{31} + r_{21}r_{32}\right)\right] \\ + E_2\left[\left(r_{21} + r_{31}r_{23}\right)\left(r_{12} + r_{13}r_{32} + r_{32} + r_{31}r_{12}\right) + \left(1 - r_{13}r_{31}\right)\left(1 - r_{23}r_{32} + r_{31} + r_{21}r_{32}\right)\right] \\ + \left(E_3 + J\right)\left[\left(r_{31} + r_{21}r_{32}\right)\left(r_{12} + r_{13}r_{32} + 1 - r_{13}r_{31}\right) + \left(r_{32} + r_{31}r_{12}\right)\left(1 - r_{23}r_{32} + r_{21} + r_{31}r_{23}\right)\right] \end{array}\right]$$

$$a_{13}^R = \left[\begin{array}{c} E_1\left[\left(1 - r_{23}r_{32}\right)\left(r_{23} + r_{21}r_{13} + 1 - r_{21}r_{12}\right) + \left(r_{12}r_{23} + r_{13}\right)\left(r_{21} + r_{31}r_{23} + r_{31} + r_{21}r_{32}\right)\right] \\ + E_2\left[\left(r_{21} + r_{31}r_{23}\right)\left(r_{23} + r_{21}r_{13}\right) + \left(r_{23} + r_{21}r_{13}\right)\left(1 - r_{23}r_{32} + r_{31} + r_{21}r_{32}\right)\right] \\ + \left(E_3 + J\right)\left[\left(r_{31} + r_{21}r_{32}\right)\left(r_{12}r_{23} + r_{13} + r_{23} + r_{21}r_{13}\right) + \left(1 - r_{21}r_{12}\right)\left(1 - r_{23}r_{32} + r_{21} + r_{31}r_{23}\right)\right] \end{array}\right]$$

$$a_{23}^R = \left[\begin{array}{c} E_1\left[\left(r_{12} + r_{13}r_{32}\right)\left(r_{23} + r_{21}r_{13} + 1 - r_{21}r_{12}\right) + \left(r_{12}r_{23} + r_{13}\right)\left(1 - r_{13}r_{31} + r_{32} + r_{31}r_{12}\right)\right] \\ + E_2\left[\left(1 - r_{13}r_{31}\right)\left(r_{23} + r_{21}r_{13}\right) + \left(r_{23} + r_{21}r_{13}\right)\left(r_{12} + r_{13}r_{32} + r_{32} + r_{31}r_{12}\right)\right] \\ + \left(E_3 + J\right)\left[\left(r_{32} + r_{31}r_{12}\right)\left(r_{12}r_{23} + r_{13} + r_{23} + r_{21}r_{13}\right) + \left(1 - r_{21}r_{12}\right)\left(r_{12} + r_{13}r_{32} + 1 - r_{13}r_{31}\right)\right] \end{array}\right]$$

$$b_1^R = 2a_{11}^R q_1 + a_{12}^R q_2 + a_{13}^R q_3$$

$$b_2^R = a_{12}^R q_1 + 2a_{22}^R q_2 + a_{23}^R q_3$$

$$b_3^R = a_{13}^R q_1 + a_{23}^R q_2 + 2a_{33}^R q_3$$

$$c^R = a_{11}^R q_1^2 + a_{12}^R q_1 q_2 + a_{22}^R q_2^2 + a_{23}^R q_2 q_3 + a_{33}^R q_3^2 + a_{13}^R q_1 q_3$$

In order to write a matrix form, let us define:

$$\mathbf{A}_e^R = \left[\begin{array}{ccc} a_{11}^R & \frac{1}{2}a_{12}^R & \frac{1}{2}a_{13}^R \\ \frac{1}{2}a_{21}^R & a_{22}^R & \frac{1}{2}a_{23}^R \\ \frac{1}{2}a_{31}^R & \frac{1}{2}a_{32}^R & a_{33}^R \end{array}\right], \ \mathbf{B}_e^R = \left[\begin{array}{c} b_1^R \\ b_2^R \\ b_3^R \end{array}\right] .$$

Then, in matrix form, Rao's criterion for *in situ* protection is:

$$\mathcal{R}_e\left(\mathbf{X}\right) = \mathbf{X}^T * \mathbf{A}_e^R * \mathbf{X} + \mathbf{X}^T * \mathbf{B}_e^R + c^R . \qquad (49)$$

D   Spreadsheet under Xcas, example of Section 4.1

Xcas Nouvelle Interface

Fich Edit Cfg Aide Outils Expression Cmds Prg Graphe Geo Tableur Phys Scolaire Tortue
/cygdrive/d/Users/figuiere/Documents/Charles/TravauxenCours/Chloé/July_2015/Calculs_Tales_Two_Diversities_28_07_2015.xws
Sauver   Config Calculs Tales Two Diversities 28 07 2015.xws : exact real RAD 12 xcas   STOP   Kbd   X

1 `restart //variables initialization`

$$[Diss,\ I,\ P1,\ P2,\ P3,\ Q,\ R,\ RTC,\ Ro1,\ Ro2,\ Ro3,\ WTC,\ Wo1,\ Wo2,\ Wo3,\ X1,\ X2,\ X3,\ r12,\ r13,\ r21,\ r23,\ r31,\ r32]$$

2

3 − Matrices and vectors

1 `R:=matrix([0,r12,r13],[r21,0,r23],[r31,r32,0]) // matrix of ecological interactions`

$$\begin{pmatrix} 0, & r12, & r13 \\ r21, & 0, & r23 \\ r31, & r32, & 0 \end{pmatrix}$$

2 `I:=matrix([1,0,0],[0,1,0],[0,0,1]) // identity matrix`

$$\begin{pmatrix} 1, & 0, & 0 \\ 0, & 1, & 0 \\ 0, & 0, & 1 \end{pmatrix}$$

3 `Q:=matrix([q1],[q2],[q3]) // vecteur of autonomous probabilities`

$$\begin{pmatrix} q1 \\ q2 \\ q3 \end{pmatrix}$$

4 `X1:=matrix([x],[0],[0]) // vecteur of policy 1`

$$\begin{pmatrix} x \\ 0 \\ 0 \end{pmatrix}$$

5 `X2 := matrix([0],[x],[0]) // vecteur of policiy 2`

$$\begin{pmatrix} 0 \\ x \\ 0 \end{pmatrix}$$

6 `X3 := matrix([0],[0],[x]) // vecteur of policy 3`

$$\begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$$

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6 `X3 := matrix([0],[0],[x]) // vecteur of policy 3`

$$\begin{pmatrix} 0 \\ 0 \\ x \end{pmatrix}$$

7 `P1:=(I-R)^(-1)*(Q+X1) // vecteur of interdependent probabilities under policy 1`

8 `P2:=(I-R)^(-1)*(Q+X2) // vecteur of interdependent probabilities under policy 2`

9 `P3:=(I-R)^(-1)*(Q+X3) // vecteur of interdependent probabilities under policy 3`

10

4 − Diversity indices

1 `WTC:=matrix([0,1,0],[0,0,0],[0,0,0]) // matrix that isolates the cross product P1*P2 in Weitzman's criterion (see expression 4 in "A tale of two diversities")`

$$\begin{pmatrix} 0, & 1, & 0 \end{pmatrix}$$

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Sauver   STOP   Kbd   X

4 – Diversity indices

1 `WTC:=matrix([0,1,0],[0,0,0],[0,0,0])` // matrix that isolates the cross product P1*P2 in Weitzman's criterion (see expression 4 in "A tale of two diversities")

$$\begin{pmatrix} 0, & 1, & 0 \\ 0, & 0, & 0 \\ 0, & 0, & 0 \end{pmatrix}$$

2 `Diss:=matrix([1],[1],[1])*(E+J)` // vecteur of dissimilarities

$$\begin{pmatrix} E+J \\ E+J \\ E+J \end{pmatrix}$$

3 `r12 := r ; r13 := r ; r21 := r ; r23 := r ; r31 := r ; r32 := r` // parameters initialization

$$(r,\ r,\ r,\ r,\ r,\ r\ )$$

4 `Q` // verification

$$\begin{pmatrix} q1 \\ q2 \\ q3 \end{pmatrix}$$

5 `R` // verification

$$\begin{pmatrix} 0, & r, & r \\ r, & 0, & r \\ r, & r, & 0 \end{pmatrix}$$

6 `Wo1 :=transpose(Diss)*P1-J*transpose(P1)*WTC*P1` // Weitzman in situ criterion under policy 1

7 `Wo2 :=transpose(Diss)*P2-J*transpose(P2)*WTC*P2` // Weitzman in situ criterion under policy 2

8 `Wo3 :=transpose(Diss)*P3-J*transpose(P3)*WTC*P3` // Weitzman in situ criterion under policy 3

9 `Q` // verification

$$\begin{pmatrix} q1 \\ q2 \\ q3 \end{pmatrix}$$

10 `R` // verification

$$\begin{pmatrix} 0, & r, & r \\ r, & 0, & r \\ r, & r, & 0 \end{pmatrix}$$

11 `factor(simplify(Wo1-Wo2))`

$$\frac{J^2 x^2 (q1-q2)}{(r+1)^2}$$

12 `factor(simplify(Wo1-Wo3))`

$$\frac{J^2 x^2 (q1 \cdot r - q2 \cdot r + q3 \cdot r + r \cdot x + q2)}{(r+1)^2 (2 \cdot r - 1)}$$

13 `RTC:=matrix([0,E,E+J],[E,0,E+J],[E+J,E+J,0])` // Dissimilarities cross matrix for Rao criterion

$$\begin{pmatrix} 0, & E, & E+J \\ E, & 0, & E+J \\ E+J, & E+J, & 0 \end{pmatrix}$$

14 `Ro1:=transpose(P1)*RTC*P1` // Rao in situ criterion under policy 1

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14 `Ro1:=transpose(P1)*RTC*P1` // *Rao in situ criterion under policy 1*

15 `Ro2:=transpose(P2)*RTC*P2` // *Rao in situ criterion under policy 2*

16 `Ro3:=transpose(P3)*RTC*P3` // *Rao in situ criterion under policy 3*

17 `factor(simplify(Ro1 - Ro2))`

$$-\frac{2 \cdot E \cdot x \cdot (q1-q2)}{(r+1)^2}$$

18 `factor(simplify(Ro1 - Ro3))`

$$-\frac{2 \cdot x \cdot (2 \cdot E \cdot q1 \cdot r - 2 \cdot E \cdot q3 \cdot r + J \cdot q1 \cdot r + J \cdot q2 \cdot r - 3 \cdot J \cdot q3 \cdot r - J \cdot r \cdot x - E \cdot q1 + E \cdot q3 - J \cdot q1 - J \cdot q2 + J \cdot q3)}{(r+1)^2 \cdot (2 \cdot r - 1)}$$

19 `factor(simplify(Ro2 - Ro3))`

$$-\frac{2 \cdot x \cdot (2 \cdot E \cdot q2 \cdot r - 2 \cdot E \cdot q3 \cdot r + J \cdot q1 \cdot r + J \cdot q2 \cdot r - 3 \cdot J \cdot q3 \cdot r - J \cdot r \cdot x - E \cdot q2 + E \cdot q3 - J \cdot q1 - J \cdot q2 + J \cdot q3)}{(r+1)^2 \cdot (2 \cdot r - 1)}$$

20

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