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A Tale of Two Diversities

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Abstract:

Efficient biodiversity management strategies aim to allocate conservation efforts so as to maximize diversity in ecological systems. Toward this end, defining a diversity criterion is an important but challenging task, as several different indices can be used as biodiversity measures. This paper elicits and compares two criteria for biodiversity conservation based on indices stemming from different disciplines: Weitzman's index in economics and Rao's index in ecology. These indices use different approaches to combine information about measures of (1) the probability distributions of the species that are present in an ecosystem (*i.e.* survival probabilities) and (2) the degree of dissimilarity between these species. As an important step toward *in situ* conservation criteria, we add to these elements information about (3) the ecological interactions that take place between species. Considering a simple three-species ecosystem, we show that criterion choice has palpable policy implications, as it can sometimes lead to divergent management recommendations. We disentangle the roles played by elements (1),(2) and (3) in the ranking of outcomes, which allows us to highlight several specificities of the two criteria. An important result is that, other things being equal, Weitzman's *in situ* ranking tends to favor robust species that are least concerned with extinction, while Rao's *in situ* ranking generally gives priority to more vulnerable species that are closer to extinction.

Keywords:

Biodiversity indices, Conservation management strategy, Ecological interactions, Public policy, Species prioritization criteria

JEL Classification: C6, Q5

1. Introduction

The way in which resources should be allocated to manage threatened species remains a controversial issue. Conservation budgets are limited and management priorities must be set. An illustrative example of one such controversial conservation expense is the Australian campaign to rescue the last few specimens of Christmas Island pipistrelle, *Pipistrellus murrayi*. Between 2004 and 2009, more than 276,000\$ was spent to support habitat corridors for the species.¹ Despite these efforts, the campaign failed and the Christmas Island pipistrelle has since gone extinct. The plight of this species has prompted an uncomfortable question: should the rescue campaign have taken place at all? In the current context of massive species extinction (e.g. Ceballos et al., 2017), an increasing number of scientists argue that the diversity and robustness of ecosystems can best be maintained by focusing management efforts on ensuring that species don't become threatened in the first place rather than on tackling lost causes.² Identifying the precise

objective(s) of conservation policy is at the crux of this issue.

The science of biodiversity conservation has grown rapidly in recent decades, in particular, on two related fronts. First, further reflection has advanced the definitions and measures of biodiversity, producing what could be called a "biodiversity index theory" (for general overviews, see Baumgärtner, 2004a,b; Magurran, 2004; Eppink and van den Bergh, 2007). Building on this first front, progress has also been made regarding 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 "prioritization solution" (e.g. the *extreme* policy in Weitzman's, 1998 Noah's Ark metaphor). It is also to make this solution operational for *in situ* conservation policies. *In situ*, species interact and as extinction is partly due to these interactions, progress has been made to take species interrelations into account when designing conservation criteria (Witting et al., 2000; Baumgärtner, 2004a; Simianer, 2008; Van der Heide et al., 2005; Courtois et al., 2014).³ As a result, at least at the conceptual level, we

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¹ See <https://www.environment.gov.au/>.

² Regarding species prioritization and related debates about conservation choices, the reader may refer to Wilson et al. (2011), Joseph et al. (2011), Carwardine et al. (2012), Schultz et al. (2013), Courtois et al. (2014, 2018), Bennett et al. (2014), Frew et al. (2016), Gerber (2016), or Lacona et al. (2017), among others.

³ Note that *in situ* is also referred to *in the wild* in the literature, cf. IUCN.

possess the means to rationalize *in situ* conservation efforts.⁴ More specifically, the problem we face is a choice between means, as the biodiversity index theory does not identify a unique, “superior” index of biodiversity. Rather, it offers a range of meaningful indices, which, when used as objective functions in optimization problems, may lead to different solutions. A key question to address is what is the conservation philosophy underlying these indices? By grounding conservation policy on one index rather than another, what weight is given to extinction probabilities, attribute dissimilarities and the role of species in the network of interactions?

Answering this question requires comparing the outcomes of *in situ* optimization exercises that use different biodiversity indices as the objective function to be maximized. An important sub-class of indices is based on data about dissimilarities between species (Rao, 1982, 1986; Weitzman, 1992, 1998; Solow et al., 1993; Hill, 2001)⁵. Gerber (2011) provides an axiomatic comparison of the last four indices, though not in a context of *in situ* protection plans and therefore, omitting the fact that species' survivals are interrelated. Rao's index was not included in this comparison, despite its importance in ecology and biology. However, the mathematical properties of quadratic entropy have been extensively studied in Champely and Chessel (2002), Pavoine et al. (2005), Rao (2010), Ricotta and Marignani (2007), Ricotta and Szeidl (2006) and Shimatani (2001).

The present paper makes an original contribution by examining the consequences of considering two alternative diversity indices as the objective function to be maximized in a prioritization framework: Weitzman's (1992, 1998) index, which is popular in several literatures including economics, and Rao's (1982) index, which is used mostly in ecology and biology, but largely ignored by economists. Both indices simultaneously account for species distribution probability and dissimilarity measures. The axiomatic properties of both indices have been elicited (Rao, 1986; Bossert et al., 2003), which gives them some transparency as measures of diversity.

Since our goal is to understand basics of protection policies, we simplify the analysis whenever possible. Simplifications concern the ecosystems studied as well as protection policies. We focus on a three-species ecosystem⁶ with ecological interactions. Weitzman's and Rao's criteria are used for the comparison of particularly simple preservation policies, in which the decision maker (e.g. a national park manager) has only enough funding to address the management of a single species. In this situation, he must decide which species should be allocated conservation funds. Should he make this decision based on, for example, the direct benefits that species provide, or the indirect benefits forwarded via ecological interactions?

The paper proceeds as follows. In Section 2, we model the two *in situ* prioritization criteria. After describing the characteristics of our three species ecosystem, we define how both indices combine different pieces of information and explain how prioritization criteria are derived from indices. Section 3 aims at disentangling the role of each of the elements embedded in the different criteria, namely (i) a autonomous survival probabilities, (ii) dissimilarities, and (iii) coefficients of ecological interactions. General insights are raised on how the two criteria value these three pieces of information. We conclude the paper with a discussion on the limits of the approach and some perspectives regarding future work on the topic.

⁴ On a practical level, Joseph et al. (2008) applied Weitzman's prioritization approach to assess New Zealand conservation allocation. Variants have been used by McCarthy et al. (2008) to allocate surveillance effort over space for preventing biological invasions.

⁵ A range of other important papers on the topic includes Weikard et al. (2006), Ricotta (2004), Sarkar (2006), Whittaker et al. (2005), Bossert et al. (2003), Crozier (1992) and Faith (1992).

⁶ As we explain later, although a two-species ecosystem would be even simpler, it would not allow us to study the role of dissimilarities on optimization outcomes. At least three species are needed for that purpose.

2. A Class of *in situ* Prioritization Problems

Consider an ecosystem with N species. Each species i , $i = 1, \dots, N$, is characterized by a survival probability P_i defined as the probability that species i does not get extinct over a given time period.⁷ Assume that survival probability depends on demographic and genetic properties of species i , on abiotic factors, on the conservation effort it receives, and, as a result of ecological interactions, on the survival probabilities of the two other species P_j , with $j \neq i$. We denote by x_i the protection effort of species i and consider $x_i \in \{0, \bar{x}\}$, meaning that a species is protected ($x_i = \bar{x} > 0$) or not ($x_i = 0$). We further assume that the simultaneous protection of more than one species is not affordable, i.e. the entire available budget is just enough to cover the protection of a single species.⁸ Without being too specific for the moment, if \mathbf{X} stands for a N -dimensional vector of efforts, with components x_i , and \mathbf{P} is the vector of linearly interdependent survival probabilities, with components P_i , the link between efforts and probabilities is a N -dimensional vector of functions P such that $\mathbf{P} = P(\mathbf{X})$.

We compare protection plans on the basis of how well they perform as measured by indices of expected diversity. We use two alternative indices: Weitzman's index, noted $W(\mathbf{P})$, and Rao's index, $R(\mathbf{P})$. Both belong to the family of expected diversity measures that aggregate dissimilarities between species. They combine, albeit in different ways, measures of, *i*) species' probability distribution, and *ii*) species' dissimilarity. Here, the probability measure considered is the survival probability of species. Given the link between interdependent probabilities and efforts, $P(\mathbf{X})$, we can construct *in situ* expected diversity indices, $W(\mathbf{X}) \equiv W(P(\mathbf{X}))$, and $R(\mathbf{X}) \equiv R(P(\mathbf{X}))$. Under this framework, the present paper makes an original contribution to the literature by exploring and comparing optimal *in situ* protection plans. We accomplish this by solving the programs $\max_{\mathbf{X}} W(\mathbf{X})$ and $\max_{\mathbf{X}} R(\mathbf{X})$ and compare their respective outcomes.

Next we address the details of \mathbf{P} , \mathbf{X} , W and R .

2.1. Interdependent Survival Probabilities

We assume each species i has an *autonomous survival probability* we denote $q_i \in [0, 1]$, $i = 1, \dots, N$. This probability can be evaluated on the basis of demographic and genetic properties of species (i.e. reproductive capacities, genetic erosion, [...]) as well as on abiotic factors impacting species survival such as geographic range and habitat breadth — examples of which can be found in Gandini et al. (2004), Alderson (2003, 2010) or Verrier et al. (2015). We assume that near 0 autonomous survival probability means that the species is *fragile* and *likely to be threatened* while close to 1 autonomous survival probability means the species is *robust* and *a priori least concerned by extinction*. Principal feature of autonomous survival probability — and this explains the qualification *autonomous* — is that it ignores the impact of species

⁷ Note that survival probability is fully related to extinction probability but may well covary with rarity. Although extinction occurs when all the populations of a taxon decline to zero, rarity does not consistently lead to high extinction risk (Harnik et al., 2012). First because species may be rare because they have small geographic ranges, narrow habitat tolerances, small populations or any combination thereof. Second because high abundance and fecundity do not consistently lead to low extinction risk (Dulvy et al., 2005). It follows that survival probability here, is neither a measure of abundance nor of species frequency. Instead, it can be assessed on the basis of the several extinction probability criteria provided by the literature, see for instance <http://www.iucnredlist.org>.

⁸ Note that we assume therefore that marginal cost of effort is symmetric. Assuming a conservation budget B , a symmetric marginal cost c and a linear budget constraint, we have $\bar{x} = B/c$. Symmetry assumption could simply be released by assuming $x_i = B/c_i$ but it will add unnecessary complexity to our model. Interested readers may refer to Courtois et al. (2018) for a detailed discussion on the impact of cost asymmetry in this class of modelling problems.

interrelationships on survival. While the ultimate causes of increased extinction in an interval of time may be abiotic, and might affect only some species directly, the intricate patterns of relationships among species in a community distribute the effects of changes in one species to others in its community. In order to take into account the impact of biotic interactions and conservation efforts so as to generate *interdependent survival probabilities*, we assume, along the lines of [Courtois et al. \(2014, 2018\)](#), a functional form to assess this probability. We denote $P_i \in [\underline{P}_i, \bar{P}_i]$, $i = 1, \dots, N$, the interdependent survival probability of species i and approximate this probability as a linear function of the protection effort x_i measured in terms of probability variation, and of $r_{ij} \equiv \partial P_i / \partial P_j$, representing the marginal ecological impact of species j on the survival probability of species i , with $|r_{ij}| < 1$. We have then:

$$P_i = q_i + x_i + \sum_{j \neq i} r_{ij} P_j \quad q_i \in [0, 1[\quad , \quad x_i \in \{0, \bar{x}\}, \quad (1)$$

meaning that interdependent survival probability P_i is the autonomous survival probability q_i of species i plus the variation of this probability due to conservation efforts x_i and the marginal impact r_{ij} any other species j has on the survival probability of species i , this impact being possibly positive as negative according to the biotic relationship.

In order to formally define the system of interdependent survival probability describing our N species ecosystem, we define:

$$\mathbf{Q} \equiv \begin{bmatrix} q_1 \\ q_2 \\ \vdots \\ q_N \end{bmatrix}, \quad \mathbf{R} \equiv \begin{bmatrix} 0 & r_{12} & \dots & r_{1N} \\ r_{21} & 0 & \dots & r_{2N} \\ \dots & \dots & \ddots & \vdots \\ r_{N1} & r_{N2} & \dots & 0 \end{bmatrix}, \quad \mathbf{P} \equiv \begin{bmatrix} P_1 \\ P_2 \\ \vdots \\ P_N \end{bmatrix}$$

$$\underline{\mathbf{P}} \equiv \begin{bmatrix} \underline{P}_1 \\ \underline{P}_2 \\ \vdots \\ \underline{P}_N \end{bmatrix}, \quad \bar{\mathbf{P}} \equiv \begin{bmatrix} \bar{P}_1 \\ \bar{P}_2 \\ \vdots \\ \bar{P}_N \end{bmatrix}, \quad \mathbf{X} \equiv \begin{bmatrix} x_1 \\ x_2 \\ \vdots \\ x_N \end{bmatrix}, \quad \bar{\mathbf{X}} \equiv \begin{bmatrix} \bar{x}_1 \\ \bar{x}_2 \\ \vdots \\ \bar{x}_N \end{bmatrix}.$$

In matrix form, the system of interdependent survival probabilities reads as:

$$\mathbf{P} = \mathbf{Q} + \mathbf{X} + \mathbf{R}\mathbf{P}, \quad (2)$$

and under the condition that matrix $\mathbf{I}^N - \mathbf{R}$ is invertible, with \mathbf{I}^N the $(N \times N)$ identity matrix, the system Eq. (2) can be solved to give:

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

Note that this condition is not particularly demanding here as it translates in a very specific relationship between marginal impact parameters. To illustrate it, in the three species case, this condition is not met iff $r_{23}r_{32} + r_{12}r_{21} + r_{13}r_{31} + r_{12}r_{31}r_{23} + r_{21}r_{13}r_{32} = 1$, i.e. a very specific equality that has no reason to be true.

We deduce that a particular protection plan \mathbf{X} induces a particular vector of survival probabilities, with $\mathbf{P} \equiv P(\mathbf{X}) \equiv [\mathbf{I} - \mathbf{R}]^{-1}(\mathbf{Q} + \mathbf{X})$ the affine mapping from efforts to probabilities.⁹ In the absence of any conservation policy, survival probabilities are $\underline{\mathbf{P}} = P(0^* \mathbf{t})$, where \mathbf{t} is a N -dimensional vector with all components equal to 1, and $0^* \mathbf{t}$ is a vector made of N zeroes. Without ecological interactions, $[\mathbf{I} - \mathbf{R}]^{-1}$ is the identity matrix, and the bounds on probabilities are $\underline{\mathbf{P}} = \mathbf{Q}$ and $\bar{\mathbf{P}} = \mathbf{P} + \bar{x}^* \mathbf{t} = \mathbf{Q} + \bar{x}^* \mathbf{t}$.

⁹Note that each element of $\mathcal{P}(\mathbf{X})$ can be explicitly computed (see [Appendix A](#) for the three species case). To compute these elements, one must ensure that the result is between 0 and 1. Two possible strategies can satisfy this requirement: 1) assuming that estimates of the model parameters in real-world scenarios naturally guarantee this condition, 2) identifying an upper bound for conservation efforts that guarantees this property. An algorithm exists for this purpose and is available from the authors on request.

2.2. Species Dissimilarities

Species are also characterized by attribute diversity and their degree of dissimilarity with other species in this regard. Dissimilarity can generally be described by distance measures between any two species or between a species and a collection of species. These distances can represent different characteristics. They can measure genetic distance, by means of DNA-DNA hybridization ([Krajewski, 1989](#); [Caccone and Powell, 1989](#)), morphological distance, or taxonomic distance. Another possibility, used in phylogenetics, is to conceive of species as terminal nodes in a tree structure. Dissimilarities are then given by corresponding branch lengths ([Faith, 1992, 1994](#)). All of these metrics share the ability to capture and measure the intuitive notion of ‘‘differences among biological entities’’ ([Wood, 2000](#)) and in what follows, we simply consider that species have attribute sets that can be either specific or shared. The more distinctive a species' attributes, the more dissimilar this species is considered to be.

For the sake of clarity and tractability, we consider in the following the simplest ecosystem that allows us to compare the two biodiversity indices, that is a system composed of three species, $N = 3$, as depicted in [Fig. 1](#):

We assume that each species has $E_i > 0$ specific attributes that are not shared with the two other species. Two species (here species 1 and 2) possibly share $J \geq 0$ common attributes. We deduce that the information about species dissimilarities is contained in the vector $\mathbf{D} = (E_1, E_2, E_3, J)$ which we use in the following in order to assess our two criteria and discuss the impact of dissimilarity. This vector contains 1) information on the species attributes that are shared between any two or more species and 2) information on species attributes that are not shared.¹⁰ We define d_{ij} , the distance between species i and j , as the number of attributes that are not shared by the two species, with $d_{ij} = d_{ji}$. By assumption, species 3 has no common attributes with species 1 and 2. We have therefore $d_{31} = d_{13} = E_3 + E_1 + J$ and $d_{32} = d_{23} = E_3 + E_2 + J$. But we allow for the possibility that species 1 and 2 may have $J \geq 0$ common attributes. So, $d_{12} = d_{21} = E_1 + E_2$.

2.3. Definitions of in situ Criteria for Conservation Priorities

The indices used in this paper are built on the ecological space presented so far. We denote Ω as the space of those parameters, and $e = (\mathbf{Q}, \mathbf{R}, \mathbf{D}) \in \Omega$ (4)

as a particular element of this parameter space. This means in particular that the mapping that transforms efforts into probabilities is configured by parts of the information included in the vector e . In what follows, we emphasize this dependence using the subscript e whenever relevant, as in the notation $P_e(\mathbf{X})$.

2.3.1. Weitzman's Criterion for in situ Protection

Let $V_e(S)$ be the diversity function of the (sub)set S of species given by the length of the (sub)tree of species in S , i.e. the number of distinct attributes contained in S . It is important to note that this function is impacted by species dissimilarity but is not itself a measure of dissimilarity *per se*. Considering the three-species ecosystem presented above:

- if S contains only one species, then

$$V_e(\{1\}) = E_1 + J, \quad V_e(\{2\}) = E_2 + J, \quad V_e(\{3\}) = E_3, \quad (5)$$

that is, the total number of attributes (which are necessarily distinctive) that characterize the species.

- When S contains only two species, then

¹⁰Dissimilarity information is conveyed in this vector and it applies to any species collection set.

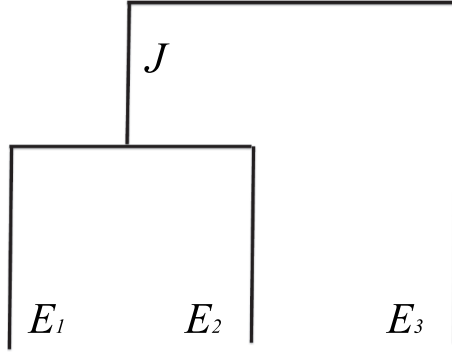


Fig. 1. Three species phylogenetic tree.

$$V_e(\{1, 2\}) = E_1 + E_2 + J, \quad V_e(\{1, 3\}) = E_1 + J + E_3, \quad V_e(\{2, 3\}) = E_2 + J + E_3, \quad (6)$$

that is, the total number of distinctive attributes that characterizes the two species.

- When S contains all species, then

$$V_e(\{1, 2, 3\}) = E_1 + E_2 + J + E_3, \quad (7)$$

that is, the total number of distinctive attributes that characterizes the three species.

Weitzman's diversity index is the expected diversity function of the ecosystem, taking into account the extinction probability of each species. In a N -species ecosystem, this expected diversity index is:

$$W_e(\mathbf{P}) = \sum_{S \subseteq N} \left(\prod_{j \in S} P_j \right) \left(\prod_{k \in N \setminus S} (1 - P_k) \right) V_e(S) \quad (8)$$

and it measures the expected length of the N -species evolutionary tree. When applied in our three-species ecosystem, the building blocks of the above expression are:

- no species disappears, an event that occurs with probability $P_1 P_2 P_3$, and the corresponding diversity is $V_e(\{1, 2, 3\})$,
- only species 1 survives, an event occurring with probability $(1 - P_2)(1 - P_3)P_1$, and the diversity is $V_e(\{1\})$,
- only species 1 and 2 survive, an event with probability $P_1 P_2 (1 - P_3)$, and the diversity is $V_e(\{1, 2\})$,
- and so on ...

We deduce that Weitzman's expected diversity in the three species ecosystem reduces to:

$$W_e(\mathbf{P}) = P_1(E_1 + J) + P_2(E_2 + J) + P_3 E_3 - P_1 P_2 J. \quad (9)$$

Since the goal is to rank conservation priorities while taking into account ecological interactions, the index must be modified in order to incorporate these interactions. We plug the relation between effort and probabilities, $P(\mathbf{X})$, into $W(\mathbf{P})$. This yields *Weitzman's in situ biodiversity criterion*, an expected diversity measure expressed as a function of effort:

$$W_e(\mathbf{X}) \equiv W_e(P_e(\mathbf{X})), \\ = P_1(\mathbf{X})(E_1 + J) + P_2(\mathbf{X})(E_2 + J) + P_3(\mathbf{X})E_3 - P_1(\mathbf{X})P_2(\mathbf{X})J. \quad (10)$$

2.3.2. Rao's Criterion for in situ Protection

Rao's index is the expected distance between any two species that are randomly drawn from a given set of species. In a N -species ecosystem, this diversity index is:

$$R_e(\mathbf{P}) = \sum_{i=1}^N \sum_{j=1}^N P_i P_j d_{ij}, \quad (11)$$

where d_{ij} is the distance between species i and j . Rao (1982) defines \mathbf{P} as a vector of probability distributions. For comparability of the two criteria and without loss of generality, we assume \mathbf{P} is a vector of survival probabilities that is to be understood as the complement to a vector of extinction probabilities.¹¹

In our three-species ecosystem, the index becomes:

$$R(\mathbf{P}) = P_1 P_2 (E_1 + E_2) + P_1 P_3 (E_1 + E_3 + J) + P_2 P_3 (E_2 + E_3 + J), \quad (12)$$

and the resulting relationship between diversity and effort is:

$$R_e(\mathbf{X}) = P_1(\mathbf{X})P_2(\mathbf{X})(E_1 + E_2) + P_1(\mathbf{X})P_3(\mathbf{X})(E_1 + E_3 + J) \\ + P_2(\mathbf{X})P_3(\mathbf{X})(E_2 + E_3 + J). \quad (13)$$

2.4. Simple in situ Protection Projects

Our objective is to compare three simple policies that concentrate efforts on either species 1, species 2 or species 3, referred to as

- Project 1:

$$\mathbf{X}_1^T = [\bar{x}, 0, 0],$$

- Project 2:

$$\mathbf{X}_2^T = [0, \bar{x}, 0],$$

- Project 3:

$$\mathbf{X}_3^T = [0, 0, \bar{x}].$$

It follows that for a given vector of parameters e , project 1 is preferred over project 2 and project 3, according to Weitzman's *in situ* criterion for protection iff:

$$W_e(\mathbf{X}_1) \geq \max\{W_e(\mathbf{X}_2), W_e(\mathbf{X}_3)\}. \quad (14)$$

That is:

$$W_e(\bar{x}, 0, 0) \geq \max\{W_e(0, \bar{x}, 0), W_e(0, 0, \bar{x})\}. \quad (15)$$

Similarly, if Rao's criterion is used to rank priorities, then project 1 is favored iff:

$$R_e(\mathbf{X}_1) \geq \max\{R_e(\mathbf{X}_2), R_e(\mathbf{X}_3)\}, \quad (16)$$

or equivalently:

$$R_e(\bar{x}, 0, 0) \geq \max\{R_e(0, \bar{x}, 0), R_e(0, 0, \bar{x})\}. \quad (17)$$

Mutatis mutandis, the same kind of formal statements can indicate the necessary and sufficient parameter conditions that lead to project 2 or 3 to be selected by each criterion. We are also in a position to study special cases in more detail, for their relevance to particular scenarios and/or because their simplicity is helpful in grasping the logic of the two *in situ* rankings.

The next section compares different optimization outcomes while keeping the analysis as simple as possible. It spares the reader the most technical details, which can be found in [Appendices B and C](#). These appendices explicitly construct the Weitzman and Rao *in situ* indices in a three-species setting.

¹¹ It is interesting to note that in the ecology literature, this probability is often assumed to be a frequency implying the additional constraint that $\sum_i P_i = 1$. This leads to the assumption that relative abundance is *per se* a good indicator of extinction risk, an assumption that is contradicted by several papers, such as [Harnik et al. \(2012\)](#) or [Dulvy et al. \(2005\)](#), as well as by most extinction risk assessment criteria that consider many other explanatory variables.

3. Disentangling the Underlying Logic of *in situ* Priorities

If a species is selected for conservation efforts, it must be because it differs from the others in some way. For each criterion, this section ranks conservation policies under several parameter configurations e , chosen in order to isolate the role played by heterogeneity in particular factors. We show that the two criteria deliver opposite conservation recommendations when heterogeneity arises from autonomous survival probabilities \mathbf{Q} , whereas they largely agree when heterogeneity arises from dissimilarities \mathbf{D} , and ecological interactions \mathbf{R} .

From a technical point of view, for a given vector of parameters e , the objective is essentially to compute:

$$W_e(\mathbf{X}_k) - W_e(\mathbf{X}_l), \\ R_e(\mathbf{X}_k) - R_e(\mathbf{X}_l),$$

for $k, l = 1, 2, 3$. All that remains is to analyze the signs of these differences. Though the calculations arrive at closed-form expressions and thus present no conceptual difficulties, the computational steps are nonetheless tedious. They were performed using a software designed for symbolic calculations (Xcas). Our Xcas spreadsheets are available upon request.

3.1. When the Criteria Diverge

3.1.1. The Influence of Autonomous Survival Probabilities(\mathbf{Q})

We start by analyzing cases in which autonomous survival probabilities are the unique source of heterogeneity among species, and examine the rankings generated by both criteria. We first consider a two-species ecosystem and subsequently extend the approach to a three-species ecosystem.

3.1.1.1. Two-species Ecosystem. Consider a class of conservation problems summarized by the list of parameters e_q , such that $J \geq 0$, $E_1 = E_2 = E$, $r_{12} = r_{21} = r$, $r_{13} = r_{31} = r_{23} = r_{32} = 0$, and $q_1 \neq q_2$. The phylogenetic tree associated with this ultrametric¹² ecosystem is depicted in Fig. 2:

Note that in this phylogenetic tree, we added additional information on autonomous survival probabilities q_i at the end of each branch as well as interaction parameters r_{ij} . Since we focus here on a two-species ecosystem, vector \mathbf{Q} and matrix \mathbf{R} become:

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

and tedious computations produce:

$$W_{e_q}(\mathbf{X}_1) - W_{e_q}(\mathbf{X}_2) = \frac{J\bar{x}}{(1+r)^2}(q_1 - q_2), \quad (18)$$

$$R_{e_q}(\mathbf{X}_1) - R_{e_q}(\mathbf{X}_2) = \frac{2E\bar{x}}{(1+r)^2}(q_2 - q_1). \quad (19)$$

Expression (18) shows that Weitzman's ranking is sensitive to the difference $q_1 - q_2$ only if $J > 0$, and becomes indifferent when $J = 0$. By contrast, according to expression (19), the sensitivity of Rao's ranking to $q_2 - q_1$ does not depend on the value of J . Assuming $J > 0$, from Eqs. (18) and (19), one can deduce the following proposition:

Proposition 1. *Let the class of conservation problems be given by the list of parameters e_q . In this case, the two diversity criteria deliver opposite rankings:*

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

$$W_{e_q}(\mathbf{X}_1) \lesseqgtr W_{e_q}(\mathbf{X}_2) \quad \Leftrightarrow \quad q_1 \lesseqgtr q_2,$$

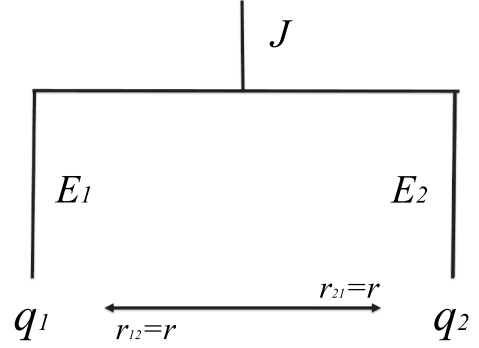


Fig. 2. Two-species ultrametric tree with $J > 0$.

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

$$R_{e_q}(\mathbf{X}_1) \lesseqgtr R_{e_q}(\mathbf{X}_2) \quad \Leftrightarrow \quad q_2 \lesseqgtr q_1.$$

How are these results explained? Ecological interactions are of little importance in this case, since both species serve identical ecological roles. These results are therefore consistent with the logic embodied in the indices alone. Weitzman's index seeks the longest expected tree. Recall that only one species is protected. If either species 1 or species 2 goes extinct, E attributes are lost but $E + J$ attributes are saved. It is therefore sensible to allocate resources to protecting the species that is initially the most secure (*i.e.* the species whose autonomous survival probability is the highest), unless $J = 0$, in which case Weitzman's criterion would clearly be indifferent regarding which species should be allocated protection efforts. Regarding the Rao criterion, the question is: how can one choose the combination of probabilities that leads to the highest expected diversity? Put more precisely, in this two-species problem, Rao seeks the largest product $P_1(\mathbf{X})P_2(\mathbf{X})$. This is best achieved when a conservation policy helps the fragile species, *i.e.* the species most likely to become endangered. Protection efforts are optimally allocated where the marginal impact is highest, therefore to species i if $P_i \leq P_j$, to species j if $P_j \leq P_i$.

3.1.1.2. Three-species Ecosystem. These results are robust to the introduction of a third species, provided that the only source of heterogeneity among species continues to be their autonomous survival probability. To avoid dissimilarities as a source of heterogeneity, we retain the same distances between species, and a good ecosystem candidate is the simple ultrametric case where $J = 0$, $E_1 = E_2 = E_3 = E$, and where q_3 can take any arbitrary value. This leads us to consider a slightly different list of parameters e'_q . The phylogenetic tree and associated information that characterizes this ecosystem is depicted in Fig. 3:

From Xcas computations, using Appendices B and C, one finds:

$$W_{e'_q}(\mathbf{X}_1) - W_{e'_q}(\mathbf{X}_2) = W_{e'_q}(\mathbf{X}_1) - W_{e'_q}(\mathbf{X}_3) = 0. \quad (20)$$

In other words, Weitzman's criterion proves to be indifferent between the three conservation policies. The reason for this indifference is that in this peculiar ecosystem, species have no common attributes. This makes conservation effort toward one species *versus* the other perfectly substitutable. Considering $G > 0$, shared attributes between the three species would modify this result — making the criterion in favor of investing in the most robust species. As for Rao's criterion, one has:

$$R_{e'_q}(\mathbf{X}_1) - R_{e'_q}(\mathbf{X}_2) = \frac{2E\bar{x}}{(r+1)^2}(q_2 - q_1), \quad (21)$$

¹² Ultrametricism here means that $E_1 + J = E_2 + J$.

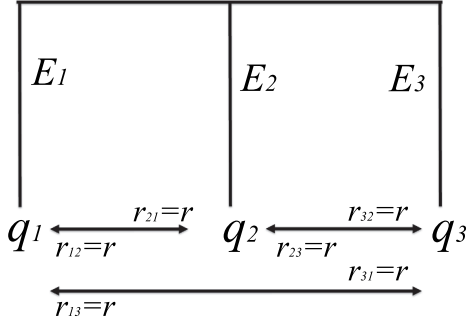


Fig. 3. Three-species ultrametric case with $J = 0$.

$$R_{e'_q}(\mathbf{X}_1) - R_{e'_q}(\mathbf{X}_3) = \frac{2E\bar{x}}{(r+1)^2}(q_3 - q_1), \quad (22)$$

$$R_{e'_q}(\mathbf{X}_2) - R_{e'_q}(\mathbf{X}_3) = \frac{2E\bar{x}}{(r+1)^2}(q_3 - q_2), \quad (23)$$

from which one directly deduces that the most fragile species ranks highest, which again confirms Proposition 1. Next, we examine the role of dissimilarity, discarding any heterogeneity in terms of autonomous survival probabilities and species interactions.

3.2. When the Criteria Converge

3.2.1. The Influence of Attributes Dissimilarity

Attribute dissimilarities are embedded in the two indices in different ways. In order to analyze the role played by \mathbf{D} , the simplest ecosystem to consider is a three-species ultrametric ecosystem in which species 1 and 2 share J common attributes and where $E_1 = E_2 = E$ and $E_3 = E + J$. Species 3 is more dissimilar than the two other species. Consider further that $q_1 = q_2 = q_3 = q > 0$ and $r_{ij} = 0$. 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:

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

and this ecosystem, denoted by parameter vector e_j , is depicted in Fig. 4:

Xcas computations deliver the following key pieces of information:

$$W_{e_j}(\mathbf{X}_1) - W_{e_j}(\mathbf{X}_2) = 0,$$

$$\begin{aligned} W_{e_j}(\mathbf{X}_3) - W_{e_j}(\mathbf{X}_1) &= W_{e_j}(\mathbf{X}_3) - W_{e_j}(\mathbf{X}_2) \\ &= Jq\bar{x} > 0, \text{ (i.e. } J > 0 \text{ and } \bar{x} > 0), \end{aligned}$$

$$R_{e_j}(\mathbf{X}_1) - R_{e_j}(\mathbf{X}_2) = 0,$$

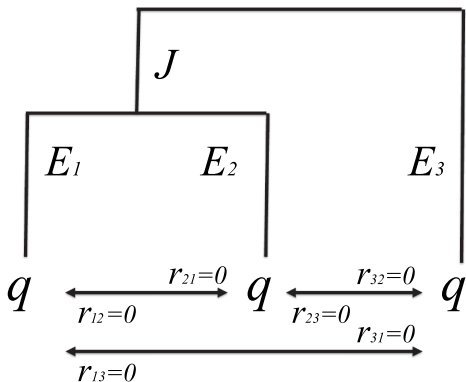


Fig. 4. Three-species ultrametric case with $J > 0$.

$$\begin{aligned} R_{e_j}(\mathbf{X}_3) - R_{e_j}(\mathbf{X}_1) &= R_{e_j}(\mathbf{X}_3) - R_{e_j}(\mathbf{X}_2) \\ &= 2Jq\bar{x} > 0. \end{aligned}$$

A conclusion immediately emerges:

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 criteria deliver the same rankings:

- They are indifferent between preserving the two least (and equivalently) dissimilar species (species 1 or 2).
- They recommend preserving the most dissimilar species (species 3).

This result seems intuitive. If only species 1 (or 2) disappears, there remains $2(E + J)$ attributes. But if only species 3 disappears, the number of remaining attributes decreases to a lower $2E + J$. In Appendix D.1, however, we show that the property emphasized in Proposition 2 is fragile. More precisely, it holds only when ecological interactions are not too strong (even if ecological interactions are not a source of heterogeneity).

3.2.2. The Influence of Ecological Interactions

Incorporating this dimension in the model is an attempt to account for the complexities of the web of life. For instance, the interactions between two species can be considered 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. In a two-species system, there are $2^2 = 4$ interaction possibilities to consider. As soon as one contemplates a three-species ecosystem, however, there are $3^3 = 27$ potential pairwise interactions between species (not even taking into account the added complexity that could be introduced by varying the intensity of each of these ecological interactions). It is evident that the number of interaction possibilities quickly explodes with the number of species in the system. In the face of this complexity, our strategy will be to focus on two illustrative cases of particular interest. To simplify matters, we assume that dissimilarities play no role and consider the simplest possible ecosystem.

3.2.2.1. Two-species Ecosystem. Consider first a situation with two interacting species, 1 and 2. The third species does not interact with species 1 or with species 2 and is considered extinct. We assume the two species share no common attributes, but possess a similar number of specific attributes, i.e. $E_1 = E_2 = E$ and $J = 0$. The phylogenetic tree associated to this ecosystem is depicted in Fig. 5:

Consider a parameter vector e_{R2} where $r_{12} \neq r_{21}$, all other r_{ij} being equal to zero, and $q_1 = q_2 = q, q_3 = 0$. The matrices \mathbf{Q} and \mathbf{R} become:

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

Computing the biodiversity criteria reveals:

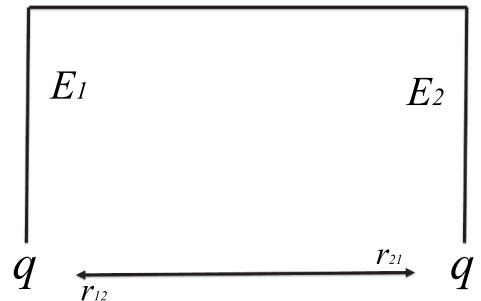


Fig. 5. Two-species ultrametric case with $J = 0$.

$$W_{e_{R2}}(\mathbf{X}_1) - W_{e_{R2}}(\mathbf{X}_2) = \frac{E\bar{x}}{1 - r_{12}r_{21}}(r_{21} - r_{12}), \quad (24)$$

$$R_{e_{R2}}(\mathbf{X}_1) - R_{e_{R2}}(\mathbf{X}_2) = \frac{2E\bar{x}(2q + \bar{x})}{(1 - r_{12}r_{21})^2}(r_{21} - r_{12}). \quad (25)$$

From these expressions, we establish the following proposition:

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 preserving the species that has the largest marginal impact on the survival of the other species:*

$$\begin{aligned} W_{e_{R2}}(\mathbf{X}_1) \geq W_{e_{R2}}(\mathbf{X}_2) &\Leftrightarrow r_{21} \geq r_{12}, \\ R_{e_{R2}}(\mathbf{X}_1) \geq R_{e_{R2}}(\mathbf{X}_2) &\Leftrightarrow r_{21} \geq r_{12}. \end{aligned}$$

In this case, the two criteria recommend preserving the species that has the largest marginal effect on the survival probability of the other species, a result that confirms a previous finding from Baumgärtner (2004a). Each criterion aims to maximize 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 preserving the prey – here species 1 – since its interaction coefficient is larger ($r_{12} < 0 < r_{21}$).
- ii) **Mutualism:** species 1 and 2 have a positive impact on each other. By definition, we have $r_{12} > 0$ and $r_{21} > 0$. Both criteria recommend preserving the species with the largest marginal benefit on the survival probability of the other species.
- iii) **Competition:** species 1 and 2 rely on a common resource in the same territory that cannot fully support both populations. By definition, we have $r_{12} < 0$ and $r_{21} < 0$. Both criteria recommend preserving the species with the lowest negative impact on the other species.

3.2.2.2. Three-species Ecosystem. When a third species is introduced, the impact of species interactions on the criteria recommendations is more difficult to study, as there is now an interplay of effects due to more complex interactions in the system. In order to illustrate this complexity, we consider a simple ecosystem of three interacting species characterized by unilateral interactions. We assume a single species, say species 1, impacts the two other species, but these two species impact neither each other nor species 1. For example, species 1 is a predator that negatively impacts two preys, species 2 and 3, but does not rely on them to survive due to the availability of other food sources, *i.e.* $r_{11} < 0$, $r_{12} = r_{13} = 0$. Species 1 could also be the prey of the two other species without being negatively impacted by them, *i.e.* $r_{11} \geq 0$, $r_{12} = r_{13} = 0$.

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 phylogenetic tree associated with this three-species ultrametric ecosystem is depicted in Fig. 6:

Here, the only distinction between the three species is how they interact. Matrices \mathbf{Q} and \mathbf{R} become:

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

The relative performance of alternative projects is measured by:

$$W_{e_{R3}}(\mathbf{X}_1) - W_{e_{R3}}(\mathbf{X}_2) = E\bar{x}(r_{21} + r_{31}), \quad (26)$$

$$W_{e_{R3}}(\mathbf{X}_1) - W_{e_{R3}}(\mathbf{X}_3) = E\bar{x}(r_{21} + r_{31}), \quad (27)$$

$$W_{e_{R3}}(\mathbf{X}_2) - W_{e_{R3}}(\mathbf{X}_3) = 0, \quad (28)$$

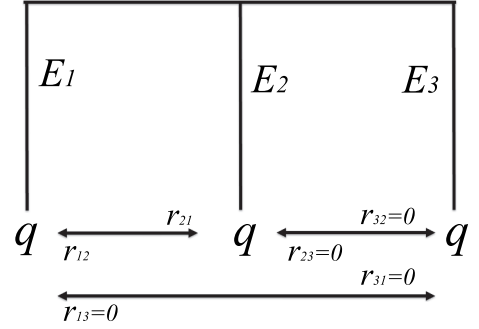


Fig. 6. Three-species ultrametric case with $J = 0$.

$$R_{e_{R3}}(\mathbf{X}_1) - R_{e_{R3}}(\mathbf{X}_2) = 2E\bar{x} \begin{bmatrix} r_{21}r_{31}(2q + \bar{x}) \\ + r_{21}(3q + \bar{x}) \\ + r_{31}(2q + \bar{x}) \end{bmatrix}, \quad (29)$$

$$R_{e_{R3}}(\mathbf{X}_1) - R_{e_{R3}}(\mathbf{X}_3) = 2E\bar{x} \begin{bmatrix} r_{21}r_{31}(2q + \bar{x}) \\ + r_{21}(2q + \bar{x}) \\ + r_{31}(3q + \bar{x}) \end{bmatrix}, \quad (30)$$

$$R_{e_{R3}}(\mathbf{X}_2) - R_{e_{R3}}(\mathbf{X}_3) = 2E\bar{x}q(r_{31} - r_{21}). \quad (31)$$

Weitzman's criterion recommends preserving species 1 rather than species 2 or 3 iff:

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

The above expressions (26) and (27) show that this is true iff $r_{21} + r_{31} > 0$, that is, if the cumulative impact of species 1 on the survival probability of the two other species is larger than the cumulative 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 confirms Proposition 3, as it recommends allocating conservation efforts to the species that is the most beneficial (or the least detrimental) to the survival of all of the other species in the ecosystem.

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

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

From expressions (29) and (30), this is true iff $r_{21}r_{31}(2q + \bar{x}) + r_{31}(2q + \bar{x}) + r_{21}(3q + \bar{x}) > 0$ and $r_{21}r_{31}(2q + \bar{x}) + r_{21}(2q + \bar{x}) + r_{31}(3q + \bar{x}) > 0$. In the case in which species 1 has a positive impact on species 2 and 3, preservation effort is allocated to species 1. When either of the above inequalities do not hold, interpreting the criterion becomes more difficult. In this case, effort is then allocated to the species that is (negatively) impacted to a greater degree by species 1. Again, we find a confirmation of the result presented in Proposition 3. However, the decision rule depicted here is no longer a simple additive formula, but a combination of additive and multiplicative components ($r_{21}r_{31}$), making interpretation difficult. Adding interrelations or additional species in the analysis greatly increases complexity through multiplicative effects (*i.e.* complementarities).

4. Interactions Between Effects

When heterogeneity arises from several dimensions at once, all of the previous criteria logics are mingled and interpreting the results becomes very challenging indeed. A fairly detailed analysis for the interested reader is given in Appendix D. Here, we briefly discuss a case in point. We let species differ in both autonomous survival probabilities (the q_i 's) and ecological interactions (the r_{ij} 's). Recall that, all else being equal, the Weitzman criterion tends to generate recommendations that protect robust species that are *a priori* the least concerned by extinction (with the largest q_i), whereas the Rao criterion generally favors fragile

Table 1
Criteria and species ranking.

	Weitzman criterion	Rao criterion
Survival probability (Q)		
If $A > B$, then	$A > B$	$B > A$
Attribute dissimilarity (D)		
If $A > B$, then	$A > B$	$A > B$
Species interaction (R)		
If $A > B$, then	$A > B$	$A > B$

species likely to be the most threatened species. On the other hand, on the basis of ecological interactions only, both criteria recommend that conservation efforts be allocated to the species with the largest positive impact on the ecosystem. Thus, an initial dissonance in rankings due to the q_i 's can vanish if this ecological interactions effect prevails. This is indeed the case and can be explored formally. See Appendix D.3.

5. Summary and Illustration

Considering a binary choice between investing in the conservation of one of two species (in an ecosystem that may contain more than two or three species) and denoting these two species A and B , the main results we obtain in the paper are summarized in Table 1:

Abusing notations, we write $A > B$ when species A has a greater survival probability (respectively attribute dissimilarity or overall net positive impact on the ecosystem through species interactions) than species B , and we write $A > B$ when the criterion favors the protection of species A . Rankings are generated under the assumption that everything else is equal, meaning that, in line 1 for example, we assume that species A has a greater survival probability than species B , but that the two species are symmetric in all other aspects.

We observe that the two criteria converge regarding attribute dissimilarity (D) and species interactions (R). Both favor species that contribute more to the diversity of the attributes contained in the ecosystem, as well as species that impart the greatest benefits, or least harm, to the ecosystem. Conversely, the criteria diverge regarding autonomous survival probability (Q) and therefore regarding how they value the relative robustness of species. While the Weitzman criterion recommends protecting the species that is *a priori* the least prone to extinction, the Rao criterion finds the opposite, recommending that conservation efforts should focus on the species that is more likely to become endangered. With respect to conservation policy, it therefore turns out that the Weitzman criterion can be considered a *triage* decision concept that seems particularly appropriate for situations involving massive extinction potential and a limited conservation budget. Conversely, the conservation philosophy underlying Rao's is to allocate funds toward the most threatened species, disregarding the chances of successfully preventing extinction. It is therefore particularly appropriate in the context of large budgets or low extinction.

We conclude the paper with an illustration of our results based on a simple simulation. Again, we consider an ecosystem that is composed of three species, as described in Fig. 7:

We assume that species 3 is more distinctive than the two others and we arbitrarily set $G = 50$, $J = 90$, $E_3 = 100$ and $E_1 = E_2 = 10$.

In what follows, we examine the binary choice of preserving one of two species contained in this ecosystem by gradually adding complexity to the parameter space considering first heterogeneity in autonomous survival probabilities (Q) and second in species interactions (R). We assume for the moment that $r_{ij} = 0, \forall i, j$, meaning that there is no interaction between species. We set $q_3 = 0.4$ meaning that species 3 is vulnerable¹³, and we assume that the autonomous survival probability of species 1 and 2 may oscillate between 0 and 1, *i.e.* between critically

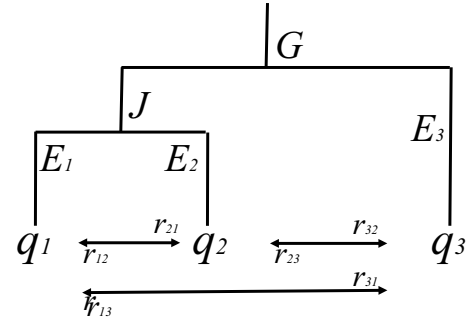


Fig. 7. Three-species ultrametric case with $J > 0$ and $G > 0$.

endangered and most robust (IUCN species status is provided in Appendix E). We focus on the choice of investing either in species 1 or 2, that is in the two less distinctive species composing this ecosystem. Isoquant curves are useful to illustrate how the two criteria value relative autonomous survival probabilities between the two species. An isoquant here is a contour line drawn through the set of points at which the same value of the criterion is obtained while changing the autonomous survival probabilities of the two species. Each isoquant depicts then the set of couples q_1, q_2 that forward the same criterion value.

Darker grey zones depict higher criteria levels, meaning that the higher the isoquant, the higher the criterion value. We observe that the Weitzman's criterion isoquants are concave with a slope greater than -1 above the bisectrix. The Rao's criterion isoquants are convex with a slope less than -1 above the bisectrix. It follows that in order to reach a superior isoquant and therefore a higher diversity, if $q_2 > q_1$ (*i.e.* above the bisectrix line), Weitzman criterion recommends investing in the protection of species 2 ($AB < AC$), while Rao's criterion recommends investing in the protection of species 1 ($AC < AB$). Conversely, below the bisectrix, Weitzman's criterion recommends investing in q_1 , while Rao's criterion recommends investing in q_2 . We confirm the result that, all else equal, Weitzman's criterion favors robust species, while Rao's criterion favors fragile ones.

Let us now increase the complexity of the problem to illustrate how the two criteria value distinctiveness (D). As species 3 is assumed to be more distinctive than the other two that share J common attributes, we now focus on the binary choice of either protecting species 1 or protecting 3. Again, we assume that no interactions exist between species, $r_{ij} = 0 \forall i, j$, but we now let q_1 and q_3 vary between 0 and 1. We assume that q_2 is equal to either 0.01 or 0.99, *i.e.* the canonical cases where species 2 is either critically endangered or extremely robust. In the first case, as species 2 is almost extinct, species 1 is almost as distinctive as species 3. In the second case, species 3 is more distinctive than species 1 as the J attributes are always secured by species 2. Isoquants for the two cases and the two criteria are depicted in Figs. 9 and 10.

We observe that when species 2 is least concerned by extinction (right-hand graphs), the slopes of the isoquants flatten, indicating that both criteria favor the protection of species 3. Notice that here, the impact of dissimilarity on criteria rankings outweighs the impact of autonomous survival probability. Even if species 1 is fragile, the two criteria recommend preserving species 3, as the J attributes of species 1 will continue to exist in the ecosystem via species 2. Interestingly, we observe that if species 2 is almost extinct, we confirm previous insights regarding autonomous survival probability.¹⁴

To conclude, we illustrate the impact of species interactions on the recommendations made by the two criteria. Considering again the binary choice between preserving species 1 or 2 and assuming $q_3 = 0.4$, *i.e.* the parameter considered in the case depicted in Fig. 8, we compare

¹⁴ The Weitzman criterion is almost indifferent between preserving the two species since G is small, making efforts to protect each species almost perfectly substitutable.

¹³ Note that we could assume q_3 to be any value between 0 and 1.

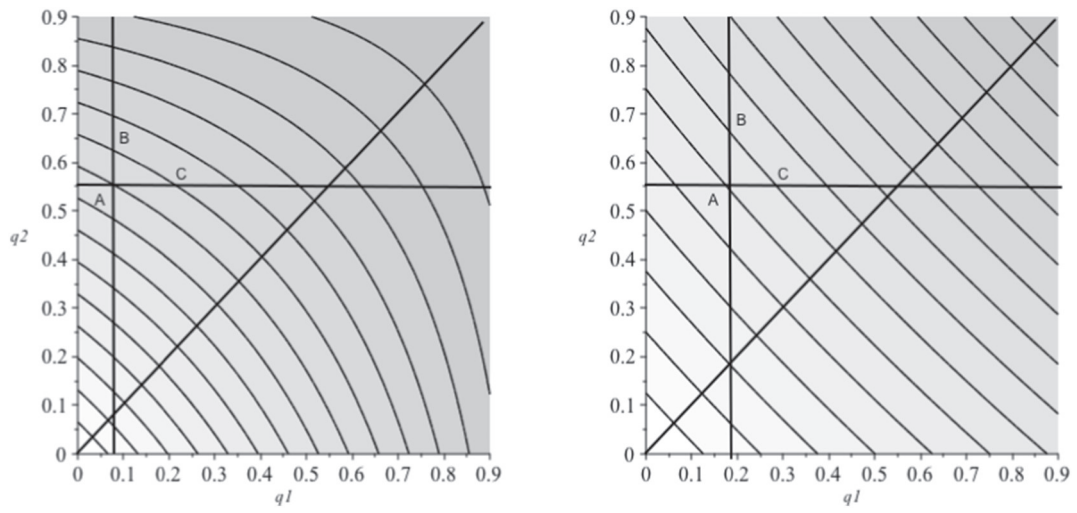


Fig. 8. Isoquants: Weitzman (left), Rao (right).

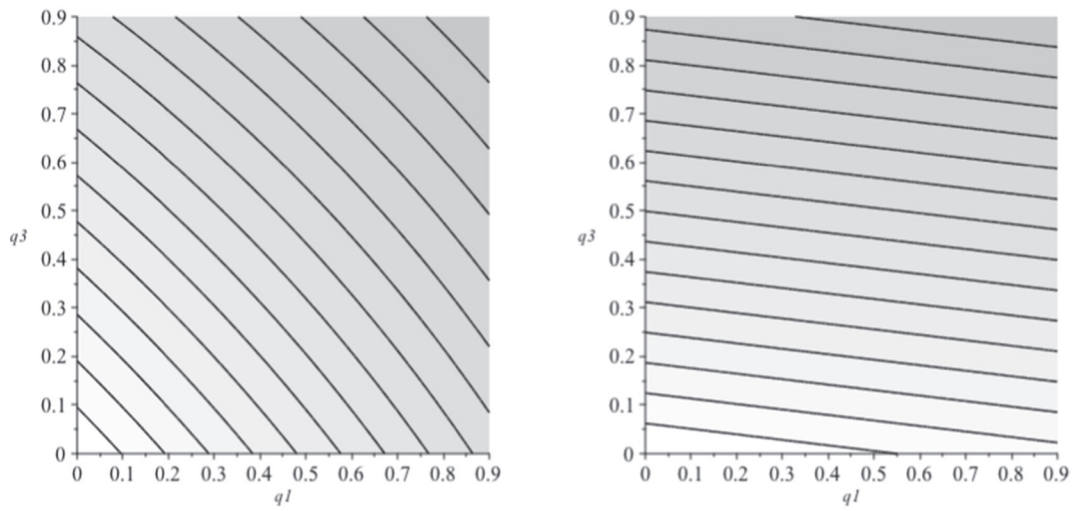


Fig. 9. Weitzman's criterion isoquants: $q_2 = 0.01$ (left), $q_2 = 0.99$ (right).

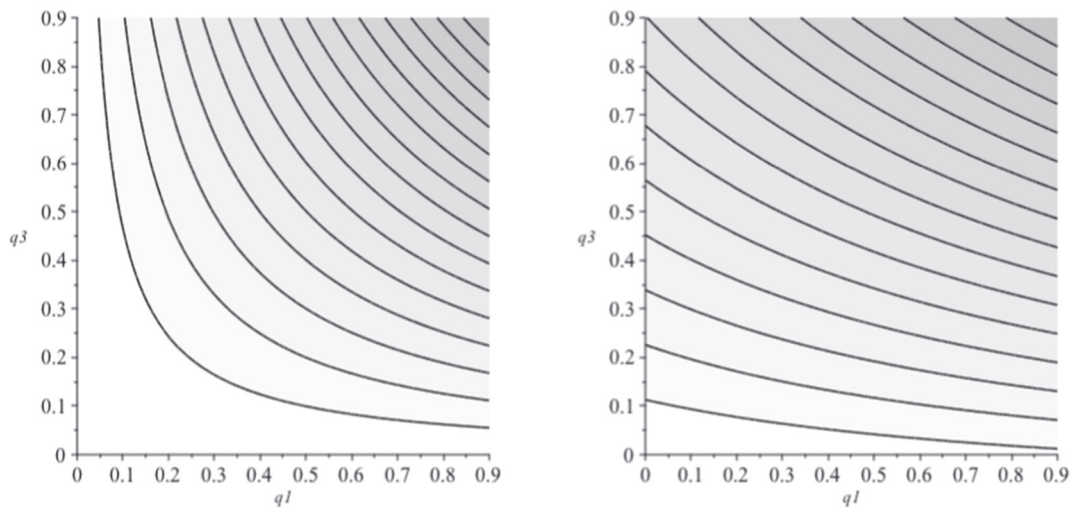


Fig. 10. Rao's criterion isoquants: $q_2 = 0.01$ (left), $q_2 = 0.99$ (right).

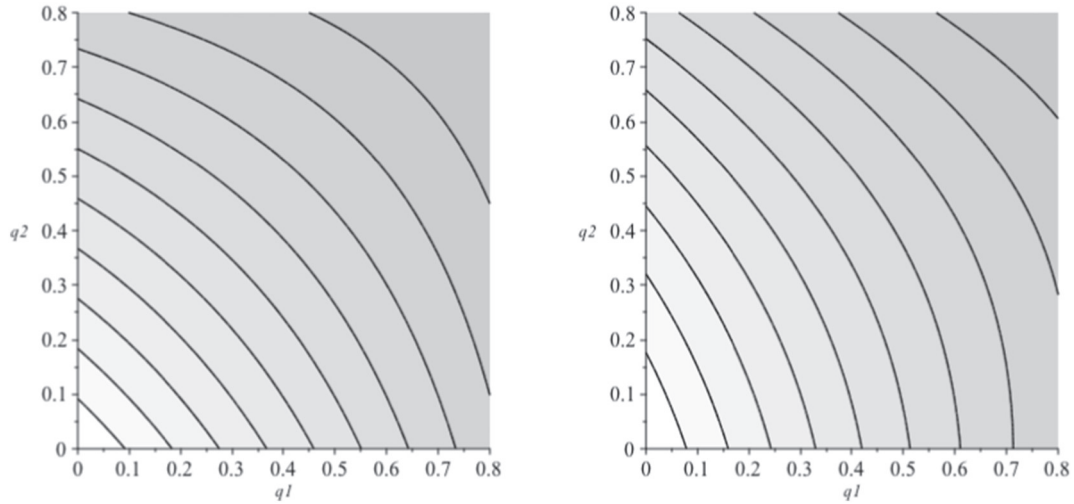


Fig. 11. Weitzman's criterion isoquants: no interaction case (left), predator-prey case (right).

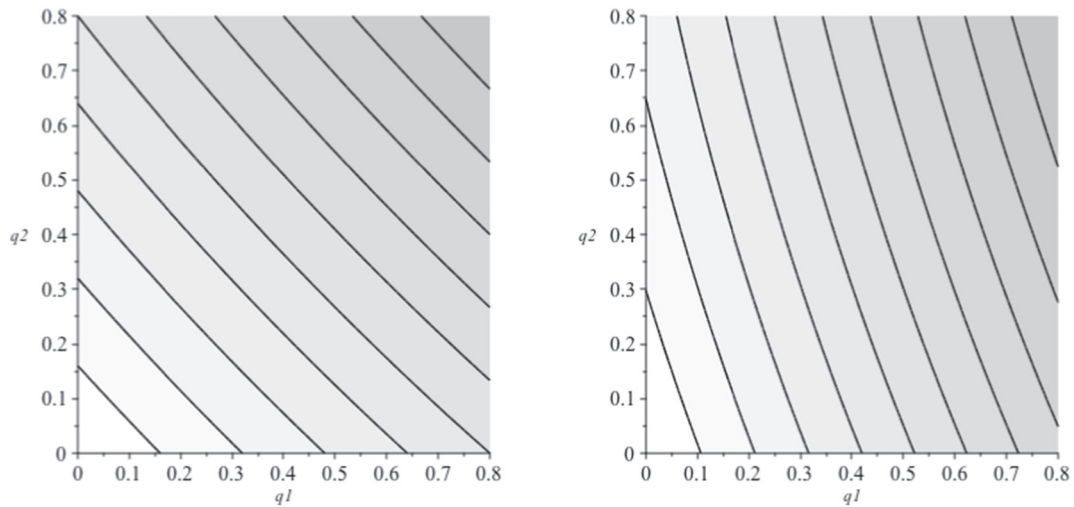


Fig. 12. Rao's criterion isoquants: no interaction case (left), predator-prey case (right).

the no interaction case ($r_{ij} = 0 \forall i, j$) and the predator-prey case where species 2 is the predator of species 1 ($r_{12} = -0.5$ and $r_{21} = 0.3$, and all remaining $r_{ij} = 0$). Isoquants for the two cases and the two criteria are depicted in Figs. 11 and 12.

Notice that when introducing species interactions, here a predator-prey relationship between species 2 and 1, both criteria's isoquants become steeper, meaning that the preservation of species 1 becomes more likely. This illustrates Proposition 3, according to which the criteria tend to allocate conservation efforts to the species that imparts the most benefits to the ecosystem. Here, species 1 is the prey and its presence positively impacts the survival probability of species 2.

6. Conclusion

This paper modifies Weitzman's and Rao's biodiversity indices, incorporating information about ecological interactions in order to render the models more appropriate for *in situ* protection plans. Using the resulting Weitzman's and Rao's *in situ* criteria, a simple framework allows us to analyze and compare the recommended conservation plans. For each *in situ* criterion, we are able to disentangle the role played by three factors: *i*) autonomous survival probabilities \mathbf{Q} , *ii*) ecological interaction \mathbf{R} and, *iii*) dissimilarity \mathbf{D} . We consider these factors both in strict isolation and in combination.

The analysis generates three important outcomes:

1. The two criteria, originating from different academic fields, combine information on \mathbf{Q} , \mathbf{R} and \mathbf{D} in different ways in order to measure biodiversity. As a consequence, they do not systematically deliver the same conservation recommendations. They diverge when differences between species arises from autonomous survival probabilities, whereas they largely agree when species heterogeneity arises from dissimilarities and/or ecological interactions.
2. When ecological interactions matter for the ranking, the favored species is the one that imparts the most benefits, or least harm, to the ecosystem. In general, the introduction of ecological interactions among more than two species can lead to complex conclusions.
3. When the three elements are combined, the policy recommended by each criterion reveals a specific trade-off between \mathbf{Q} , \mathbf{R} and \mathbf{D} .

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 feasibly receive protection. The analytical interpretation of the rankings in this case would probably be lost, but such an analysis does not seem to pose any computational problems.

At a more fundamental level, further consideration should be given to the objectives of conservation policies. Each biodiversity index is, by construction, a measure of a certain vision of biodiversity and therefore of conservation. It is interesting to learn that, all else being equal, there is a tendency for Weitzman's criterion to favor robust species, and for

Rao's criterion to favor fragile ones. The choice of one criterion over the other therefore depends on the policy perspective adopted. If the available conservation budget is large and the opportunity exists to save a great many species, then Rao's criterion is the most appropriate choice. If the conservation budget is limited and the potential for species extinction is as drastic as that of the narrative of Noah's Ark, Weitzman's criterion should be seriously considered. In order to arrive at a unique policy solution, it will therefore be necessary to develop a criterion for selecting from among biodiversity indices themselves. The present paper demonstrates that such a meta-criterion would essentially determine the trade-off that is ultimately made between robust and fragile species in conservation management.

Acknowledgments

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Appendix A. The System of Interdependent Probabilities

Solving the system Eq. (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:

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

$$P_2(\mathbf{X}) = \frac{(q_2 + x_2)(1 - r_{13}r_{31}) + (q_1 + x_1)(r_{21} + r_{31}r_{23}) + (q_3 + x_3)(r_{21}r_{13} + r_{23})}{1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}} \quad (33)$$

$$P_3(\mathbf{X}) = \frac{(q_1 + x_1)(r_{31} + r_{32}r_{21}) + (q_2 + x_2)(r_{12}r_{31} + r_{32}) + (q_3 + x_3)(1 - r_{12}r_{21})}{1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}} \quad (34)$$

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

In vector notations, probabilities as functions of efforts are:

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

with $\Lambda = [\mathbf{I} - \mathbf{R}]^{-1}$.

Appendix B. Three-species Weitzman's Criterion for *in situ* Protection When Distances are Ultrametric

In a three-species model, considering parameter vector $e = (\mathbf{Q}, \mathbf{R}, \mathbf{D}) \in \Omega$, Weitzman's expected diversity as a function of efforts is:

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

Assuming distances are ultrametric, $E_1 = E_2 = E$ and $E_3 = E + J$, with $E > 0$ and $J \geq 0$, we have:

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

Using Eqs. (32), (33) and (34), we obtain the following value for a vector of effort \mathbf{X} :

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

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

Appendix C. Three-species Rao's Criterion for *in situ* Protection When Distances are Ultrametric

For parameter vector $e = (\mathbf{Q}, \mathbf{R}, \mathbf{D}) \in \Omega$, and given $P(\mathbf{X}) \equiv \Lambda^*(\mathbf{Q} + \mathbf{X})$, Rao's index for *in situ* protection is:

$$R_e(\mathbf{X}) = P_1(\mathbf{X})P_2(\mathbf{X})(E_1 + E_2) + P_1(\mathbf{X})P_3(\mathbf{X})(E_1 + E_3 + J) + P_2(\mathbf{X})P_3(\mathbf{X})(E_2 + E_3 + J) \\ = 2[(P_1(\mathbf{X})P_2(\mathbf{X}) + P_1(\mathbf{X})P_3(\mathbf{X}) + P_2(\mathbf{X})P_3(\mathbf{X}))E + (P_1(\mathbf{X}) + P_2(\mathbf{X}))P_3(\mathbf{X})J]$$

and considering ultrametric distances such that $E_1 = E_2 = E$ and $E_3 = E + J$, with $J \geq 0$ and $E > 0$, we obtain:

$$R_e(\mathbf{X}) = 2[(P_1(\mathbf{X})P_2(\mathbf{X}) + P_1(\mathbf{X})P_3(\mathbf{X}) + P_2(\mathbf{X})P_3(\mathbf{X}))E + (P_1(\mathbf{X}) + P_2(\mathbf{X}))P_3(\mathbf{X})J].$$

Using system Eqs. (32), (33), and (34), the value of the criterion for a vector of effort \mathbf{X} is:

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

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

Appendix D. Interactions Between Effects

D.1. Autonomous Survival Probabilities and Dissimilarities

Let us examine the combination of autonomous survival probabilities and dissimilarity. Consider a slight departure from the parameter configuration e_q in Section 3.1.1. In the new list of parameters e_{qJ} , the unique difference arises from parameter J , which is no longer null, $J > 0$, and $r_{ij} = r$, when $i \neq j$. The vector \mathbf{Q} and the matrix \mathbf{R} are:

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

The relative performance of policies can be deduced from:

$$W_{e_{qJ}}(\mathbf{X}_1) - W_{e_{qJ}}(\mathbf{X}_2) = \frac{J\bar{x}}{(1+r)^2}(q_1 - q_2), \quad (35)$$

$$W_{e_{qJ}}(\mathbf{X}_1) - W_{e_{qJ}}(\mathbf{X}_3) = \frac{J\bar{x}[r(q_1 + q_3 + x) + q_2(1 - r)]}{(1+r)^2(2r - 1)}, \quad (36)$$

$$W_{e_{qJ}}(\mathbf{X}_2) - W_{e_{qJ}}(\mathbf{X}_3) = \frac{J\bar{x}[r(q_2 + q_3 + x) + q_1(1 - r)]}{(1+r)^2(2r - 1)}, \quad (37)$$

$$R_{e_{qJ}}(\mathbf{X}_1) - R_{e_{qJ}}(\mathbf{X}_2) = \frac{2E\bar{x}}{(1+r)^2}(q_2 - q_1), \quad (38)$$

$$\begin{aligned} R_{e_{qJ}}(\mathbf{X}_1) - R_{e_{qJ}}(\mathbf{X}_3) &= \frac{2J\bar{x}[r(3q_3 - q_1 - q_2) + r\bar{x} - (q_3 - q_1 - q_2)]}{(1+r)^2(2r - 1)} \\ &+ \frac{2E\bar{x}}{(1+r)^2}(q_3 - q_1), \end{aligned} \quad (39)$$

$$\begin{aligned} R_{e_{qJ}}(\mathbf{X}_2) - R_{e_{qJ}}(\mathbf{X}_3) &= \frac{2J\bar{x}[r(3q_3 - q_1 - q_2) + r\bar{x} - (q_3 - q_1 - q_2)]}{(r+1)^2(2r - 1)} \\ &+ \frac{2E\bar{x}}{(1+r)^2}(q_3 - q_2). \end{aligned} \quad (40)$$

When the choice to be made involves species 1 and 2, we again find that Weitzman's logic favors robust species, whereas Rao's index favors weak species.

The conclusions are more nuanced when a third species is introduced, and they depend on the importance of ecological interactions: Weitzman's index favors species 3 only if $r < 1/2$ ¹⁵. In other words, dissimilarity prevails when ecological interactions are not too strong. The conclusion is even more complex when it comes to Rao's index. Whatever the recommendation, it is reversed when r crosses the value $1/2$. As a particular case, now let the autonomous probabilities of survival be identical. The relative policy performances (Eqs. (35) to (40)) simplify to:

$$W_{e'_{qJ}}(\mathbf{X}_1) - W_{e'_{qJ}}(\mathbf{X}_2) = 0, \quad (41)$$

$$W_{e'_{qJ}}(\mathbf{X}_1) - W_{e'_{qJ}}(\mathbf{X}_3) = \frac{J\bar{x}[r(q + \bar{x}) + q]}{(1+r)^2(2r - 1)}, \quad (42)$$

$$W_{e'_{qJ}}(\mathbf{X}_2) - W_{e'_{qJ}}(\mathbf{X}_3) = \frac{J\bar{x}[r(q + \bar{x}) + q]}{(1+r)^2(2r - 1)}, \quad (43)$$

$$R_{e'_{qJ}}(\mathbf{X}_1) - R_{e'_{qJ}}(\mathbf{X}_2) = 0, \quad (44)$$

¹⁵ Note that the system of interdependent probabilities (Eq. (2)) cannot be solved when $r = 1/2$.

$$R_{e_{qJ}}(\mathbf{X}_1) - R_{e_{qJ}}(\mathbf{X}_3) = \frac{2J\bar{x}[r(q + \bar{x}) + q]}{(1+r)^2(2r-1)}, \quad (45)$$

$$R_{e_{qJ}}(\mathbf{X}_2) - R_{e_{qJ}}(\mathbf{X}_3) = \frac{2J\bar{x}[r(q + \bar{x}) + q]}{(1+r)^2(2r-1)}. \quad (46)$$

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

D.2. Ecological Interactions and Dissimilarities

Now, combine the heterogeneity of ecological interactions with dissimilarities. Consider a parameter 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:

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

The relative policy performances can be deduced from:

$$W_{e_{rJ}}(\mathbf{X}_1) - W_{e_{rJ}}(\mathbf{X}_2) = \bar{x} \frac{(E+J)(1-r_{12}r_{21}) - J(2q+\bar{x})}{(1-r_{12}r_{21})^2} (r_{21} - r_{12}), \quad (47)$$

$$W_{e_{rJ}}(\mathbf{X}_1) - W_{e_{rJ}}(\mathbf{X}_3) = \bar{x}(E+J) \frac{(1+r_{12}-r_{12}r_{21}-r_{12}^2r_{21})r_{21}}{(1-r_{12}r_{21})^2} \quad (48)$$

$$- \bar{x}J \frac{(r_{12}q + 2q + \bar{x})r_{21} + q}{(1-r_{12}r_{21})^2}, \quad (49)$$

$$W_{e_{rJ}}(\mathbf{X}_2) - W_{e_{rJ}}(\mathbf{X}_3) = \bar{x}(E+J) \frac{(1+r_{21}-r_{12}r_{21}-r_{12}r_{21}^2)r_{12}}{(1-r_{12}r_{21})^2} \quad (50)$$

$$- \bar{x}J \frac{(r_{21}q + 2q + \bar{x})r_{12} + q}{(1-r_{12}r_{21})^2}, \quad (51)$$

$$R_{e_{rJ}}(\mathbf{X}_1) - R_{e_{rJ}}(\mathbf{X}_2) = \frac{2E\bar{x}(2q+\bar{x})}{(1-r_{12}r_{21})^2} (r_{21} - r_{12}), \quad (52)$$

$$R_{e_{rJ}}(\mathbf{X}_1) - R_{e_{rJ}}(\mathbf{X}_3) = 2\bar{x}(E+J) \frac{q(r_{12}r_{21}^2 + r_{12}^2r_{21} + 2r_{12}r_{21} - r_{12} - 1)}{(1-r_{12}r_{21})^2} \quad (53)$$

$$+ 2\bar{x} \frac{Er_{21}(qr_{12} + q + \bar{x}) - Jq(1+r_{21})}{(1-r_{12}r_{21})^2}, \quad (54)$$

$$R_{e_{rJ}}(\mathbf{X}_2) - R_{e_{rJ}}(\mathbf{X}_3) = 2\bar{x}(E+J) \frac{q[r_{12}r_{21}^2 + r_{12}^2r_{21} + 2r_{12}r_{21} - r_{21} - 1]}{(1-r_{12}r_{21})^2} \quad (55)$$

$$+ 2\bar{x} \frac{Er_{12}(qr_{21} + q + \bar{x}) - Jq(1+r_{12})}{(1-r_{12}r_{21})^2}. \quad (56)$$

When the comparison involves only species 1 and 2, which are perfectly substitutable from the point of view of their dissimilarities, and for low values of J , the conclusion is unambiguous: both indices favor the species with the largest ecological impact. When species 3 is introduced, the conclusions become ambiguous. To illustrate, assume that all ecological impacts are non-negative ($r_{12} \geq 0, r_{21} \geq 0$). In this case, both the Weitzman and the Rao criteria prioritize species 3 over species 1 (or species 2) when the ecological impact of the latter is sufficiently weak. However, the indices may also diverge in their recommendations. For instance, when the autonomous survival probability q is sufficiently close to 0, the Rao index clearly abandons species 3 in favor of either of the other two. This conclusion cannot be drawn from Weitzman's index under the same condition on q .

D.3. Autonomous Survival Probabilities and Ecological Interactions

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

$$\begin{aligned}
W_{eqR}(\mathbf{X}_1) - W_{eqR}(\mathbf{X}_2) = & J \frac{\bar{x}(1 + r_{12}r_{21})}{(1 - r_{12}r_{21})^2} (q_1 - q_2) \\
& + J \frac{2\bar{x}}{(1 - r_{12}r_{21})^2} (q_2r_{12} - q_1r_{21}) \\
& + \frac{\bar{x}[(E + J)(1 - r_{12}r_{21}) - J\bar{x}]}{(1 - r_{12}r_{21})^2} (r_{21} - r_{12}),
\end{aligned} \tag{58}$$

$$\begin{aligned}
R_{eqR}(\mathbf{X}_1) - R_{eqR}(\mathbf{X}_2) = & \frac{2E\bar{x}(1 + r_{12}r_{21})}{(1 - r_{12}r_{21})^2} (q_2 - q_1) \\
& - \frac{4E\bar{x}}{(1 - r_{12}r_{21})^2} (q_2r_{12} - q_1r_{21}) \\
& + \frac{2E\bar{x}^2}{(1 - r_{12}r_{21})^2} (r_{21} - r_{12}).
\end{aligned} \tag{59}$$

Of course, when $r_{21} = r_{12} = r$, one again finds the results presented in Section 3.1.1. Recall that using the Weitzman index generates a recommendation to protect the strongest species (*i.e.* the species with the largest q_i), whereas using the Rao index generates a recommendation to protect the weakest species (Proposition 1). As soon as $r_{21} \neq r_{12}$, these results must be qualified. They now become more complex functions of not only the q_i s, but also the r_{ij} s. In order to grasp these qualifications, imagine that species 1 is the strongest species ($q_1 > q_2$). We know from Proposition 1 that, when $r_{21} = r_{12} = r$, the Weitzman index (respectively Rao index) suggests that 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 prioritize species 2 (see Proposition 3). However, if $q_1 > q_2$, from expressions (58) and (59), Rao clearly recommends species 2, whereas Weitzman's conclusion is ambiguous. Eventually the conclusion reveals a trade-off between two opposite effects, and this trade-off depends, among other things, on the importance of J and 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 $q_1 < q_2$. In this case, Weitzman clearly prioritizes species 2. Rao's ranking, on the other hand, embodies two opposing 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 these opposing forces. As can be deduced from expression (59), contrary to Weitzman's trade-off, Rao's conclusion does not depend on J .

Appendix E. IUCN Species Extinction Status

IUCN assumes that the probability of extinction in the wild is: $\geq 50\%$ in 10 years for critically endangered species, $\geq 20\%$ in 20 years for endangered species and $\geq 10\%$ in 100 years for vulnerable species. In line with Mooers et al. (2008), we can make projections at 50 and 100 years of these data and extrapolate species extinction probabilities for near threatened and least concern species. We obtain the following extinction probabilities:

Table E1
IUCN species extinction status. Sources: <http://www.iucnredlist.org/> and Mooers et al. (2008).

IUCN Categories	IUCN 50	IUCN 100
Critically endangered	0.97	0.999
Endangered	0.42	0.667
Vulnerable	0.05	0.05
Near threatened	0.004	0.01
Least concerned	0.00005	0.001

References

- Alderson, L., 2003. Criteria for the recognition and prioritisation of breeds of special genetic importance. *Anim. Genet. Resour. Info* 33, 1–9.
- Alderson, L., 2010. Breeds at risk: criteria and classification. In: Joint ERF/ERFP/RBI/RBST, workshop summary report, London, 16–17 February 2010.
- Baumgärtner, S., 2004a. Optimal investment in multi-species protection: interacting species and ecosystem health. *Ecohealth* 1, 101–110.
- Baumgärtner, S., 2004b. Measuring the diversity of what? And for what purpose? A conceptual comparison of ecological and economic measures of biodiversity. In: IIEE Heidelberg, working paper, pp. 1–22.
- Bennett, J.R., Elliott, G., Mellish, B., Joseph, L.N., Tulloch, A.I., Probert, W.J.M., Di Fonzo, M.M.I., Monks, J.M., Possingham, H.P., Maloney, R., 2014. Balancing phylogenetic diversity and species numbers in conservation prioritization, using a case study of threatened species in New Zealand. *Biol. Conserv.* 174, 47.
- Bossert, W., Pattanaik, P.K., Xu, Y., 2003. Similarity of options and the measurement of diversity. *J. Theor. Polit.* 405–421.
- Caccone, A., Powell, J.R., 1989. DNA divergence among hominoids. *Evolution* 43 (5), 925–942.
- Carwardine, J., O Connor, T., Legge, S., Mackey, B., Possingham, H.P., Martin, T.G., 2012. Prioritizing threat management for biodiversity conservation. *Conserv. Lett.* 5, 196–204.
- Ceballos, G., Ehrlich, P., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci.* 114 (30), 6089–6096.
- Champely, S., Chessel, D., 2002. Measuring biological diversity using Euclidean metrics. *Environ. Ecol. Stat.* 9, 167–177.
- Courtois, P., Figuières, C., Mulier, C., 2014. Conservation priorities when species interact: the Noah's Ark metaphor revisited. *PLoS One* 9 (9).
- Courtois, P., Figuières, C., Mulier, C., Weill, W., 2018. A cost-benefit approach for prioritizing invasive species. *Ecol. Econ.* 146, 607–620.
- Crozier, R.H., 1992. Genetic diversity and the agony of choice. *Biol. Conserv.* 61, 11–15.
- Dulvy, N., Jennings, S., Goodwin, N., Grant, A., Reynolds, J., 2005. Comparison of threat and exploitation status in north-east Atlantic marine populations. *J. Appl. Ecol.* 42, 883–891.
- Eppink, F.V., van den Bergh, J.C.J.M., 2007. Ecological theories and indicators in economic models of biodiversity loss and conservation: a critical review. *Ecol. Econ.* 61 (2-3), 284–293.
- Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1–10.
- Faith, D.P., 1994. Genetic diversity and taxonomic priorities for conservation. *Biol. Conserv.* 68 (1), 69–74.
- Frew, K., Nils Peterson, M., Stevenson, K., 2016. Are we working to save the species our children want to protect? Evaluating species attribute preferences among children. *Oryx* 1.
- Gandini, G., Ollivier, L., Danell, B., Distl, O., Geogoudis, A., Groeneveld, E., Martyniuk, E., Van Arendonk, J., Woolliams, J., 2004. Criteria to assess the degree of endangerment of livestock breeds in Europe. *Livest. Prod. Sci.* 91, 173–182.
- Gerber, N., 2011. Biodiversity measures based on species-level dissimilarities: a methodology for assessment. *Ecol. Econ.* 70 (12), 2275–2281.
- Gerber, L.R., 2016. Conservation triage or injurious neglect in endangered species

- recovery. *Proc. Natl. Acad. Sci.* 113 (13), 3563.
- Harnik, P.G., Simpson, C., Payne, J.L., 2012. Long-term differences in extinction risk among the seven forms of rarity. *Proc. Biol. Sci.* 279 (1749), 4969–4976.
- Hill, R. J., 2001. *Measuring Biological Diversity*. Unpublished Manuscript, UNSW, Sydney, Australia.
- Joseph, L.N., Maloney, R.F., Possingham, H.P., 2008. Optimal allocation of resources among threatened species: a project prioritization protocol. *Conserv. Biol.* 23 (2), 328–338.
- Joseph, L.N., Maloney, R., Watson, J.E.M., Possingham, H.P., 2011. Securing nonflagship species from extinction. *Conserv. Lett.* 4, 324–325.
- Krajewski, C., 1989. Phylogenetic relationships among cranes (Gruiformes: Gruidae) based on DNA hybridization. *Auk*, CVI 603–618.
- Lacona, G., Maloney, R.F., Chadés, L., Bennett, J.R., Seddon, P.J., Possingham, H.P., 2017. Prioritizing revived species: what are the conservation management implications of de-extinction? *Funct. Ecol.* 31 (5), 1041–1048. <https://doi.org/10.1111/1365-2435.12720>.
- Magurran, A., 2004. *Measuring Biological Diversity*. Blackwell Publishing, Oxford, UK, pp. 256.
- McCarthy, M.A., Thompson, C.J., Garnett, T., 2008. Optimal investment in conservation of species. *J. Appl. Ecol.* 45, 1428–1435.
- Moers, A., Faith, D.P., Maddison, W.P., 2008. Converting endangered species categories to probabilities of extinction for phylogenetic conservation prioritization. *PLoS ONE* 3.
- Pavoine, S., Ollier, S., Pontier, D., 2005. Measuring diversity from dissimilarities with Rao's quadratic entropy: are any dissimilarities suitable? *Theor. Popul. Biol.* 67 (4), 231–239.
- Rao, C.R., 1982. Diversity and dissimilarity coefficients: a unified approach. *Theor. Popul. Biol.* 21, 24–43.
- Rao, C.R., 1986. *Rao's Axiomatization of Diversity Measures*. Wiley StatsRef: Statistics Reference Online.
- Rao, C.R., 2010. Quadratic entropy and analysis of diversity. *Indian J. Stat.* 72 (1), 70–80.
- Ricotta, C., 2004. A parametric diversity measure combining the relative abundances and taxonomic distinctiveness of species. *Divers. Distrib.* 10, 143–146.
- Ricotta, C., Marignani, M., 2007. Computing diversity with Rao's quadratic entropy: a change of perspective. *Divers. Distrib.* 13 (2), 237–241.
- Ricotta, C., Szeidl, L., 2006. Towards a unifying approach to diversity measures: bridging the gap between Shannon entropy and Rao's quadratic index. *Theor. Popul. Biol.* 70, 237–243.
- Sarkar, S., 2006. Ecological diversity and biodiversity as concepts for conservation planning: comments on Ricotta. *Acta Biotheor.* 54, 133–140.
- Schultz, J.A., Darling, E.S., Côté, I.M., 2013. What is an endangered species worth? Threshold costs for protecting imperilled fishes in Canada. *Mar. Policy* 42, 125.
- Shimatani, K., 2001. On the measurement of species diversity incorporating species differences. *Oikos* 93, 135–147.
- Simianer, H., 2008. Accounting for non-independence of extinction probabilities in the derivation of conservation priorities based on Weitzman's diversity concept. *Conserv. Genet.* 9 (1), 171–179.
- Solow, A., Polasky, S., Broadus, J., 1993. On the measurement of biological diversity. *J. Environ. Econ. Manag.* 24, 60–68.
- Van der Heide, M.C., van den Bergh, J.C.J.M., van Ierland, E.C., 2005. Extending Weitzman's economic ranking of biodiversity protection: combining ecological and genetic considerations. *Ecol. Econ.* 55, 218–223.
- Verrier, E., Audiot, A., Bertrand, C., Chapuis, H., Charvolin, E., Danchin-Burge, C., Danvy, S., Gourdine, J.L., Gaultier, P., Guémené, D., Laloë, D., Lenoir, H., Leroy, G., Naves, M., Patin, S., Sabbagh, M., 2015. Assessing the risk status of livestock breeds: a multi-indicator method applied to 178 French local breeds belonging to ten species. *Anim. Genet. Resour.* 57, 105–118.
- Weikard, H.P., Punt, M., Wesseler, J., 2006. Diversity measurement combining relative abundances and taxonomic distinctiveness of species. *Divers. Distrib.* 12, 215–217.
- Weitzman, M.L., 1992. On diversity. *Q. J. Econ.* 107 (2), 363–405.
- Weitzman, M.L., 1998. The Noah's Ark problem. *Econometrica* 66 (6), 1279–1298.
- Whittaker, R.J., Araujo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M., Willis, K.J., 2005. Conservation biogeography: assessment and prospect. *Divers. Distrib.* 11, 323.
- Wilson, H.B., Joseph, L.N., Moore, A.L., Possingham, H.P., 2011. When should we save the most endangered species? *Ecol. Lett.* 14, 886–890.
- Witting, L., Tomiuk, J., Loeschcke, V., 2000. Modelling the optimal conservation of interacting species. *Ecol. Model.* 125, 123–143.
- Wood, P.M., 2000. *Biodiversity and Democracy: Rethinking Society and Nature*. University of British Columbia Press, Vancouver, Canada.