A Tale of Two Diversities

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Abstract

This paper analyses simple biodiversity protection plans regarding to how well they perform from the perspective of biodiversity, using for that matter alternatively Weitzman's and Rao's criterions, two biodiversity indices stemming from different disciplines. Both indices rest on pieces of information about (1) species survival probability, (2) some measure of distinctiveness between species. And each index has its own way to combine these data. Because we modelize interdependent probabilities, we arrive at what we call *in situ* versions of those criterions, which eventually are functions of protection efforts only. We show that choosing a particular *in situ* criterion has policy implications, for they sometimes deliver diverging protection recommendations. And we disentangle the role played by the data in their ranking logics, which helps us to highlight their major characteristics and differences as measurement of biodiversity.

Keywords: conservation priorities, ecological interactions.

JEL Classification: C6, Q5.

1 Introduction

Choosing species for prioritization is an extremely complex issue, which implies underlying interrogations about the value of biodiversity. They are worth asking, however, in a context of shrinking conservation funds worldwide. The recent 12th Meeting of the Conference of Parties to the Convention on Biological diversity, held in October 2014, has again expressed an urgent call to increase mobilization of financial resources at international and domestic levels from a large variety of sources, including major productive sectors (Chiarolla & Lapeyre, 2014). In order to get this funding on political agendas, information on the "rate of return" of investing funds to conservation, along with careful definition and prioritization of conservation targets will be crucially needed (Pearce, 2005,

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Indeed, a rational use of scarce money on biodiversity conservation rests on a prioritization of its components, *i.e.* a ranking of the categories of species or habitats for conservation. Such a maximization methodology has been popularized by Weitzman (1998) and his "Noah's ark problem"[1]. It is a cost-effective method helping Noah to board species on his arch, using a biodiversity function to be maximized, subjected to a budget constraint. Of course, the outcome of such a ranking methodology is strongly influenced not only by the constraint imposed on the problem, but first and foremost by the initial choice of the objective function retained for defining biodiversity. Actually, in the subsequent literature this method has raised two research questions: *i*) which meaningful index to use in order to measure biological diversity?, *ii*) in addition to the budget limitation, how to incorporate a constraint that properly reflects ecological interactions between species?

As for the first question, numerous measures of biodiversity have been proposed, notably by ecologists and economists. Yet, little has been done so far to compare their outcomes in terms of diversity prioritization. As noticed by Aulong, Erdlenbruch and Figuières (2005) and Baumgärtner (2007), measuring biodiversity requires prior value judgements on the character and purpose attributed to biodiversity. An important sub-class of indices, advocated in Wood (2000), is based on data about pairwise dissimilarities between species (Rao, 1986, Weitzman, 1992, Solow et al, 1993, Hill, 2001, Gerber, 2011). 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.

Regarding the second question, the Noah's ark approach - whatever the biodiversity index used in the objective function - can also be met with scepticism regarding its capacity to account for ecological interactions and therefore to tackle seriously *in situ* conservation issues (Mainwaring, 2001, Weikard 2002). In successive papers, Baumgartner (2004), Van der Heide et al (2006) and Simanier (2008) already noticed that accounting for species interactions may reverse Weitzman's conservation ranking, and even suggested to turn to other types of indices in order to rank biodiversity conservation issues. In Courtois, Figuières and Mulier (2014), we develop a general model for ranking *in situ* conservation projects accounting for species interactions. But the diversity function was left unspecified, which does not allow to understand the issues related to the choice of a particular index within an in situ protection context.

This is the task we challenge in this paper. Using the framework developed by Courtois et al (2014), two diversity indices will be scrutinized: 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. Both indices account simultaneously for abundances and dissimi-

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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), Weitzman (1992), Solow, Polasky and Broadus (1993), Bossert, Pattanaik and Xu (2003).

larity 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. Both Rao's entropy and Weitzman's index have an axiomatic characterization, which establishes their transparency as diversity measures (Rao, 1986, Bossert, Pattanaik and Xu, 2002).

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 the comparison of extreme preservation policies where, say, the manager of a natural park must choose between allocating his whole budget only to a single species. The second section of this paper modelizes the type of *in situ* prioritization problems we are dealing with. After describing the characteristics of our three species ecosystem, we define how both indices combine this information in their general form and how they may be used for ranking species for in situ conservation. The third section aims at disentangling the role of the different parameters that compose the indicators, namely (i) the autonomous survival probabilities, (ii) the measure of dissimilarity, (iii) the coefficients of ecological interaction. We end this paper with a discussion over the limit and perspectives of this approach.

2 A class of *in situ* prioritization problems

Consider an ecoystem with three species. The protection plans we analyze in this paper are as simple as possible: protection efforts are binary, *i.e.* a species is protected or not; and the entire available budget is enough to finance the protection of one species, no more, no less. Protection plans for two or three species are not affordable. Without being too specific for the moment - more details will appear below - if $\mathbf{X}$ stands for a 3-dimensional vector whose components indicate protection efforts granted to species, and $\mathbf{P}$ is the vector of survival probabilities, then the link between efforts and probabilities is a 3-dimensional vector of functions $\mathcal{P}(\mathbf{X})$.

We then compare conservation plans regarding to how well they perform from the perspective of indices of expected biodiversity. We shall invoke alternatively two different indexes of expected biodiversity, Weitzman's index, noted W, and Rao's index, R. Both belong to the familly of diversity measures aggregating dissimilarities between species. Both combine in a different way (1) species survival probability, and (2) some measure of distinctiveness between species. In our framework, we integrate and articulate information about ecological interactions and protection efforts in order to express new *in situ* expected diversity indices, $\mathcal{W}(\mathbf{X}) \equiv W(\mathbf{P}(\mathbf{X}))$, and $\mathcal{R}(\mathbf{X}) \equiv R(\mathbf{P}(\mathbf{X}))$. And the logic of optimal *in situ* protection plans is to solve the programs $\max_{\mathbf{X}} \mathcal{W}(\mathbf{X})$

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[2] As explained later, a two-species ecosystem would be even simpler, but would not allow to study the role of dissimilarities on the results. At least three species are needed for that purpose.

or $\max_{\mathbf{X}} \mathcal{R}(\mathbf{X})$.

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

2.1 Species interdependent survival probabilities

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 date have to be modified to give *interdependent survival probabilities,* denoted as $P_i \in \left[\underline{P}_i, \overline{P}_i\right]$. These probabilities are linear functions of the protection efforts $x_i \in \{0, \overline{x}\}$, $i = 1,2,3$, measured in terms of probability variations, and of numbers r_{ij}, representing the marginal ecological impact of species j on the survival probability of species i. It is reasonable to 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 the following:

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

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 of probabilities reads as:

$$\mathbf{P} = \mathbf{Q} + \mathbf{X} + \mathbf{R} * \mathbf{P}. \tag{1}$$

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 (1) can be solved[3] to give:

$$\mathbf{P} = [\mathbf{I} - \mathbf{R}]^{-1} * (\mathbf{Q} + \mathbf{X}) . \tag{2}$$

Thus, a particular protection plan $\mathbf{X}$ induces a vector of survival probabilities. Recall that $\mathcal{P}(\mathbf{X}) \equiv [\mathbf{I} - \mathbf{R}]^{-1} * (\mathbf{Q} + \mathbf{X})$ refers to the affine mapping

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

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

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). In a three species case, survival probabilities without protection policies are therefore:

$$\underline{\mathbf{P}} = \mathcal{P}\left(0 * \iota^{\mathbf{3}}\right) \ , \tag{3}$$

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

2.2 Species dissimilarities

Species are also characterized by their *dissimilarities*, which at a general level are pairwise distances between any two species. Those distances capture and measure the intuitive notion of "differences among biological entities" (Wood, 2000). It is here useful to refer to the library metaphor as in Weitzman (1998), under which each species can be understood as a library, that is a collection of books. 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 books, do not influence directly each species survival probabilities, but enters in a different way in the measure provided by biodiversity indices.

We will consider ultrametric distances among species. The 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). 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[4] (Pavoine et al., 2004, 2005); by contrast, in the ultrametric case Rao's index reaches its maximum value when all species are granted some attention.

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 distances are thus 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.

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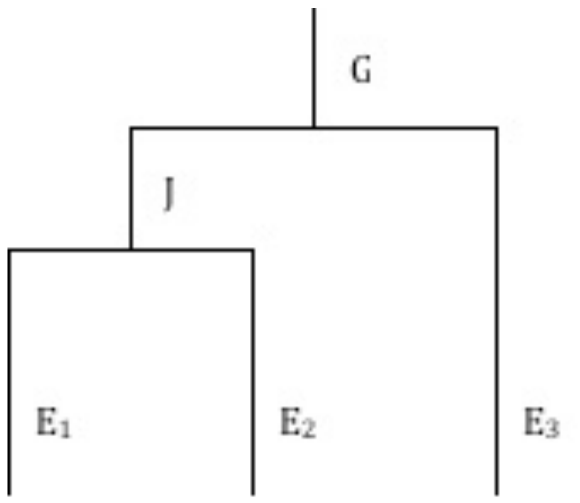
[4] In an extreme example, with one variable measured as source of distinctiveness among species, quadratic entropy is equal to the variance and retains species showing the extreme values of this variable.

In the three species case, such dissimilarities translate into a phylogenetic tree representation with proportional branches as shown in Figure 1 below.

Figure 1: Ultrametric tree with three species



In this case:

- E_i, the number of "books" specific to species (library) i and only species i (with $i = 1, 2, 3$),
- J, the number of "books" specific to species 1 and 2,
- G, the number of "books" common to 1, 2 and 3 (here set arbitrarily close to zero, and thus species 3 has no common books with species 1 and 2).

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

$$\begin{aligned} M_1 &= E_1 + J + G\ , \\ M_2 &= E_2 + J\ + G, \\ M_3 &= E_3 + G, \end{aligned}$$

where J is the number of books that libraries have in common, and E_1 the number of books contained in library 1 but neither in library 2 nor in library 3.

Considering d_{ij} as 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 :

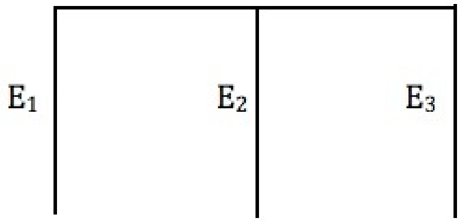
$$\begin{aligned} & d_{12} = d_{21} = E_1 = E_2 = E, \\ & d_{13} = d_{31} = d_{23} = d_{32} = E_2 + J = E_1 + J = E_3 \end{aligned}$$

Distances between three species i, k, l are ultrametric if and only if for all i, k, l we can verify :

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

With $J = 0$ 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: 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 distinctiveness. As J raises away from 0, we are able to represent the role of distinctiveness among species for both indicators since $E_1 = E_2 \neq E_3$.

2.3 Definition 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 used 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 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:

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

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

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

Since the goal is goal is 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 $\mathcal{P}(\mathbf{X}) \equiv \mathbf{\Lambda} * (\mathbf{Q} + \mathbf{X})$ between efforts and probabilities into $W(\mathbf{P})$. This results in what may be further called *Weitzman's biodiversity index for in situ preservation*:

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

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

$$\mathcal{W}_e(\mathbf{X}) = \mathbf{X} * \mathbf{A}_e^W * \mathbf{X}^T + \mathbf{B}_e^W * \mathbf{X}^T + c^W \ . \tag{4}$$

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 (4). Hence we explicitly mention this dependence *via* subscripts, as in $\mathcal{W}_e(\mathbf{X})$.

Rao's index used for *in situ* protection Rao's index in our three-species ecosystem is :

$$\begin{aligned} R(\mathbf{P}) &= P_1P_2(E_1+E_2) + P_1P_3(E_1+E_3+J) + P_2P_3(E_2+E_3+J) \ , \\ &= 2P_1P_2E + 2P_1P_3(E+J) + 2P_2P_3(E+J) \ , \\ &= 2\left[(P_1P_2+P_1P_3+P_2P_3)E + (P_1+P_2)P_3J\right] \ . \end{aligned}$$

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

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

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

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

where the notation emphasizes again a dependence with respect to the vector e of parameters.

2.4 Rankings of *in situ* protection projects

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

- Project 1:
$$\mathbf{X}_1 = [\overline{x}, 0, 0] \ ,$$
- Project 2:
$$\mathbf{X}_2 = [0, \overline{x}, 0] \ ,$$
- Project 3:
$$\mathbf{X}_3 = [0, 0, \overline{x}] \ .$$

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

$$\mathcal{W}_e\left(\mathbf{X}_1\right) \geq \max\left\{\mathcal{W}_e\left(\mathbf{X}_2\right), \mathcal{W}_e\left(\mathbf{X}_3\right)\right\} \ . \tag{5}$$

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

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

Thus we would prefer the preservation of species 1 to the species 2 or 3 if the value of Weitzman's index is higher than its value when preserving species 2 or species 3.

Ranking of projects according to Rao : If Rao's criterion is used to rank priorities, then project 1 is favored iff:

$$\mathcal{R}_e\left(\mathbf{X}_1\right) \geq \max\left\{\mathcal{R}_e\left(\mathbf{X}_2\right), \mathcal{R}_e\left(\mathbf{X}_3\right)\right\} \ , \tag{6}$$

or equivalently:

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

Thus we would prefer the preservation of species 1 to the species 2 or 3 if the value of Rao's index is higher than its value when preserving species 2 or species 3.

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 role of $\mathbf{Q}$, $\mathbf{R}$ and D in both in-situ indices

3.1 The influence of autonomous survival probabilities ($\mathbf{Q}$)

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

In this setting, we consider a vector e_1, representing parameters configuration in which $J > 0$, $r_{12} = r_{21} = r$ and $q_1 \neq q_2$ in order to isolate the role played by autonomous survival probability in a two species ultrametric case. In this setting, the matrices $\mathbf{Q}$ and $\mathbf{R}$ become:

$$\mathbf{Q}_{e_1} \equiv \begin{bmatrix} q_1 \\ q_2 \\ 0 \end{bmatrix}, \ \mathbf{R}_{e_1} \equiv \begin{bmatrix} 0 & r & 0 \\ r & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}.$$

Proposition 1 *Let the parameters be given by the vector e_1 in a two-species ecosystem. In this case, the two diversity indices deliver opposite rankings:*

- *Weitzman's preserves the "strongest" species, i.e. the in-situ ranking verifies:*
$$\mathcal{W}_{e_1}(\mathbf{X}_1) \gtreqless \mathcal{W}_{e_1}(\mathbf{X}_2) \quad \Leftrightarrow \quad q_1 \gtreqless q_2$$
- *whereas Rao's preserves the "weakest"' species, i.e. the in situ ranking verifies:*
$$\mathcal{R}_{e_1}(\mathbf{X}_1) \gtreqless \mathcal{R}_{e_1}(\mathbf{X}_2) \quad \Leftrightarrow \quad q_2 \gtreqless q_1$$

Proof. Appendix D. ■

Therefore with identical - or without - interactions between species and no efforts allocated to one or the other species survival probability, Weitzman would retain the most robust species - with the higher autonomous survival probability - whereas Rao would retain the most fragile species - presenting the lower autonomous survival probability.

Such results are not surprising, given the original purpose of both indicators. Weitzman' seeks the longest expected tree and only one species can be protected. If only one species goes extinct, E "books" are lost but $E + J$ are safe. It is wise then to affect protection resources on the species which is 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 objective is different. This index wishes to provide the least variance possible in the survival probabilities of species, in order to keep as much species as possible in the ecosystem. It will thus tend naturally to help the weakest species, in order to maximize the chances of keeping this species into the web of life.

As a third and substituable species is introduced into the framework (i.e. keeping the same distances between species 1, 2 and 3, and thus $J = 0$ and $G = 0$), those results are confirmed (Proof in Appendix D.1). In a second step, we will examine the role of dissimilarity, holding constant autonomous survival probabilities and all species interactions to zero.

3.2 The influence of dissimilarity (D)

Dissimilarities between species play a different role depending on the indicators. In our ultrametric case and in a two species framework, such dissimilarities are identical and can not explain differences in rankings (species are perfectly substitutable from the point of view of their distinctiveness). The role of dissimilarity only appears as we add a third species into the framework, and provided that the number of common genes between species 1 and 2 get away from zero $(J > 0)$ (figure 1).

Considering the parameter vector e_2 in which $q_1 = q_2 = q_3 = q$ and in the absence of interactions (i.e, $r_{ij} = 0, \forall i, j$) in the ultrametric case where $E_1 = E_2 = E, E_3 = E + J$, the matrices $\mathbf{Q}$ and $\mathbf{R}$ become:

$$\mathbf{Q}_{e_2} \equiv \begin{bmatrix} q \\ q \\ q \end{bmatrix}, \ \mathbf{R}_{e_2} \equiv \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}.$$

Proposition 2 *Let the parameters be given by the vector e_2. In a 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) distinctive species (species 1 or 2).*
- *They recommend to preserve the most distinctive species (species 3).*

Proof. Remark that $\mathcal{W}_{e_2}(\mathbf{X}_1) = \mathcal{W}_{e_2}(\mathbf{X}_2)$ and $\mathcal{R}_{e_2}(\mathbf{X}_1) = \mathcal{R}_{e_2}(\mathbf{X}_2)$ .Therefore the two indices preserves indifferently species 1 or 2. We now need to show when the two indices recommend to preserve species 3 rather than species 1 or 2. Without loss of generality, let us focus on the ranking between species 1 and 3. Weitzman index recommends to preserve species 1 iff:

$$\mathcal{W}_{e_2}(\mathbf{X}_1) > \mathcal{W}_{e_2}(\mathbf{X}_3) \Leftrightarrow -Jxq > 0 \Leftrightarrow Jxq < 0$$

which is impossible, and therefore, Weitzman would preserve species 3 rather than species 1.
Rao index recommends to preserve species 1 iff:

$$\mathcal{R}_{e_2}(\mathbf{X}_1) > \mathcal{R}_{e_2}(\mathbf{X}_2) \Leftrightarrow -2J^2xq > 0$$

which is again impossible, and thus, Rao would preserve the most distinctive species 3 rather than species 1. ■

In the vector of ecological interactions $\mathbf{R}_{e_2}$, if non null but identical interactions r are introduced, both indices lead to the same general conclusions, but with an additional stronger constraint depending mostly on the strength of interactions. Indeed, both indices would retain the most distinctive species if and only if $r < 1/2$, and the least distinctive species otherwise (see the proof in appendix).

3.3 The influence of ecological interactions

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 comtemplates a three-species ecosystem, there are $3^3 = 27$ potential pairwise interactions between species. The number of possibilities quickly explodes with the number of species. In face of this complexity, our strategy will be to focus on a small number of cases of particular interest. And to simplify matter we assume away any role for dissimilarities, *i.e.* $G = 0$ and $J = 0$.

3.3.1 Bilateral interactions and a "silent species"

Let us first consider a situation with two interacting species 1 and 2, and another third, "silent" species - i.e. which doesn't interact with neither species 1 nor species 2. Consider a parameter vector e_3 where $r_{12} \neq r_{21}$, all the other r being equal to zero, and $q_1 = q_2 = q_3 = q$. The matrices $\mathbf{Q}$ and $\mathbf{R}$ become :

$$\mathbf{Q}_{e_3} \equiv \begin{bmatrix} q \\ q \\ q \end{bmatrix}, \ \mathbf{R}_{e_3} \equiv \begin{bmatrix} 0 & r_{12} & 0 \\ r_{21} & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}.$$

Proposition 3 *In a three-species ecosystem in which only species 1 and 2 interact but not species 3, both indicators would preserve the interacting species with the* larger beneficial impact on the other species, or the lower overall negative impact*. For Weitzman, this impact should in addition be positive, otherwise it would preserve the "silent" species 3.*

- *Weitzman's in situ ranking preserves species 1 rather than 2 or 3 when:*

$$\mathcal{W}_{e_4}(\mathbf{X}_1) \gtreqless \max\{\mathcal{W}_{e_4}(\mathbf{X}_2), \mathcal{W}_{e_4}(\mathbf{X}_3)\} \Leftrightarrow \begin{cases} r_{21} > r_{12} \\ r_{21} > 0 \end{cases}$$

- *With J=0, Rao's in situ ranking preserves species 1 rather than 2 or 3 when:*

$$\mathcal{R}_{e_4}(\mathbf{X}_1) \gtreqless \max\{\mathcal{R}_{e_4}(\mathbf{X}_2), \mathcal{R}_{e_4}(\mathbf{X}_3)\} \Leftrightarrow r_{21} > r_{12}$$

Proof. See Appendix

■

With Rao's index, we preserve the species with the largest impact on the other species. With Weitzman's, an additional constraint is imposed on the interactions and account for the existence of this new incomer in the ecosystem: it would preserve species 1 if its impact on species 2 is positive, and larger than the impact of species 2 on species 1. Otherwise, Weitzman's index would retain the "silent" species 3 rather than preserving species with negative impacts on each other.

The general message is thus that in a three species ecosystem in which only two species interact, both indices tend to preserve the species with the largest marginal benefit (or the lowest marginal cost) on the other species. 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. So $r_{21} > 0$ whereas $r_{12} < 0$. In this case, both indices would preserve the prey - here species 1 - since its interaction coefficient with species 2 is positive ($r_{21} > 0$) and larger than the impact of species 1 on 2 (since $r_{12} < 0$).

ii) *Mutualism*: in this case species 1 and 2 impact positively on each other, and therefore $r_{12} > 0$ and $r_{21} > 0$. Here both indices would retain the species with the largest collective marginal impact.

iii) *Competition*: two species have to share a common resource in the same living area that cannot fully support both populations, hence $r_{12} < 0$ and $r_{21} < 0$. Here both indices would retain the species with the lowest negative impact on the other species.

Thus the introduction of a third, "silent" species 3 will impose stricter conditions for retaining species 1 rather than the others, even if only species 1 and 2 interacts. For Weitzman, interactions of species 1 on species 2 must be strictly beneficial to species 2, otherwise it would retain species 3, which can't harm any of the other species. As a consequence, the introduction of a third, non interacting species in our ecosystem is far from trivial. This specific three-species ecosystem is actually an extension of a two-species ecosystem, in which only species 1 and 2 are present (See proof in Appendix D.2). However, if we decide to include two instead of one bilateral interaction in our three species ecosystem, things can get a bit more tricky.

3.3.2 Two bilateral interactions and no "silent" species

With two bilateral interactions, every species are potentially in interaction. In this case, two species are impacting the third species, and one species impacts the two others. Given the potential complexity of those interrelations, we illustrate the choices made by the two indices using the predator-prey relationship.

For example, we choose to have one predator (1) and two preys (2 and 3). Here, the interactions are double-sided, since the predator impacts negatively its two preys, and therefore is simultaneously positively impacted by the two prey species.

$$\begin{aligned}&(1)\ 1 \overset{-}{\longrightarrow}\ 2 \text{ and } 1 \overset{-}{\longrightarrow}\ 3\ ,\\&(2)\ 2 \overset{+}{\longrightarrow} 1 \text{ and } 3 \overset{+}{\longrightarrow} 1\ .\end{aligned}$$

We are thus in the case where:

$$\left\{\begin{array}{l} r_{21}<0 \text{ and } r_{31}<0 \\ r_{12}>0 \text{ and } r_{13}>0 \end{array}\right. .$$

The difficulty with such a situation is to be able to consider simultaneously those interactions inside our two indices of biodiversity. Indeed, with four different and simultaneous interaction coefficients, the strength of cross effects between coefficient can't be disentangled and discussed. One solution to this problem, although very imperfect, is to look at interactions successively rather than simultaneously. In our one predator- two preys system, successive interactions can be described as follow: first, the predator feeds on the two preys, and thus impact them both negatively; next, the two preys benefit to the predator, and thus have a positive impact on the predator.

We will thus need to look successively at the cases where $r_{21} \neq r_{31}$, and then $r_{12} \neq r_{13}$.We have thus 2 vectors of parameters e_5 and e_6, leading to the following matrices $\mathbf{Q}$ and $\mathbf{R}$:

$$\mathbf{Q}_{e_5,e_6} \equiv \begin{bmatrix} q \\ q \\ q \end{bmatrix} \ , \ \mathbf{R}_{e_5} \equiv \begin{bmatrix} 0 & 0 & 0 \\ r_{21} & 0 & 0 \\ r_{31} & 0 & 0 \end{bmatrix} \ , \ \mathbf{R}_{e_6} \equiv \begin{bmatrix} 0 & r_{12} & r_{13} \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} \ .$$

Using 5 and 6, and applying successively the vector of parameters e_5 and e_6, the choices of both indices are the following. With parameter e_5, and thus $r_{21} \neq r_{31}$:

$$\begin{aligned}
\mathcal{W}_{e_5}(\mathbf{X}_1) &> \mathcal{W}_{e_5}(\mathbf{X}_2) &\Leftrightarrow\quad & r_{21}+r_{31}>0\ ,\\
\mathcal{W}_{e_5}(\mathbf{X}_1) &> \mathcal{W}_{e_5}(\mathbf{X}_3) &\Leftrightarrow\quad & r_{21}+r_{31}>0\ ,\\
\mathcal{R}_{e_5}(\mathbf{X}_1) &> \mathcal{R}_{e_5}(\mathbf{X}_2) &\Leftrightarrow\quad & (r_{21}r_{31}+r_{31})(2q+x)+r_{21}(3q+x)>0\ ,\\
\mathcal{R}_{e_5}(\mathbf{X}_1) &> \mathcal{R}_{e_5}(\mathbf{X}_3) &\Leftrightarrow\quad & (r_{21}r_{31}+r_{21})(2q+x)+r_{31}(3q+x)>0\ ,\\
\mathcal{R}_{e_5}(\mathbf{X}_2) &> \mathcal{R}_{e_5}(\mathbf{X}_3) &\Leftrightarrow\quad & r_{31}>r_{21}
\end{aligned}$$

With parameter e_6, and thus $r_{12} \neq r_{13}$:

$$\begin{aligned}
\mathcal{W}_{e_6}(\mathbf{X}_1) &> \mathcal{W}_{e_6}(\mathbf{X}_2) &\Leftrightarrow\quad & r_{12}<0\ ,\\
\mathcal{W}_{e_6}(\mathbf{X}_1) &> \mathcal{W}_{e_6}(\mathbf{X}_3) &\Leftrightarrow\quad & r_{13}<0\ ,\\
\mathcal{W}_{e_6}(\mathbf{X}_2) &> \mathcal{W}_{e_6}(\mathbf{X}_3) &\Leftrightarrow\quad & r_{12}>r_{13}\ ,\\
\mathcal{R}_{e_6}(\mathbf{X}_1) &> \mathcal{R}_{e_6}(\mathbf{X}_2) &\Leftrightarrow\quad & -qr_{13}-r_{12}(3q+x)>0\ ,\\
\mathcal{R}_{e_6}(\mathbf{X}_1) &> \mathcal{R}_{e_6}(\mathbf{X}_3) &\Leftrightarrow\quad & -qr_{12}-r_{13}(3q+x)>0\ ,\\
\mathcal{R}_{e_6}(\mathbf{X}_2) &> \mathcal{R}_{e_6}(\mathbf{X}_3) &\Leftrightarrow\quad & r_{12}>r_{13}
\end{aligned}$$

Those results allows us to illustrate a specific case of predator-prey relationship. In the depicted case where species 1 is a predator and 2 and 3 are two preys, we have two types of information about species interactions which may be used successively :

1. How much does the predator impacts the preys 2 and 3 ? Predator 1 feeds on the preys 2 and 3, and impacts them negatively. Thus we have $r_{31} < 0$ and $r_{21} < 0$

- Weitzman would never preserve species 1, and would be indifferent between preserving the prey species 2 or 3. As a consequence, in this simple configuration, Weitzman can't help us in order to choose one or the other prey.
- Rao would never preserve species 1, but however helps us to choose between the prey species 2 and 3. Indeed, in the case where $r_{31} < 0$ and $r_{21} < 0$, Rao would preserve the prey species 2 iff $r_{31} > r_{21}$, *i.e.* if the prey 2 is affected more negatively by the predator than the prey 3, which makes sense.

  ⇒Therefore, as seen earlier, no index would recommend to preserve the predator in this ecosystem. Which prey species must be selected for conservation is still unclear for Weitzman, whereas Rao's index decide to preserve the prey which is the most threatened by the predator. In order to refine this logic, we would need another information about the benefits for the predator of each preys.

2. How much do preys 2 and 3 benefit to predator 1? Species 2 and 3 impacts predator 1 positively to a certain degree, and thus we know that $r_{13} > 0$ and $r_{12} > 0$.This adds another layer of information about the interactions, which will helps us to refine which of the 2 prey species must be preserved

- Weitzman is now able to choose between preserving species 2 and 3 : It would preserve the species which has the largest positive impact on the the predator, and thus would preserve species 2 rather than 3 iff $r_{12} > r_{13}$.
- Similarly, Rao recommands to selects for preservation the prey which benefits the most the predator, i.e. $r_{12} > r_{13}$.

  ⇒Therefore, Weitzman chooses among the two prey using information on which of the two has the largest impact on the predator. Rao decide to retain the prey which has the largest impact on the predator AND which suffers the largest impact by the predator.

This very simplified case where bilateral relations are characterized by predator-prey relationships are relatively easy to describe. However, it is much more difficult for both indices to decide over preservation of one species in the apparently simplest case of commensalism (bilateral positive impacts), and competition (bilateral negative impacts). Indeed, the two successive steps would lead to retain potentially two different species at each step, without the capacity of deciding over which of the two must be chosen for conservation.

In addition to this difficulty, this successive treatment of the question leads to overstate or understate the value of the final survival probabilities, to which we should apply the effort for preservation. Indeed, the effect of the two preys 2 and 3 on the predator 1 should be accounted for when calculating the new survival probabilities for species 1, 2 and 3, and the step at which we apply the protection effort $\overline{x}$ will thus be important.

4 Discussion

Our simplified framework allows us to conclude over simple characteristics of two diversity objective functions, and disentangle the respective roles of autonomous survival probabilities q, ecological interaction r and dissimilarity considered in strict isolation, for each of the two indexes. However, the reality of such choices is much more complex than this structure.

The object of this discussion is to put those simple, yet important results into perspective. Indeed, once we allow two different categories of parameter to vary (say ecological interactions r and dissimilarity J), results are not as clear as when we considered the variations of a single parameter. In many cases, it seem that the parameters contained in vector e can influence the outcome of the index in isolation, but also in combination. To see this, we describe two different examples in which we introduce dissimilarity in addition to another dimension (autonomous survival probabilities q in the first example, and ecological interactions r set equal accross the three species, in the second example). We observe that the rankings ends up to depend on this variable rather than dissimilarity.

Autonomous survival probabilities q and dissimilarity, $J > 0$: our first example looks at the combination of survival probabilities and dissimilarity. The introduction of dissimilarity with a $J > 0$ impose additional restrictions on Weitzman's retained choice. Indeed, Weitzman's *in situ* ranking is indifferent between preserving species 1, 2 or 3 when $J = 0$. However, as soon as $J > 0$, the ranking verifies:

$$\mathcal{W}_{e_3}\left(\mathbf{X}_1\right) \gtreqless \max\left\{\mathcal{W}_{e_3}\left(\mathbf{X}_2\right), \mathcal{W}_{e_3}\left(\mathbf{X}_3\right)\right\} \Leftrightarrow -\left(q_2\left(\frac{1-r}{r}\right)+q_3+x\right) \gtrless q_1, q_2, \text{for all } r$$

and is therefore dependent on the variables q_1, q_2, and q_3, whereas Rao's in situ ranking is inchanged and still verifies for all r:

$$\mathcal{R}_{e_3}\left(\mathbf{X}_1\right) \geq \max\left\{\mathcal{R}_{e_3}\left(\mathbf{X}_2\right), \mathcal{R}_{e_3}\left(\mathbf{X}_3\right)\right\} \Leftrightarrow q_1 < \max\left\{q_2, q_3\right\} \ .$$

The proof of those statements is in Appendix E.1.

Interaction coefficient $r \neq 0$ and dissimilarities, $J > 0$: in this second example, we combine interaction coefficients - set equal accross species - with dissimilarity. Similarly, this new configuration leads to impose additional restrictions on the choice of species, this time for the two indices. Consider the parameter vector e_7, in which $q_1 = q_2 = q_3 = q$ and $r_{ij} = r, \forall i, j$,with $r \neq 0$. This is a very specific case of interactions, in which all interactions are set equal, but not necessarily equal to zero. The matrices $\mathbf{Q}$ and $\mathbf{R}$ thus become:

$$\mathbf{Q}_{e_7} \equiv \begin{bmatrix} q \\ q \\ q \end{bmatrix}, \mathbf{R}_{e_7} \equiv \begin{bmatrix} 0 & r & r \\ r & 0 & r \\ r & r & 0 \end{bmatrix}.$$

In this peculiar ecosystem the two diversity indices:

- are indifferent between preserving species 1 or species 2.
- recommend to preserve species 3 when $r < 1/2$, species 1 or 2 else.

The Proof is in Appendix E.

Therefore, when dissimilarity is introduced with equivalent r, the conservation choice depends on the interactions rather than the number of common genes J. Thus, when two parameters are used in combination instead of being in isolation, the results may be refined or even modified.

In addition, if the interactions are considered as successive in their occurence, this framework should be adapted in order to account for this sequentiality in the calculus of interdependant survival probabilities, and may well impact on the final choice.

Appendix

A The system of interdependent probabilities

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

$$P_1(\mathbf{X}) = \frac{(q_1 + x_1)(1 - r_{23}r_{32}) + (q_2 + x_2)(r_{12} + r_{13}r_{32}) + (q_3 + x_3)(r_{12}r_{23} + r_{13})}{1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}} \tag{7}$$

$$P_2(\mathbf{X}) = \frac{(q_2 + x_2)(1 - r_{13}r_{31}) + (q_1 + x_1)(r_{21} + r_{31}r_{23}) + (q_3 + x_3)(r_{21}r_{13} + r_{23})}{1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}} \tag{8}$$

$$P_3(\mathbf{X}) = \frac{(q_1 + x_1)(r_{31} + r_{32}r_{21}) + (q_2 + x_2)(r_{12}r_{31} + r_{32}) + (q_3 + x_3)(1 - r_{12}r_{21})}{1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}} \tag{9}$$

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:

$$\mathcal{P}\left(\mathbf{X}\right) \equiv \left[\begin{array}{c} P_1\left(\mathbf{X}\right) \\ P_2\left(\mathbf{X}\right) \\ P_3\left(\mathbf{X}\right) \end{array}\right] = \mathbf{\Lambda} * \left(\mathbf{Q} + \mathbf{X}\right) \ .$$

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:

$$\begin{aligned} W\left(\mathbf{P}\right) = {} & P_1P_2P_3\left(E_1+E_2+J+E_3+G\right) + \left(1-P_2\right)\left(1-P_3\right)P_1\left(E_1+J+G\right) \\ & + \left(1-P_1\right)\left(1-P_3\right)P_2\left(E_2+J+G\right) + \left(1-P_1\right)\left(1-P_2\right)P_3\left(E_3+G\right) \\ & + P_1P_2\left(1-P_3\right)\left(E_1+E_2+J+G\right) + P_1P_3\left(1-P_2\right)\left(E_1+J+E_3+G\right) \\ & + P_2P_3\left(1-P_1\right)\left(E_2+J+E_3+G\right) \ . \end{aligned}$$

Since G is close to zero, this expression simplifies to

$$\begin{aligned} W = {} & P_1P_2P_3\left(E_1+E_2+J+E_3\right) + \left(1-P_2\right)\left(1-P_3\right)P_1\left(E_1+J\right) \\ & + \left(1-P_1\right)\left(1-P_3\right)P_2\left(E_2+J\right) + \left(1-P_1\right)\left(1-P_2\right)P_3E_3 \\ & + P_1P_2\left(1-P_3\right)\left(E_1+E_2+J\right) + P_1P_3\left(1-P_2\right)\left(E_1+J+E_3\right) \\ & + P_2P_3\left(1-P_1\right)\left(E_2+J+E_3\right) \ . \end{aligned}$$

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

$$W\left(\mathbf{P}\right) = P_1\left(E_1+J\right) + P_2\left(E_2+J\right) + P_3E_3 - P_1P_2J \ .$$

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

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

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

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

More precisely, using (7), (8) and (9):

$$\mathcal{W}\left(\mathbf{X}\right) = \frac{1}{\phi}\left[\begin{array}{c} \left(E+J\right)\left(\begin{array}{c} \left(q_1+x_1\right)\left(1-r_{23}r_{32}\right) + \left(q_2+x_2\right)\left(r_{12}+r_{13}r_{32}\right) + \left(q_3+x_3\right)\left(r_{12}r_{23}+r_{13}\right) \\ + \left(q_2+x_2\right)\left(1-r_{13}r_{31}\right) + \left(q_1+x_1\right)\left(r_{21}+r_{31}r_{23}\right) + \left(q_3+x_3\right)\left(r_{21}r_{13}+r_{23}\right) \\ + \left(q_1+x_1\right)\left(r_{31}+r_{32}r_{21}\right) + \left(q_2+x_2\right)\left(r_{12}r_{31}+r_{32}\right) + \left(q_3+x_3\right)\left(1-r_{12}r_{21}\right) \end{array}\right) \\ -\frac{J}{\phi}\left[\begin{array}{c} \left(q_1+x_1\right)\left(1-r_{23}r_{32}\right) \\ + \left(q_2+x_2\right)\left(r_{12}+r_{13}r_{32}\right) \\ + \left(q_3+x_3\right)\left(r_{12}r_{23}+r_{13}\right) \end{array}\right] * \left[\begin{array}{c} \left(q_2+x_2\right)\left(1-r_{13}r_{31}\right) \\ + \left(q_1+x_1\right)\left(r_{21}+r_{31}r_{23}\right) \\ + \left(q_3+x_3\right)\left(r_{21}r_{13}+r_{23}\right) \end{array}\right] \end{array}\right] \tag{10}$$

with $\phi = \left(1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}\right)^2$.
We can rewrite this general form as follows:

$$\mathcal{W}\left(\mathbf{X}\right) = \left\{ \begin{array}{c} a_{11}^{W}x_1^2 + a_{22}^{W}x_2^2 + a_{33}^{W}x_3^2 + a_{12}^{W}x_1x_2 + a_{13}^{W}x_1x_3 + a_{23}^{W}x_2x_3 \\ +b_1^{W}x_1 + b_2^{W}x_2 + b_3^{W}x_3 + c^{W} \end{array} \right. \tag{11}$$

where

$$\begin{aligned}
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} \left(E + J\right)\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} \left(E + J\right)\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} \left(E + J\right)\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[\begin{array}{c} 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) \\ +2q_3\left(r_{12}r_{23} + r_{13}\right)\left(r_{21}r_{13} + r_{23}\right) \end{array} \right] \end{array} \right] \\
c^{W} &= \left[\begin{array}{c} \left(E + J\right)\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]
\end{aligned}$$

Finally, a matrix form expression would be more compact. 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:

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

C Rao's criterion for in situ protection

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

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

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

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

Using the survival probability system (7), (8), and (9), we obtain the following form for Rao's index:

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

This form can be rewritten as :

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

where

$$
\begin{aligned}
\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
\end{aligned}
$$

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:

$$
\mathcal{R}_e\left(\mathbf{X}\right) = \mathbf{X} * \mathbf{A}_e^R * \mathbf{X}^T + \mathbf{B}_e^R * \mathbf{X}^T + c^R \ . \tag{13}
$$

D Proof of Proposition 1

Considering vector e_1, matrices $\mathbf{A}_e^W$ and $\mathbf{B}_e^W$ shrink to

$$\mathbf{A}_e^W = \begin{bmatrix} -\frac{J}{\phi^2} r & -\frac{J}{2\phi^2}\left(1+r^2\right) & 0 \\ -\frac{J}{2\phi^2}\left(1+r^2\right) & -\frac{J}{\phi^2} r & 0 \\ 0 & 0 & 0 \end{bmatrix},$$

$$\mathbf{B}_e^W = \begin{bmatrix} \frac{(E+J)}{\phi}(1+r) - \frac{J}{\phi^2}(2rq_1 + (1+r^2)q_2) \\ \frac{(E+J)}{\phi}(1+r) - \frac{J}{\phi^2}(2rq_2 + (1+r^2)q_1) \\ 0 \end{bmatrix}.$$

According to Weitzman's *in situ* ranking inequality in the case where $q_1 \neq q_2$ and every other parameters being equal (vector e_1) and considering that $1 - r_{12}r_{21} > 0$, effort is allocated to species 1 iff:

$$\mathcal{W}_{e_1}(\mathbf{X}_1) > \mathcal{W}_{e_1}(\mathbf{X}_2) \;\Leftrightarrow\; \mathbf{X}_1 * \mathbf{A}_{e_1}^W * \mathbf{X}_1^T + \mathbf{B}_{e_1}^W * \mathbf{X}_1^T > \mathbf{X}_2 * \mathbf{A}_{e_1}^W * \mathbf{X}_2^T + \mathbf{B}_{e_1}^W * \mathbf{X}_2^T$$

- When $J \neq 0$, this inequality is true when

$$\frac{Jx}{(1+r)^2}(q_1 - q_2) > 0\ ,$$

$$\Leftrightarrow q_1 > q_2$$

- When $J = 0$, choice is independent of intrinsic survival probabilities. The ranking inequality is never fulfilled and effort is indifferently allocated to the protection of one species or the other.

Rao's *in situ* ranking is:

$$\mathcal{R}_{e_1}(\mathbf{X}_1) > \mathcal{R}_{e_1}(\mathbf{X}_2) \;\Leftrightarrow\; \mathbf{X}_1 * \mathbf{A}_{e_1}^R * \mathbf{X}_1^T + \mathbf{B}_{e_1}^R * \mathbf{X}_1^T > \mathbf{X}_2 * \mathbf{A}_{e_1}^R * \mathbf{X}_2^T + \mathbf{B}_{e_1}^R * \mathbf{X}_2^T\ ,$$

$$\Leftrightarrow \quad (1-r)^2 (q_2 - q_1) > 0\ ,$$

and thus

$$\mathcal{R}_{e_1}(\mathbf{X}_1) > \mathcal{R}_{e_1}(\mathbf{X}_2) \quad \Leftrightarrow \quad q_2 > q_1\ .$$

D.1 Proof of Proposition on survival probability with three species

When introducing a third species and considering only differences in survival probabilities, the parameters are given by vector e_3, with $r_{ij} = r, \forall i, j$, and $q_1 \neq q_2 \neq q_3$. The matrices $\mathbf{Q}$ and $\mathbf{R}$ become:

$$\mathbf{Q}_{e_3} \equiv \begin{bmatrix} q_1 \\ q_2 \\ q_3 \end{bmatrix},\ \mathbf{R}_{e_3} \equiv \begin{bmatrix} 0 & r & r \\ r & 0 & r \\ r & r & 0 \end{bmatrix}.$$

In a three-species ecosystem where only autonomous survival probability differ, both indicators deliver opposite rankings. Weitzman preserves the species with the highest survival probability, whereas Rao preserves the species with the lowest autonomous survival probability.

Proof. For Weitzman, using 5 in the case where all r are equivalent and $q_1 \neq q_2 \neq q_3$, we can write :

$$\begin{aligned} &\mathcal{W}_{e_3}(\mathbf{X}_1) > \mathcal{W}_{e_3}(\mathbf{X}_2) \\ &\qquad \Leftrightarrow Jx(q_1 - q_2)(1+r)^{-2} > 0 \\ &\qquad \Leftrightarrow q_1 > q_2, \text{ for all } r \end{aligned}$$

and

$$\begin{aligned} \mathcal{W}_{e_3}(\mathbf{X}_1) &> \mathcal{W}_{e_3}(\mathbf{X}_3) \\ &\Leftrightarrow \\ Jx(rx + rq_1 - rq_2 + rq_3 + q_2)\left(2r^3 + 3r^2 - 1\right)^{-1} &> 0 \end{aligned}$$

As $2r^3 + 3r^2 - 1 > 0$, for all $r > 1/2$, and $2r^3 + 3r^2 - 1 < 0$ for all $r < 1/2$, we must verify:

$$\begin{aligned} &(1) \quad rx + rq_1 - rq_2 + rq_3 + q_2 > 0, \text{for all } r > 1/2 \Leftrightarrow q_1 > -\left(q_2 \frac{(1-r)}{r} + q_3 + x\right) \ , \\ &(2) \quad rx + rq_1 - rq_2 + rq_3 + q_2 < 0, \text{ for all } 0 < r < 1/2 \Leftrightarrow q_1 < -\left(q_2 \frac{(1-r)}{r} + q_3 + x\right) \ , \\ &(3) \quad rx + rq_1 - rq_2 + rq_3 + q_2 < 0, \text{for all } r < 0 \Leftrightarrow q_1 > -\left(q_2 \frac{(1-r)}{r} + q_3 + x\right) \ . \end{aligned}$$

Indeed:

$$\begin{aligned} rx + rq_1 - rq_2 + rq_3 + q_2 &< 0 \Leftrightarrow r(x + q_1 + q_3) - rq_2 + q_2 < 0 \ , \\ &\Leftrightarrow r(x + q_1 + q_3) < -q_2(1-r) \ . \end{aligned}$$

And, because $r < 0$

$$\begin{aligned} &\Leftrightarrow \quad (x + q_1 + q_3) > -q_2 \frac{(1-r)}{r}, \\ &\Leftrightarrow \quad q_1 > -\left(q_2 \frac{(1-r)}{r} + q_3 + x\right), \text{ for all } r < 0 \ . \end{aligned}$$

Thus for $r > 1/2$, we must verify :

$$\begin{aligned} &\begin{cases} q_1 > q_2 \\ q_1 > -\left(q_2 \frac{(1-r)}{r} + q_3 + x\right) \end{cases} \\ &\Leftrightarrow q_1 > \max\left\{q_2, -\left(q_2 \frac{(1-r)}{r} + q_3 + x\right)\right\} \\ &\Leftrightarrow q_1 > q_2 \end{aligned}$$

Thus for $r < 1/2$, we must verify :

$$\begin{cases} q_1 > q_2 \\ q_1 > -\left(q_2 \frac{(1-r)}{r} + q_3 + x\right) \end{cases}$$

$$\Leftrightarrow q_2 < q_1 < -\left(q_2 \left(\frac{1-r}{r}\right) + q_3 + x\right)$$

Therefore, Weitzman preserves species 1 rather than species 2 or 3 when :

$$q_2 < q_1 < -\left(q_2 \left(\frac{1-r}{r}\right) + q_3 + x\right)$$

For Rao, using expression 6 in the case where all r are equivalent and $q_1 \neq q_2 \neq q_3$, we can write :

$$\begin{aligned} &\mathcal{R}_{e_3}(\mathbf{X}_1) \geq \mathcal{R}_{e_3}(\mathbf{X}_2) \\ &\qquad \Leftrightarrow -\frac{2Ex}{(1+r)^2}(q_1 - q_2) > 0 \\ &\qquad \Leftrightarrow q_1 < q_2 \end{aligned}$$

and

$$\begin{aligned} &\mathcal{R}_{e_3}(\mathbf{X}_1) \geq \mathcal{R}_{e_3}(\mathbf{X}_3) \\ &\qquad \Leftrightarrow -\frac{2Ex}{(1+r)^2}(q_1 - q_3) > 0 \\ &\qquad \Leftrightarrow q_1 < q_3 \end{aligned}$$

Therefore, Rao preserves species 1 rather than species 2 and 3 iff :

$$q_1 < \min\{q_2, q_3\}$$

■

D.2 Proof of Proposition 2 species ecosystem with bilateral interactions ??

In the case where $r_{12} \neq r_{21}$, every other parameters being equal (vector e_2) and considering that $1 - r_{12}r_{21} > 0$, Weitzman would retain species one for preservation iff:

$$\mathcal{W}_{e_2}(\mathbf{X}_1) > \mathcal{W}_{e_2}(\mathbf{X}_2) \;\;\Leftrightarrow\;\; \mathbf{X}_1 * \mathbf{A}^w_{e_2} * \mathbf{X}_1^T + \mathbf{B}^w_{e_2} * \mathbf{X}_1^T > \mathbf{X}_2 * \mathbf{A}^w_{e_2} * \mathbf{X}_2^T + \mathbf{B}^w_{e_2} * \mathbf{X}_2^T,$$

$$\begin{aligned} &\Leftrightarrow (E+J)\left(\frac{(q+x)(1+r_{21}) + q(1+r_{12})}{1 - r_{12}r_{21}}\right) - J\frac{(q+x)q + q^2 r_{12} + (q+x)^2 r_{21} + q r_{12} r_{21}(q+x)}{(1 - r_{12}r_{21})^2} \\ &> (E+J)\left(\frac{q(1+r_{21}) + (q+x)(1+r_{12})}{1 - r_{12}r_{21}}\right) - J\frac{q(q+x) + q^2 r_{21} + (q+x)^2 r_{12} + (q+x) r_{12} r_{21} q}{(1 - r_{12}r_{21})^2} \end{aligned}$$

$$\Leftrightarrow (E+J)\left(\frac{q+x+qr_{21}+xr_{21}+q+qr_{12}}{1-r_{12}r_{21}}\right)-J\frac{q^2r_{21}+2qxr_{21}+x^2r_{21}+q^2r_{12}+q^2r_{12}r_{21}+qr_{12}r_{21}x}{\left(1-r_{12}r_{21}\right)^2}$$
$$> (E+J)\left(\frac{q+qr_{21}+q+x+qr_{12}+xr_{12}}{1-r_{12}r_{21}}\right)-J\frac{q^2r_{21}+r_{12}q^2+2r_{12}qx+r_{12}x^2+r_{12}r_{21}q^2+xr_{12}r_{21}q}{\left(1-r_{12}r_{21}\right)^2}$$
$$\Leftrightarrow (E+J)\left(\frac{xr_{21}}{1-r_{12}r_{21}}\right)-J\frac{2qxr_{21}+x^2r_{21}}{\left(1-r_{12}r_{21}\right)^2} > (E+J)\left(\frac{xr_{12}}{1-r_{12}r_{21}}\right)-J\frac{2r_{12}qx+r_{12}x^2}{\left(1-r_{12}r_{21}\right)^2}$$
$$\Leftrightarrow \left(\frac{E+J}{1-r_{12}r_{21}}\right)x\left(r_{21}-r_{12}\right)+\frac{Jx\left(2q+x\right)}{\left(1-r_{12}r_{21}\right)^2}\left(r_{12}-r_{21}\right)>0$$
$$\Leftrightarrow \left(r_{21}-r_{12}\right)\left[\frac{(E+J)\left(1-r_{12}r_{21}\right)-J\left(2q+x\right)}{\left(1-r_{12}r_{21}\right)^2}\right]>0$$
$$\Leftrightarrow \left(r_{21}-r_{12}\right)\left[(E+J)\left(1-r_{12}r_{21}\right)-J\left(2q+x\right)\right]>0$$

Rao's in situ ranking would retain species 1 for preservation iff :

$$\mathcal{R}_{e_2}\left(\mathbf{X}_1\right)>\mathcal{R}_{e_2}\left(\mathbf{X}_2\right) \;\Leftrightarrow\; \mathbf{X}_1*\mathbf{A}^r_{e_2}*\mathbf{X}_1^T+\mathbf{B}^r_{e_2}*\mathbf{X}_1^T > \mathbf{X}_2*\mathbf{A}^r_{e_2}*\mathbf{X}_2^T+\mathbf{B}^r_{e_2}*\mathbf{X}_2^T\ ,$$
$$\Leftrightarrow\; \left(q+x+r_{12}q+r_{12}\right)\left(q+r_{21}q+r_{21}x\right)>\left(q+r_{12}q+r_{12}x\right)\left(q+x+r_{21}q+r_{21}\right)\ ,$$
$$\Leftrightarrow\; q\left(r_{12}-r_{21}\right)+x^2\left(r_{21}-r_{12}\right)+2qx\left(r_{21}-r_{12}\right)>0\ ,$$
$$\Leftrightarrow\; \left(r_{21}-r_{12}\right)\left(x^2+2qx-q\right)>0\ ,$$

and thus

$$r_{21}>r_{12}$$

D.3 Proof : three species ecosystem, only two species interact

Proof. Weitzman index recommends to preserve species 1 iff:

$$\mathcal{W}_{e_4}\left(\mathbf{X}_1\right)\gtreqless\max\left\{\mathcal{W}_{e_4}\left(\mathbf{X}_2\right),\mathcal{W}_{e_4}\left(\mathbf{X}_3\right)\right\}$$

It preserves species 1 rather than species 2 iff :

$$\mathcal{W}_{e_4}\left(\mathbf{X}_1\right)\gtreqless\mathcal{W}_{e_4}\left(\mathbf{X}_2\right)\Leftrightarrow r_{12}<r_{21}$$

It preserves species 1 to species 3 iff :

$$\mathcal{W}_{e_4}\left(\mathbf{X}_1\right)\gtreqless\mathcal{W}_{e_4}\left(\mathbf{X}_3\right)\Leftrightarrow r_{21}r_{12}+r_{21}>0\Leftrightarrow r_{21}\left(1+r_{12}\right)>0\Leftrightarrow r_{21}>0$$

Therefore, Weitzman preserves species 1 rather than species 2 AND 3 iff

$$\mathcal{W}_{e_4}\left(\mathbf{X}_1\right)\gtreqless\max\left\{\mathcal{W}_{e_4}\left(\mathbf{X}_2\right),\mathcal{W}_{e_4}\left(\mathbf{X}_3\right)\right\}\Leftrightarrow\left\{\begin{array}{c} r_{12}<r_{21}\\ r_{21}>0\end{array}\right.$$

Rao index recommends to preserve species 1 iff:

$$\mathcal{R}_{e_4}(\mathbf{X}_1) \gtreqless \max\{\mathcal{R}_{e_4}(\mathbf{X}_2), \mathcal{R}_{e_4}(\mathbf{X}_3)\}$$

It preserves species 1 rather than species 2 iff :

$$\mathcal{R}_{e_4}(\mathbf{X}_1) > \mathcal{R}_{e_4}(\mathbf{X}_2) \Leftrightarrow (r_{12} - r_{21})(qr_{12}r_{21} - (3q + x)) > 0$$

Supposing that $qr_{12}r_{21} - 3q - x > 0$, we can write :

$$q(r_{12}r_{21} - 3) > x \Leftrightarrow (r_{12}r_{21} - 3) > \frac{x}{q}$$

which is impossible since $r_{12}r_{21} - 3 < 0$,as we know that $r_{12}r_{21} - 1 < 0$. Therefore, $qr_{12}r_{21} - 3q - x < 0$ for all r_{21} and r_{12}. Consequently,

$$\begin{aligned}\mathcal{R}_{e_4}(\mathbf{X}_1) > \mathcal{R}_{e_4}(\mathbf{X}_2) &\Leftrightarrow (r_{12} - r_{21})(qr_{12}r_{21} - (3q + x)) > 0\\ &\Leftrightarrow r_{12} - r_{21} < 0\\ &\Leftrightarrow r_{12} < r_{21}\end{aligned}$$

Rao preserves species 1 rather than species 3 iff :

$$\mathcal{R}_{e_4}(\mathbf{X}_1) > \mathcal{R}_{e_4}(\mathbf{X}_3) \Leftrightarrow r_{21}\left((1 + r_{12})^2 + \frac{q + x}{q}\right) > r_{12}$$

Thus Rao preserves species 1 rather than species 2 and 3 iff

$$\begin{aligned}\mathcal{R}_{e_4}(\mathbf{X}_1) &\gtreqless \max\{\mathcal{R}_{e_4}(\mathbf{X}_2), \mathcal{R}_{e_4}(\mathbf{X}_3)\} \Leftrightarrow \left\{\begin{array}{c} r_{21} > r_{12} \\ r_{21}\left((1 + r_{12})^2 + \frac{q+x}{q}\right) > r_{12}\end{array}\right.\\ &\Leftrightarrow r_{21} > r_{12}\end{aligned}$$

■

E Co-Influence of interactions and distinctiveness

Proof. Remark that $\mathcal{W}_{e_4}(\mathbf{X}_1) = \mathcal{W}_{e_4}(\mathbf{X}_2)$ and $\mathcal{R}_{e_4}(\mathbf{X}_1) = \mathcal{R}_{e_4}(\mathbf{X}_2)$: the two indices still preserves indifferently species 1 or 2. Without loss of generality, let us focus on the ranking between species 1 and 3.

Weitzman index recommends to preserve species 1 iff:

$$\mathcal{W}_{e_4}(\mathbf{X}_1) > \mathcal{W}_{e_4}(\mathbf{X}_3) \Leftrightarrow Jx(qr + rx + q)\left(2r^3 + 3r^2 - 1\right)^{-1} > 0$$

- notice that $2r^3 + 3r^2 - 1 > 0$ iff $r \in]1/2, 1]$. We deduce that:
- when $r \in]1/2, 1]$, $\mathcal{W}_{e_4}(\mathbf{X}_1) > \mathcal{W}_{e_4}(\mathbf{X}_3)$ if $x > -q\frac{(1+r)}{r}$ which is always true

- when $r \in]-1, 1/2[$, $\mathcal{W}_{e_4}(\mathbf{X}_1) > \mathcal{W}_{e_4}(\mathbf{X}_3)$ if $x < -q\frac{(1+r)}{r}$ which is impossible
  Thus Weitzman preserves 1 instead for $r \in]1/2, 1]$,and preserves 3 for $r \in]-1, 1/2[$.

Rao index recommends to preserve species 1 iff:

$$\mathcal{R}_{e_4}(\mathbf{X}_1) > \mathcal{R}_{e4}(\mathbf{X}_2) \Leftrightarrow 2J^2 x (qr + rx + q) \left(2r^3 + 3r^2 - 1\right)^{-1} > 0$$

- again, notice that $2r^3 + 3r^2 - 1 > 0$ iff $r \in]1/2, 1]$. We deduce that:
- when $r \in]1/2, 1]$, $\mathcal{W}_{e_4}(\mathbf{X}_1) > \mathcal{W}_{e_4}(\mathbf{X}_3)$ if $x > -q\frac{(1+r)}{r}$ which is always true
- when $r \in]-1, 1/2[$, $\mathcal{W}_{e_4}(\mathbf{X}_1) > \mathcal{W}_{e_4}(\mathbf{X}_3)$ if $x < -q\frac{(1+r)}{r}$ which is impossible.

  Thus Rao preserves 1 instead for $r \in]1/2, 1]$,and preserves 3 for $r \in]-1, 1/2[$

■

E.1 Co-influence of survival proability and distinctiveness

Proof.

- For Weitzman, using 5 in the case where all r are equivalent and $q_1 \neq q_2 \neq q_3$, and $J > 0$ we can write :

$$\begin{aligned} &\mathcal{W}_{e_3}(\mathbf{X}_1) > \mathcal{W}_{e_3}(\mathbf{X}_2) \\ &\qquad \Leftrightarrow Jx (q_1 - q_2)(1 + r)^{-2} > 0 \\ &\qquad \Leftrightarrow q_1 > q_2, \text{ for all } r \end{aligned}$$

and

$$\begin{aligned}&\mathcal{W}_{e_3}\left(\mathbf{X}_1\right) > \mathcal{W}_{e_3}\left(\mathbf{X}_3\right)\\ &\qquad \Leftrightarrow Jx\left(rx + rq_1 - rq_2 + rq_3 + q_2\right)\left(2r^3 + 3r^2 - 1\right)^{-1} > 0\end{aligned}$$

As $2r^3 + 3r^2 - 1 > 0,$ for all $r > 1/2,$ and $2r^3 + 3r^2 - 1 < 0$ for all $r < 1/2,$ we must verify :

(1) $rx + rq_1 - rq_2 + rq_3 + q_2 > 0,$ for all $r > 1/2 \Leftrightarrow q_1 > -\left(q_2 \dfrac{(1-r)}{r} + q_3 + x\right)$

(2) $rx + rq_1 - rq_2 + rq_3 + q_2 < 0,$ for all $0 < r < 1/2 \Leftrightarrow q_1 < -\left(q_2 \dfrac{(1-r)}{r} + q_3 + x\right)$

(3) $rx + rq_1 - rq_2 + rq_3 + q_2 < 0,$ for all $r < 0 \Leftrightarrow q_1 > -\left(q_2 \dfrac{(1-r)}{r} + q_3 + x\right)$

Indeed, $rx + rq_1 - rq_2 + rq_3 + q_2 < 0 \Leftrightarrow r\left(x + q_1 + q_3\right) - rq_2 + q_2 < 0$

$$\begin{aligned}&\Leftrightarrow r\left(x + q_1 + q_3\right) < -q_2\left(1-r\right)\\ &\Leftrightarrow \left(x + q_1 + q_3\right) > -q_2 \frac{(1-r)}{r}, \text{as } r < 0\\ &\Leftrightarrow q_1 > -\left(q_2 \frac{(1-r)}{r} + q_3 + x\right), \text{ for all } r < 0\end{aligned}$$

Thus for $r > 1/2$, we must verify :

$$\begin{aligned}&\begin{cases} q_1 > q_2 \\ q_1 > -\left(q_2 \frac{(1-r)}{r} + q_3 + x\right) \end{cases}\\ &\Leftrightarrow q_1 > \max\left\{q_2, -\left(q_2 \frac{(1-r)}{r} + q_3 + x\right)\right\}\\ &\Leftrightarrow q_1 > q_2\end{aligned}$$

Thus for $r < 1/2$, we must verify :

$$\begin{aligned}&\begin{cases} q_1 > q_2 \\ q_1 > -\left(q_2 \frac{(1-r)}{r} + q_3 + x\right) \end{cases}\\ &\Leftrightarrow q_2 < q_1 < -\left(q_2\left(\frac{1-r}{r}\right) + q_3 + x\right)\end{aligned}$$

Therefore, Weitzman preserves species 1 rather than species 2 or 3 when :

$$q_2 < q_1 < -\left(q_2\left(\frac{1-r}{r}\right) + q_3 + x\right)$$

For Rao, using expression 6 in the case where all r are equivalent and $q_1 \neq q_2 \neq q_3$, we can write :

$$\begin{aligned}&\mathcal{R}_{e_3}\left(\mathbf{X}_1\right) \geq \mathcal{R}_{e_3}\left(\mathbf{X}_2\right)\\ &\qquad \Leftrightarrow -\frac{2Ex}{\left(1+r\right)^2}\left(q_1 - q_2\right) > 0\\ &\qquad \Leftrightarrow q_1 < q_2\end{aligned}$$

and

$$\begin{aligned}\mathcal{R}_{e_3}(\mathbf{X}_1) &\geq \mathcal{R}_{e_3}(\mathbf{X}_3) \\ &\Leftrightarrow -\frac{2Ex}{(1+r)^2}(q_1 - q_3) > 0 \\ &\Leftrightarrow q_1 < q_3\end{aligned}$$

■

Therefore, Rao preserves species 1 rather than species 2 and 3 iff :

$$q_1 < \min\{q_2, q_3\} \ .$$

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