

A Tale of Two Diversities

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Abstract

Efficient biodiversity management strategies aim to allocate conservation efforts in order 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 combine in different ways, information about measures of (1) species' probability distribution and (2) species' dissimilarity. As an important step toward *in situ* protection criteria, to these elements we add information about (3) the ecological interactions between species. Considering a simple three-species ecosystem, we show that criterion choice has palpable policy implications, as it can sometimes lead to diverging management recommendations. We disentangle the role played by elements (1), (2) and (3) in the ranking outcomes, which allows us to highlight some specificities of the two criteria. An important result is that, other things equal, Weitzman's *in situ* ranking tends to favor robust species least concerned by extinction, while Rao's *in situ* ranking generally gives priority to species the more concerned.

Keywords

biodiversity indices, conservation management strategy, ecological interactions, public policy, species prioritization criteria.

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. Important progress has been made 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 Baumgartner, 2004a,b, Magurran, 2004, Eppink and van der Berg., 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 *Noah's ark metaphor*, 1998). 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, Baumgartner, 2004a, Simianer, 2008, van der Heide, 2008, van den Bergh and van Ierland, 2005, Courtois et al., 2014).³ As a result, at least at the conceptual level, we 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 trophic interactions ?

Answering this question requires comparing the outcomes of *in situ* optimization exercises that use different biodiversity indexes 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

41 properties of quadratic entropy have been extensively studied in Rao (2010), Ricotta and Marig-
42 nani (2007), Ricotta and Szeidl (2006), Pavoine et al. (2005), Champely and Chessel (2002) and
43 Shimatani (2001).

44 Using prioritization framework, the present paper makes an original contribution by exam-
45 ining the consequences of considering two alternative diversity indices as the objective function
46 to be maximized: Weitzman (1992)' s index, which is popular in several literatures including
47 economics, and Rao (1982)' s index, which is used mostly in ecology and biology, but largely
48 ignored by economists. Both indices simultaneously account for species distribution probability
49 and dissimilarity measures. Rao's index is defined as the expected dissimilarity between all pairs
50 of species composing a collection of species, whereas Weitzman's index is defined as the expected
51 length of the evolutionary tree associated with a collection of species. The axiomatic proper-
52 ties of both indices have been elicited (Rao, 1986, Bossert et al., 2003), which gives them some
53 transparency as measures of diversity.

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

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

69 **2 A class of *in situ* prioritization problems**

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

80 probabilities, with components P_i , the link between efforts and probabilities is a N-dimensional
 81 vector of functions \mathcal{P} such that $\mathbf{P} = \mathcal{P}(\mathbf{X})$.

82 We compare protection plans on the basis of how well they perform as measured by indices of
 83 expected diversity. We use two alternative indices: Weitzman's index, noted $W(\mathbf{P})$, and Rao's
 84 index, $R(\mathbf{P})$. Both belong to the family of expected diversity measures that aggregate dissimi-
 85 larities between species. Both indices combine, albeit in different ways, measures of, *i*) species'
 86 probability distribution, and *ii*) species' dissimilarity. Here, the probability measure considered
 87 is the survival probability of species. Given the link between interdependent probabilities and
 88 efforts, $\mathcal{P}(\mathbf{X})$, we can construct *in situ* expected diversity indices, $\mathcal{W}(\mathbf{X}) \equiv W(\mathcal{P}(\mathbf{X}))$, and
 89 $\mathcal{R}(\mathbf{X}) \equiv R(\mathcal{P}(\mathbf{X}))$. Under this framework, the present paper makes an original contribution to
 90 the literature by exploring and comparing optimal *in situ* protection plans. We accomplish this
 91 by solving the programs $\max_{\mathbf{X}} \mathcal{W}(\mathbf{X})$ and $\max_{\mathbf{X}} \mathcal{R}(\mathbf{X})$ and compare their respective outcomes.

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

93 2.1 Interdependent survival probabilities

94 We assume each species i has an *autonomous survival probability* we denote $q_i \in [0, 1]$, $i = 1, \dots, N$.
 95 This probability can be evaluated on the basis of demographic and genetic properties of species
 96 (ie. reproductive capacities, genetic erosion, [...]) as well as on abiotic factors impacting species
 97 survival such as geographic range and habitat breadth - examples of which can be found in
 98 Gandini et al. (2004), Alderson (2003, 2010) or Verrier et al. (2015). We assume that near
 99 0 autonomous survival probability means that the species is *fragile* and *likely to be threatened*
 100 while close to 1 autonomous survival probability means the species is *robust* and *a priori least*
 101 *concerned by extinction*. Principal feature of autonomous survival probability - and this explains
 102 the qualification *autonomous* - is that it ignores the impact of species interrelationships on
 103 survival. While the ultimate causes of increased extinction in an interval of time may be abiotic,
 104 and might affect only some species directly, the intricate patterns of relationships among species
 105 in a community distribute the effects of changes in one species to others in its community.
 106 In order to take into account the impact of biotic interactions and conservation efforts so as
 107 to generate *interdependent survival probabilities*, we assume, along the lines of Courtois et al.
 108 (2014, 2018), a functional form to assess this probability. We denote $P_i \in [\underline{P}_i, \bar{P}_i]$, $i = 1, \dots, N$,
 109 the interdependent survival probability of species i and approximate this probability as a linear
 110 function of the protection effort x_i measured in terms of probability variation, and of $r_{ij} \equiv$
 111 $\partial P_i / \partial P_j$, representing the marginal ecological impact of species j on the survival probability of
 112 species i , with $|r_{ij}| < 1$. We have then:

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

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

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

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

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

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

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

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

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

122 Note that this condition is not particularly demanding here as it translates in a very specific
 123 relationship between marginal impact parameters. To illustrate it, in the three species case, this
 124 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
 125 equality that has no reason to be true.

126 We deduce that a particular protection plan \mathbf{X} induces a particular vector of survival proba-
 127 bilities. Denoting $\mathcal{P}(\mathbf{X}) \equiv \mathbf{P} \equiv [\mathbf{I} - \mathbf{R}]^{-1} * (\mathbf{Q} + \mathbf{X})$ the affine mapping from efforts to probabili-
 128 ties, *i.e.* the expression of the survival probability system as a function of efforts. Each element
 129 of $\mathcal{P}(\mathbf{X})$ can be explicitly computed (see Appendix A for the three species case).⁹ Survival
 130 probabilities in the absence of any conservation policy are therefore:

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

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

134 2.2 Species dissimilarities

135 Species are also characterized by attributes diversity and their dissimilarity. Dissimilarity can
 136 generally be described by distance measures between any two species or between a species and a
 137 collection of species. These distances can represent different characteristics. They can measure

138 genetic distance, by means of DNA-DNA hybridization (Krajewski, 1989, Cacccone and Powell,
139 1989), morphological distance, or taxonomic distance. Another possibility, used in phylogenetics,
140 is to conceive of species as terminal nodes in a tree structure. Dissimilarities are then given by
141 corresponding branch lengths (Faith, 1992, 1994). All of these metrics share the ability to capture
142 and measure the intuitive notion of “differences among biological entities” (Wood, 2000) and in
143 what follows, we simply consider that species have a set of attributes that can be either specific
144 or commonly shared. The more distinctive attributes a species exhibits, the more dissimilar this
145 species is considered.

146 For the sake of clarity and of tractability, we consider in the following the simplest ecosystem
147 that allows us to compare the two biodiversity indices, that is a system composed of three
148 species, $N = 3$, as depicted in Figure 1:

149

150 **[Insert Figure 1.]**

151

152 We assume each species has $E_i > 0$ specific attributes that are not shared with the two other
153 species. Two species (here species 1 and 2) possibly share $J \geq 0$ common attributes. We deduce
154 that the information about species dissimilarities is contained in the vector $\mathbf{D} = (E_1, E_2, E_3, J)$
155 which we use in the following in order to assess our two criteria and discuss the impact of
156 dissimilarity. This vector contains 1) informations on species attributes that are shared between
157 any two or more species and 2) informations on species attributes that are not shared.¹⁰ We
158 define d_{ij} , the distance between species i and j , as the number of attributes that are not shared
159 by the two species, with $d_{ij}=d_{ji}$. By assumption, species 3 has no common attributes with
160 species 1 and 2. We have therefore $d_{31} = d_{13} = E_3 + E_1 + J$ and $d_{32} = d_{23} = E_3 + E_2 + J$.
161 But we allow for the possibility that species 1 and 2 may have $J \geq 0$ common attributes. So,
162 $d_{12} = d_{21} = E_1 + E_2$.

163 **2.3 Definitions of *in situ* criteria for conservation priorities**

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

$$e = (\mathbf{Q}, \mathbf{R}, \mathbf{D}) \in \Omega, \quad (5)$$

166 a particular element of this parameters space. This means in particular that the mapping that
167 transforms efforts into probabilities is configured by parts of the information included in the
168 vector e . In the sequel we shall emphasize this dependence using a subscript e whenever relevant,
169 as in the notation $\mathcal{P}_e(\mathbf{X})$.

170 **Weitzman’s criterion for *in situ* protection** Let $V_e(S)$ be the diversity function of the
171 (sub)set S of species given by the length of the (sub)tree made of species in S , that is the
172 number of distinct attributes contained in S . This is important to note that this function is
173 impacted by species dissimilarity but is not *per se* a measure of dissimilarity. Considering the
174 three species ecosystem presented above:

175 • if S contains only one species, then

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

176 that is, the total number of attributes (which are necessarily distinctive) carried out by the
177 species.

178 • When S has only two species, then

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

179 that is, the total number of distinctive attributes carried out by the two species.

180 • When S has all species, then

$$V_e(\{1, 2, 3\}) = E_1 + E_2 + J + E_3 \quad (8)$$

181 that is, the total number of distinctive attributes carried out by the three species.

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

$$W_e(\mathbf{P}) = \sum_{S \subseteq N} \left(\prod_{j \in S} P_j \right) \left(\prod_{k \in N \setminus S} (1 - P_k) \right) V_e(S) \quad (9)$$

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

- 187 • no species disappears, an event that occurs with probability $P_1 P_2 P_3$, and the corresponding
188 diversity is $V_e(\{1, 2, 3\})$,
- 189 • only species 1 survives, an event occurring with probability $(1 - P_2)$
190 $(1 - P_3) P_1$, and the diversity is $V_e(\{1\})$,
- 191 • only species 1 and 2 survive, an event with probability $P_1 P_2 (1 - P_3)$, and the diversity is
192 $V_e(\{1, 2\})$,
- 193 • and so on...

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

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

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

$$\begin{aligned} \mathcal{W}_e(\mathbf{X}) &\equiv W_e(\mathcal{P}_e(\mathbf{X})) , \\ &= P_1(\mathbf{X}) (E_1 + J) + P_2(\mathbf{X}) (E_2 + J) + P_3(\mathbf{X}) E_3 - P_1(\mathbf{X}) P_2(\mathbf{X}) J . \end{aligned} \quad (11)$$

199 **Rao's criterion for *in situ* protection** Rao's index is the expected distance between any
 200 two species that are randomly drawn from a given set of species. In a N -species ecosystem, this
 201 diversity index is:

$$R_e(\mathbf{P}) = \sum_{i=1}^N \sum_{j=1}^N P_i P_j d_{ij}, \quad (12)$$

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

206 In our three-species ecosystem, the index becomes:

$$R(\mathbf{P}) = P_1 P_2 (E_1 + E_2) + P_1 P_3 (E_1 + E_3 + J) + P_2 P_3 (E_2 + E_3 + J), \quad (13)$$

207 and the resulting relationship between diversity and effort is:

$$\begin{aligned} \mathcal{R}_e(\mathbf{X}) &= P_1(\mathbf{X}) P_2(\mathbf{X}) (E_1 + E_2) + P_1(\mathbf{X}) P_3(\mathbf{X}) (E_1 + E_3 + J) \\ &+ P_2(\mathbf{X}) P_3(\mathbf{X}) (E_2 + E_3 + J). \end{aligned} \quad (14)$$

208 2.4 Simple *in situ* protection projects

209 Our purpose is to compare three simple policies that concentrate efforts on either species 1,
 210 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:

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

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

$$\mathcal{W}_e(\mathbf{X}_1) \geq \max\{\mathcal{W}_e(\mathbf{X}_2), \mathcal{W}_e(\mathbf{X}_3)\}. \quad (15)$$

213 That is:

$$\mathcal{W}_e(\bar{x}, 0, 0) \geq \max\{\mathcal{W}_e(0, \bar{x}, 0), \mathcal{W}_e(0, 0, \bar{x})\}. \quad (16)$$

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

$$\mathcal{R}_e(\mathbf{X}_1) \geq \max\{\mathcal{R}_e(\mathbf{X}_2), \mathcal{R}_e(\mathbf{X}_3)\}, \quad (17)$$

215 or equivalently:

$$\mathcal{R}_e(\bar{x}, 0, 0) \geq \max \mathcal{R}_e(0, \bar{x}, 0), \mathcal{R}_e(0, 0, \bar{x}) . \quad (18)$$

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

221

222 The next section compares different optimization outcomes while keeping the analysis as
223 simple as possible. It spares too technical details to the reader. Those details can be found in
224 Appendices B and C, which explicitly construct Weitzman and Rao *in situ* indices in a three-
225 species setting.

226 **3 Disentangling the underlying logic of in-situ priorities**

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

234 From a technical point of view, for a given vector of parameters e , the whole challenge of this
235 paper boils down to the computation of differences such as:

$$\begin{aligned} \mathcal{W}_e(\mathbf{X}_k) - \mathcal{W}_e(\mathbf{X}_l) , \\ \mathcal{R}_e(\mathbf{X}_k) - \mathcal{R}_e(\mathbf{X}_l) , \end{aligned}$$

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

241 **3.1 When the criteria disagree**

242 **3.1.1 The influence of autonomous survival probabilities (\mathbf{Q})**

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

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

251

252 [Insert Figure 2.]

253

Note that we added in this phylogenetic tree, additional informations 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:

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

254 and tedious computations produce:

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

$$\mathcal{R}_{e_q}(\mathbf{X}_1) - \mathcal{R}_{e_q}(\mathbf{X}_2) = \frac{2E\bar{x}}{(1+r)^2} (q_2 - q_1) . \quad (20)$$

255 Expression (19) shows that Weitzman's ranking is sensitive to the difference $q_1 - q_2$ only if $J > 0$,
 256 and becomes indifferent when $J = 0$. By contrast, according to expression (20) the sensitivity of
 257 Rao's ranking to $q_2 - q_1$ does not depend on the value of J . Assuming $J > 0$, from (19) and (20)
 258 one can deduce:

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

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

$$\mathcal{W}_{e_q}(\mathbf{X}_1) \gtrless \mathcal{W}_{e_q}(\mathbf{X}_2) \Leftrightarrow q_1 \gtrless q_2 ,$$

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

$$\mathcal{R}_{e_q}(\mathbf{X}_1) \gtrless \mathcal{R}_{e_q}(\mathbf{X}_2) \Leftrightarrow q_2 \gtrless q_1 .$$

261 How are these results explained? Ecological interactions are of little importance in this first
 262 example, since both species serve identical ecological roles. These results are therefore consistent
 263 with the logic embodied in the indices alone. Weitzman's index seeks the longest expected tree.
 264 Recall that only one species is protected. If either species 1 or species 2 goes extinct, E attributes
 265 are lost but $E + J$ are safe. It is therefore sensible to allocate protection resources to the species

266 which is initially the most secure (*i.e.* the species whose autonomous survival probability is the
267 highest), unless $J = 0$, in which case Weitzman's criterion would clearly be indifferent regarding
268 which species should be afforded protection efforts. Regarding Rao criterion, the question is: how
269 can one choose the combination of probabilities that leads to the highest expected diversity? Put
270 more precisely, in this two-species problem, Rao seeks the largest product $P_1(\mathbf{X})P_2(\mathbf{X})$. This
271 is best achieved when a conservation policy helps the fragile species, *i.e.* the most likely to be
272 threatened. Indeed, the marginal impact of increasing P_i is equal to P_j . And protection efforts
273 are optimally allocated where the marginal impact is highest, therefore to species i if $P_i \leq P_j$.

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

281

282 **[Insert Figure 3.]**

283

284 From Xcas computations, using Appendix B and C, one finds:

$$\mathcal{W}_{e'_q}(\mathbf{X}_1) - \mathcal{W}_{e'_q}(\mathbf{X}_2) = \mathcal{W}_{e'_q}(\mathbf{X}_1) - \mathcal{W}_{e'_q}(\mathbf{X}_3) = 0 . \quad (21)$$

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

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

$$\mathcal{R}_{e'_q}(\mathbf{X}_1) - \mathcal{R}_{e'_q}(\mathbf{X}_3) = \frac{2E\bar{x}}{(r+1)^2} (q_3 - q_1) , \quad (23)$$

$$\mathcal{R}_{e'_q}(\mathbf{X}_2) - \mathcal{R}_{e'_q}(\mathbf{X}_3) = \frac{2E\bar{x}}{(r+1)^2} (q_3 - q_2) , \quad (24)$$

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

294 **3.2 When the criteria agree**

295 **3.2.1 The influence of attributes dissimilarity**

Attribute dissimilarities are embedded differently in the two indices. 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:

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

296 and this ecosystem, denoted by parameter vector e_J , is depicted in Figure 4:

297

298 [insert Figure 4.]

299

300

Xcas computations deliver the following key pieces of information:

301

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

$$\begin{aligned} \mathcal{W}_{e_J}(\mathbf{X}_3) - \mathcal{W}_{e_J}(\mathbf{X}_1) &= \mathcal{W}_{e_J}(\mathbf{X}_3) - \mathcal{W}_{e_J}(\mathbf{X}_2) \\ &= Jq\bar{x} > 0, \quad (\text{since } J > 0 \text{ and } \bar{x} > 0), \end{aligned}$$

302

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

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

303 A conclusion immediately emerges:

304 **Proposition 2** *Let the class of conservation problems be given by the list of parameters e_J .*

305 *In this three-species ecosystem where dissimilarities are the only source of heterogeneity among*
 306 *species, the two diversity criteria deliver the same rankings:*

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

310 This result seems intuitive. If only species 1 (or 2) disappears, there remains $2(E + J)$ at-
 311 tributes. But if only species 3 disappears, the number of safe attributes decreases to a lower
 312 $2E + J$. In Appendix D.1, however, we show that the property emphasized in Proposition 2 is
 313 fragile. More precisely, it holds only when ecological interactions are not too strong (even if
 314 ecological interactions are not a source of heterogeneity).

315 **3.2.2 The influence of ecological interactions**

316 Incorporating this dimension in the model is an attempt to account for the complexities of the web
 317 of life. For instance, the interactions between two species can be considered unilateral, *e.g.* species
 318 1 impacts species 2 but not *vice versa*, or bilateral, *e.g.* species 1 impacts species 2 and species 2
 319 impacts species 1. In a two-species system, there are $2^2 = 4$ interaction possibilities to consider.
 320 As soon as one contemplates a three-species ecosystem, however, there are $3^3 = 27$ potential
 321 pairwise interactions between species (not even taking into account the added complexity that
 322 could be introduced by varying the intensity of each of these ecological interactions). It is evident
 323 that the number of interaction possibilities quickly explodes with the number of species in the
 324 system. In the face of this complexity, our strategy will be to focus on two illustrative cases of
 325 particular interest. To simplify matters, we assume that dissimilarities play no role and consider
 326 the simplest possible ecosystem.

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 Figure 5:

[insert Figure 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 :

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

327 Computing the biodiversity criteria reveals:

$$\mathcal{W}_{e_{R2}}(\mathbf{X}_1) - \mathcal{W}_{e_{R2}}(\mathbf{X}_2) = \frac{E\bar{x}}{1 - r_{12}r_{21}}(r_{21} - r_{12}), \quad (25)$$

$$\mathcal{R}_{e_{R2}}(\mathbf{X}_1) - \mathcal{R}_{e_{R2}}(\mathbf{X}_2) = \frac{2E\bar{x}(2q + \bar{x})}{(1 - r_{12}r_{21})^2}(r_{21} - r_{12}). \quad (26)$$

328 From these expressions we can establish the following proposition:

329 **Proposition 3** *Let the class of conservation problems be given by the list of parameters e_{R2} .*
 330 *The two criteria deliver the same ranking of policies \mathbf{X}_1 and \mathbf{X}_2 . They recommend preserving*
 331 *the species that has the largest marginal impact on the survival of the other species:*

$$\begin{aligned} \mathcal{W}_{e_{R2}}(\mathbf{X}_1) \begin{matrix} \geq \\ \leq \end{matrix} \mathcal{W}_{e_{R2}}(\mathbf{X}_2) &\Leftrightarrow r_{21} \begin{matrix} \geq \\ \leq \end{matrix} r_{12}, \\ \mathcal{R}_{e_{R2}}(\mathbf{X}_1) \begin{matrix} \geq \\ \leq \end{matrix} \mathcal{R}_{e_{R2}}(\mathbf{X}_2) &\Leftrightarrow r_{21} \begin{matrix} \geq \\ \leq \end{matrix} r_{12}. \end{aligned}$$

332 In this case, the two criteria recommend preserving the species that has the largest marginal
 333 effect on the survival probability of the other species, a result that confirms a previous finding
 334 from Baumgartner (2004a). Each criterion aims to maximize the survival probability of the
 335 ecosystem as a whole. This result can be illustrated using the principal categories of interactions
 336 between our two species.

337 i) *Predation*: species 2, a predator, feeds on species 1, its prey. By definition we have $r_{21} > 0$ and
 338 $r_{12} < 0$. Both criteria recommend preserving the prey - here species 1 - since its interaction
 339 coefficient is larger ($r_{12} < 0 < r_{21}$).

340 ii) *Mutualism*: species 1 and 2 have a positive impact on each other. By definition we have
 341 $r_{12} > 0$ and $r_{21} > 0$. Both criteria recommend preserving the species with the largest
 342 marginal benefit on the survival probability of the other species.

343 iii) *Competition*: species 1 and 2 rely on a common resource in the same territory that cannot
 344 fully support both populations. By definition we have $r_{12} < 0$ and $r_{21} < 0$. Both criteria
 345 recommend preserving the species with the lowest negative impact on the other species.

346 **Three-species ecosystem** When a third species is introduced, the impact of interactions on
 347 criteria recommendations is more difficult to study, as there is now an interplay of effects due
 348 to more complex interactions in the system. In order to illustrate this complexity we consider a
 349 simple ecosystem of three interacting species characterized by unilateral interactions. We assume
 350 a single species, say species 1, impacts the two other species, but these two species impact neither
 351 each other nor species 1. For example, species 1 is a predator that negatively impacts two preys,
 352 species 2 and 3, but does not rely on them to survive due to the availability of other food sources,
 353 *i.e.* $r_{i1} < 0$, $r_{i2} = r_{i3} = 0$. Species 1 could also be the prey of the two other species without
 354 being negatively impacted by them, *i.e.* $r_{i1} \geq 0$, $r_{i2} = r_{i3} = 0$.

355 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
 356 coefficients beside r_{21} and r_{31} are null. The phylogenetic tree associated with this three-species
 357 ultrametric ecosystem is depicted in Figure 6:

358

359 **[insert Figure 6.]**

360

361 Therefore, the only distinction between the three species in this case is how they interact.

362 Matrices \mathbf{Q} and \mathbf{R} become :

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

363 The relative performance of alternative policies is measured by:

$$\mathcal{W}_{e_{R3}}(\mathbf{X}_1) - \mathcal{W}_{e_{R3}}(\mathbf{X}_2) = E\bar{x}(r_{21} + r_{31}), \quad (27)$$

$$\mathcal{W}_{e_{R3}}(\mathbf{X}_1) - \mathcal{W}_{e_{R3}}(\mathbf{X}_3) = E\bar{x}(r_{21} + r_{31}), \quad (28)$$

$$\mathcal{W}_{e_{R3}}(\mathbf{X}_2) - \mathcal{W}_{e_{R3}}(\mathbf{X}_3) = 0, \quad (29)$$

$$\mathcal{R}_{e_{R3}}(\mathbf{X}_1) - \mathcal{R}_{e_{R3}}(\mathbf{X}_2) = 2E\bar{x} \begin{bmatrix} r_{21}r_{31}(2q + \bar{x}) \\ +r_{21}(3q + \bar{x}) \\ +r_{31}(2q + \bar{x}) \end{bmatrix}, \quad (30)$$

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

$$\mathcal{R}_{e_{R3}}(\mathbf{X}_2) - \mathcal{R}_{e_{R3}}(\mathbf{X}_3) = 2E\bar{x}q(r_{31} - r_{21}). \quad (32)$$

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

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

364 The above expressions (27) and (28) show that this is true iff $r_{21} + r_{31} > 0$, that is, if the
 365 cumulative impact of species 1 on the survival probability of the two other species is larger than
 366 the cumulative impact of these species on all other species (which is null here as we assume
 367 $r_{12} = r_{13} = r_{23} = r_{32} = 0$). This result confirms Proposition 3, as it recommends allocating
 368 conservation efforts to the species that is the most beneficial (or the least detrimental) to the
 369 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:

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

370 From expressions (30) and (31), this is true iff $r_{21}r_{31}(2q + \bar{x}) + r_{31}(2q + \bar{x}) + r_{21}(3q + \bar{x}) > 0$
 371 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
 372 impact on species 2 and 3, preservation effort is allocated to species 1. When either of the above
 373 inequalities do not hold, interpreting the criterion becomes more difficult. In this case, effort
 374 is then allocated to the species that is (negatively) impacted to a greater degree by species 1.
 375 Again we find a confirmation of the result presented in Proposition 3. However, the decision
 376 rule depicted here is no longer a simple additive formula, but a combination of additive and
 377 multiplicative components ($r_{21}r_{31}$), making interpretation challenging. Adding interrelations or
 378 additional species in the analysis greatly increases complexity through complementarities and
 379 multiplicative effects.

380 4 Interactions between effects

381 When heterogeneity arises from several dimensions at once, all of the previous criteria logics are
 382 mingled and interpreting the results becomes very challenging indeed. A fairly detailed analysis

383 for the interested reader is given in Appendix D. Here we briefly discuss a case in point. We let
384 species differ in both autonomous survival probabilities (the q_i s) and ecological interactions (the
385 r_{ij} s). Recall that, all else being equal, the Weitzman criterion tends to generate recommendations
386 that protect robust species that are *a priori* the least concerned by extinction (with the largest
387 q_i), whereas the Rao criterion generally favors fragile species likely to be the most threatened
388 species. On the other hand, on the basis of ecological interactions only, both criteria recommend
389 that conservation efforts be allocated to the species with the largest positive impact on the
390 ecosystem. Thus, an initial dissonance in rankings due to the q_i s can vanish if this ecological
391 interactions effect prevails. This is indeed the case and can be explored formally. See Appendix
392 D.3.

393 5 Summary and illustration

394 Considering a binary choice between investing in the conservation of one of two species (in an
395 ecosystem that may be larger than a two or three species one), and denoting these two species,
396 A and B , major results are summarized in Table 1:

	Weitzman Criterion	Rao Criterion
Survival probability (Q) If $A > B$, then	$A \succ B$	$B \succ A$
Attributes dissimilarity (D) If $A > B$, then	$A \succ B$	$A \succ B$
Species interaction (R) If $A > B$, then	$A \succ B$	$A \succ B$

Table 1: Criteria and species ranking

397 Abusing notations, we write $A > B$ when species A has a bigger survival probability
398 (respectively attributes dissimilarity or overall net positive impact on the ecosystem through
399 species interactions) than species B and $A \succ B$ when the criterion favors the protection of
400 species A . Rankings are provided everything else equal meaning that in line 1 for example,
401 we assume species A has a bigger survival probability than species B but the two species are
402 symmetric regarding any other aspects.

403 The criteria converge regarding attribute dissimilarity (**D**) and species interactions (**R**). Both
404 favor species contributing the more to the diversity of attributes contained in the ecosystem as
405 well as species that impart the most benefits or the least harm to the ecosystem. Conversely, the
406 criteria diverge regarding autonomous survival probability (**Q**) and therefore on how they value
407 the relative robustness of species. While Weitzman criterion recommends to preserve the species
408 which *a priori* are the least concerned with extinction, Rao criterion advocates the opposite,
409 recommending to dedicate conservation efforts to species the more likely to get threatened. For

410 conservation policy, it comes out that Weitzman criterion is a *triage* decision concept that seems
411 particularly appropriate for situations of massive extinction and limited conservation budget.
412 Conversely, the conservation philosophy underlying Rao's is to allocate funds toward the most
413 threatened species disregarding chances of success. It is therefore particularly appropriate if
414 budget is unlimited or if extinction is marginal.

415
416 We end the paper with an illustration of our results considering a larger parameter space.
417 Assume again an ecosystem composed of three species as described in Figure 7:

418
419 **[insert Figure 7.]**

420
421 where we arbitrarily consider $G = 50$, $J = 90$, $E_3 = 100$ and $E_1 = E_2 = 10$.¹³ By
422 assumption, species 3 is more distinctive than the two others. We study in the following the
423 binary choice of preserving one of two species composing this ecosystem by gradually adding
424 complexity in the parameter space. Let us first focus on species robustness (\mathbf{Q}) and analyze
425 the binary choice of either preserving species 1 or species 2 assuming for the moment that
426 $r_{ij} = 0, \forall i, j$. We set $q_3 = 0.4$ meaning that species 3 is vulnerable while autonomous survival
427 probability of species 1 and 2 may oscillate between 0 and 1, that is between the critically
428 endangered status to the least concerned status (IUCN species status is provided in Appendix
429 E).¹⁴ Isoquant curves are useful to illustrate how the two criteria value relative autonomous
430 survival probabilities.

431

432 **[insert Figure 8.]**

433

434 Darker grey zones depict higher criteria levels meaning that the higher the isoquant, the
435 higher the criterion value. Observe that Weitzman's isoquants are concave with a slope bigger
436 than -1 above the bisectrix. Rao's isoquants are convex with a slope lower than -1 above
437 the bisectrix. It follows that for reaching a superior isoquant, if $q_2 > q_1$ (*i.e.* above the
438 bisectrix line), Weitzman criterion recommends to invest in species 2 ($AB < AC$) while Rao's
439 recommends to invest in species 1 ($AC < AB$). Conversely, below the bisectrix, Weitzman's
440 recommends to invest in q_1 while Rao recommends to invest in q_2 . We confirm the result that
441 everything else equal, Weitzman's favors robust species while Rao's favors fragile ones.

442 Let us now increase complexity and illustrate how the two criteria value distinctiveness. As
443 species 3 is assumed more distinctive than the two others that share J common attributes,
444 we focus now on the binary choice to either protect species 1 or 3. Again, we assume no
445 interactions, $r_{ij} = 0 \forall i, j$, but now let oscillate q_1 and q_3 between 0 and 1. We assume q_2 is
446 either equal to 0.01 or 0.99, that is the canonical cases where species 2 is critically endangered
447 and least concerned by extinction. In the first case, as species 2 is almost extinct, species 1 is
448 almost as distinctive as species 3. In the second case, species 3 is more distinctive than species
449 1 as the J attributes are always secured by species 2. Isoquants for the two cases and the two

450 criteria are depicted in Figure 9 and 10.

451

452 **[insert Figure 9.]**

453

454 **[insert Figure 10.]**

455

456 We observe that when species 2 is least concerned by extinction (right graphs), the slope of
457 isoquants flattens making the two criteria favor the protection of species 3. Notice that here,
458 the impact of dissimilarity on criteria rankings outweighs the impact of autonomous survival
459 probability. Even if species 1 is fragile, the two criterion recommend here to preserve species 3
460 as the J attributes of species 1 will be brought by species 2. Interestingly, we observe that if
461 species 2 is almost extinct, that is species 1 and 3 are almost as dissimilar, we confirm previous
462 insights on autonomous survival probability.¹⁵

463

464 To end, we illustrate the impact of species interactions on recommendations made by the two
465 criteria. Considering again the binary choice between preserving species 1 or 2 and assuming
466 $q_3 = 0.4$, that is the parameter considered in the case depicted in Figure 8, we compare the no
467 interaction case ($r_{ij} = 0 \forall i, j$) and the predator-prey case where species 2 is the predator of
468 species 1 ($r_{12} = -0.5$ and $r_{21} = 0.3$, all remaining $r_{ij} = 0$). Isoquants for the two cases and the
469 two criteria are depicted in Figure 11 and 12.

470

471 **[insert Figure 11.]**

472

473 **[insert Figure 12.]**

474

475 Notice that introducing species interactions, here a predator prey relationship between species
476 2 and 1, both criterion's isoquants get steeper meaning that the preservation of species 1 becomes
477 more likely. This illustrate Proposition 3 according to the criteria tend to put conservation efforts
478 in the species that imparts the most benefits to the ecosystem. Here, species 1 is the prey and
479 it benefits the survival of species 2.

480 **6 Conclusion**

481 This paper modifies Weitzman's and Rao's biodiversity indices, incorporating information about
482 ecological interactions in order to render the models more suitable for *in situ* protection plans.
483 Using the resulting Weitzman's and Rao's *in situ* criteria, a simple framework allows us to
484 analyze and compare the recommended conservation plans. For each *in situ* criterion, we are
485 able to disentangle the role played by three factors: *i*) autonomous survival probabilities \mathbf{Q} ,

486 *ii*) ecological interaction **R** and, *iii*) dissimilarity **D**. We consider these factors both in strict
487 isolation and in combination.

488 The analysis generates three important outcomes:

- 489 1. The two criteria, originating from different academic fields, combine the pieces of informa-
490 tion **Q**, **R** and **D** in different ways in order to measure biodiversity. As a consequence, they
491 do not systematically deliver the same conservation recommendations. They disagree when
492 differences between species arises from autonomous survival probabilities, whereas they
493 largely agree when heterogeneity arises from dissimilarities and/or ecological interactions.
- 494 2. When ecological interactions matter for the ranking, the favored species is the one that
495 imparts the most benefits or the least harm to the ecosystem. In general, the introduction
496 of ecological interactions among more than two species can lead to complex conclusions.
- 497 3. When the three elements are combined, the policy advocated by each index reveals a specific
498 trade-off between **Q**, **R** and **D**.

499 From a practical point of view, an interesting follow-up to this research would be to consider
500 any number of species, among which only a subset can receive protection. The analytical inter-
501 pretation of the rankings in this case would probably be lost, but such an analysis does not seem
502 to pose any computational problems.

503 At a more fundamental level, further consideration should be given to the objective of con-
504 servation policies. Each biodiversity index is, by construction, a measure of a certain vision of
505 biodiversity and therefore of conservation. It is interesting to learn that, all else being equal, there
506 is a tendency for Weitzman's criterion to favor robust species, and for Rao's criterion to favor
507 fragile ones. Using one criterion versus the other depends on the policy perspective we adopt. If
508 budget is large and we have the opportunity to save a large range of species, Rao's criterion is
509 certainly the most appropriate. If budget is limited and extinction is drastic as in Noah's Ark
510 paradigm, Weitzman's criterion is to be taken seriously into consideration. In order to arrive at
511 a unique policy solution, it will be necessary to develop a criterion for selecting among biodiver-
512 sity indices themselves. The present paper demonstrates that such a criterion would essentially
513 determine the trade-off made between robust and fragile species in conservation management.

514 Appendix

515 **A The system of interdependent probabilities**

516 Solving the system (2) of ecological interactions for P_1, P_2 and P_3 as functions of $\mathbf{X} = (x_1, x_2, x_3)^T$ gives
517 :

$$P_1(\mathbf{X}) = \frac{(q_1 + x_1)(1 - r_{23}r_{32}) + (q_2 + x_2)(r_{12} + r_{13}r_{32}) + (q_3 + x_3)(r_{12}r_{23} + r_{13})}{1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}} \quad (33)$$

$$P_2(\mathbf{X}) = \frac{(q_2 + x_2)(1 - r_{13}r_{31}) + (q_1 + x_1)(r_{21} + r_{31}r_{23}) + (q_3 + x_3)(r_{21}r_{13} + r_{23})}{1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}} \quad (34)$$

$$P_3(\mathbf{X}) = \frac{(q_1 + x_1)(r_{31} + r_{32}r_{21}) + (q_2 + x_2)(r_{12}r_{31} + r_{32}) + (q_3 + x_3)(1 - r_{12}r_{21})}{1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}} \quad (35)$$

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

In vector notations, probabilities as functions of efforts are:

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

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

522 **B Three-species Weitzman's criterion for in situ protection**
523 **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:

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

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

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

524 Using (33), (34) and (35), we obtain the following value for a vector of effort \mathbf{X} :

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

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

526 C Three-species Rao's criterion for *in situ* protection when dis- 527 tances are ultrametric

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

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

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:

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

530 Using system (33), (34), and (35), the value of the criterion for a vector of effort \mathbf{X} is:

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

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

532 D Interactions between effects

533 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:

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

534 The relative performance of policies can be deduced from:

$$\mathcal{W}_{e_{qJ}}(\mathbf{X}_1) - \mathcal{W}_{e_{qJ}}(\mathbf{X}_2) = \frac{J\bar{x}}{(1+r)^2} (q_1 - q_2), \quad (36)$$

$$\mathcal{W}_{e_{qJ}}(\mathbf{X}_1) - \mathcal{W}_{e_{qJ}}(\mathbf{X}_3) = \frac{J\bar{x} [r(q_1 + q_3 + x) + q_2(1-r)]}{(1+r)^2(2r-1)}, \quad (37)$$

$$\mathcal{W}_{e_{qJ}}(\mathbf{X}_2) - \mathcal{W}_{e_{qJ}}(\mathbf{X}_3) = \frac{J\bar{x} [r(q_2 + q_3 + x) + q_1(1-r)]}{(1+r)^2(2r-1)}, \quad (38)$$

$$\mathcal{R}_{e_{qJ}}(\mathbf{X}_1) - \mathcal{R}_{e_{qJ}}(\mathbf{X}_2) = \frac{2E\bar{x}}{(1+r)^2} (q_2 - q_1), \quad (39)$$

$$\begin{aligned} \mathcal{R}_{e_{qJ}}(\mathbf{X}_1) - \mathcal{R}_{e_{qJ}}(\mathbf{X}_3) &= \frac{2J\bar{x} [r(3q_3 - q_1 - q_2) + r\bar{x} - (q_3 - q_1 - q_2)]}{(1+r)^2(2r-1)} \\ &\quad + \frac{2E\bar{x}}{(1+r)^2} (q_3 - q_1), \end{aligned} \quad (40)$$

$$\begin{aligned} \mathcal{R}_{e_{qJ}}(\mathbf{X}_2) - \mathcal{R}_{e_{qJ}}(\mathbf{X}_3) &= \frac{2J\bar{x} [r(3q_3 - q_1 - q_2) + r\bar{x} - (q_3 - q_1 - q_2)]}{(1+r)^2(2r-1)} \\ &\quad + \frac{2E\bar{x}}{(1+r)^2} (q_3 - q_2). \end{aligned} \quad (41)$$

535

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

538 The conclusions are more nuanced when a third species is introduced, and they depend on the im-
539 portance of ecological interactions: Weitzman's index favors species 3 only if $r < 1/2$ ¹⁶. In other words,
540 dissimilarity prevails when ecological interactions are not too strong. The conclusion is even more complex
541 when it comes to Rao's index. Whatever the recommendation, it is reversed when r crosses the value $1/2$.
542 As a particular case, now let the autonomous probabilities of survival be identical. The relative policy

543 performances (36) to (41) simplify to:

$$\mathcal{W}_{e'_{qJ}}(\mathbf{X}_1) - \mathcal{W}_{e'_{qJ}}(\mathbf{X}_2) = 0, \quad (42)$$

$$\mathcal{W}_{e'_{qJ}}(\mathbf{X}_1) - \mathcal{W}_{e'_{qJ}}(\mathbf{X}_3) = \frac{J\bar{x}[r(q+\bar{x})+q]}{(1+r)^2(2r-1)}, \quad (43)$$

$$\mathcal{W}_{e'_{qJ}}(\mathbf{X}_2) - \mathcal{W}_{e'_{qJ}}(\mathbf{X}_3) = \frac{J\bar{x}[r(q+\bar{x})+q]}{(1+r)^2(2r-1)}, \quad (44)$$

$$\mathcal{R}_{e'_{qJ}}(\mathbf{X}_1) - \mathcal{R}_{e'_{qJ}}(\mathbf{X}_2) = 0, \quad (45)$$

$$\mathcal{R}_{e'_{qJ}}(\mathbf{X}_1) - \mathcal{R}_{e'_{qJ}}(\mathbf{X}_3) = \frac{2J\bar{x}[r(q+\bar{x})+q]}{(1+r)^2(2r-1)}, \quad (46)$$

$$\mathcal{R}_{e'_{qJ}}(\mathbf{X}_2) - \mathcal{R}_{e'_{qJ}}(\mathbf{X}_3) = \frac{2J\bar{x}[r(q+\bar{x})+q]}{(1+r)^2(2r-1)}. \quad (47)$$

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

547 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:

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

548 The relative policy performances can be deduced from:

$$\mathcal{W}_{e_{RJ}}(\mathbf{X}_1) - \mathcal{W}_{e_{RJ}}(\mathbf{X}_2) = \bar{x} \frac{(E+J)(1-r_{12}r_{21}) - J(2q+\bar{x})}{(1-r_{12}r_{21})^2} (r_{21} - r_{12}), \quad (48)$$

$$\mathcal{W}_{e_{RJ}}(\mathbf{X}_1) - \mathcal{W}_{e_{RJ}}(\mathbf{X}_3) = \bar{x}(E+J) \frac{(1+r_{12}-r_{12}r_{21}-r_{12}^2r_{21})r_{21}}{(1-r_{12}r_{21})^2} \quad (49)$$

$$- \bar{x}J \frac{(r_{12}q + 2q + \bar{x})r_{21} + q}{(1-r_{12}r_{21})^2}, \quad (50)$$

$$\mathcal{W}_{e_{RJ}}(\mathbf{X}_2) - \mathcal{W}_{e_{RJ}}(\mathbf{X}_3) = \bar{x}(E+J) \frac{(1+r_{21}-r_{12}r_{21}-r_{12}r_{21}^2)r_{12}}{(1-r_{12}r_{21})^2} \quad (51)$$

$$- \bar{x}J \frac{(r_{21}q + 2q + \bar{x})r_{12} + q}{(1-r_{12}r_{21})^2}, \quad (52)$$

$$(53)$$

$$\mathcal{R}_{e_{RJ}}(\mathbf{X}_1) - \mathcal{R}_{e_{RJ}}(\mathbf{X}_2) = \frac{2E\bar{x}(2q + \bar{x})}{(1 - r_{12}r_{21})^2}(r_{21} - r_{12}), \quad (54)$$

$$\mathcal{R}_{e_{RJ}}(\mathbf{X}_1) - \mathcal{R}_{e_{RJ}}(\mathbf{X}_3) = 2\bar{x}(E + J) \frac{q(r_{12}r_{21}^2 + r_{12}^2r_{21} + 2r_{12}r_{21} - r_{12} - 1)}{(1 - r_{12}r_{21})^2} \quad (55)$$

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

$$\mathcal{R}_{e_{RJ}}(\mathbf{X}_2) - \mathcal{R}_{e_{RJ}}(\mathbf{X}_3) = 2\bar{x}(E + J) \frac{q[r_{12}r_{21}^2 + r_{12}^2r_{21} + 2r_{12}r_{21} - r_{21} - 1]}{(1 - r_{12}r_{21})^2} \quad (57)$$

$$+ 2\bar{x} \frac{Er_{12}(qr_{21} + q + \bar{x}) - Jq(1 + r_{12})}{(1 - r_{12}r_{21})^2}. \quad (58)$$

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

559 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:

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

560 Computations for rankings of species 1 and 2 yield:

$$\begin{aligned}
\mathcal{W}_{e_{qR}}(\mathbf{X}_1) - \mathcal{W}_{e_{qR}}(\mathbf{X}_2) &= J \frac{\bar{x}(1 + r_{12}r_{21})}{(1 - r_{12}r_{21})^2} (q_1 - q_2) \\
&+ J \frac{2\bar{x}}{(1 - r_{12}r_{21})^2} (q_2r_{12} - q_1r_{21}) \\
&+ \frac{\bar{x}[(E + J)(1 - r_{12}r_{21}) - J\bar{x}]}{(1 - r_{12}r_{21})^2} (r_{21} - r_{12}) ,
\end{aligned} \tag{59}$$

$$\begin{aligned}
\mathcal{R}_{e_{qR}}(\mathbf{X}_1) - \mathcal{R}_{e_{qR}}(\mathbf{X}_2) &= \frac{2E\bar{x}(1 + r_{12}r_{21})}{(1 - r_{12}r_{21})^2} (q_2 - q_1) \\
&- \frac{4E\bar{x}}{(1 - r_{12}r_{21})^2} (q_2r_{12} - q_1r_{21}) \\
&+ \frac{2E\bar{x}^2}{(1 - r_{12}r_{21})^2} (r_{21} - r_{12}) .
\end{aligned} \tag{60}$$

561 Of course, when $r_{21} = r_{12} = r$, one again finds the results presented in Section 3.1.1. Recall that using
562 the Weitzman index generates a recommendation to protect the strongest species (i.e. the species with
563 the largest q_i), whereas using the Rao index generates a recommendation to protect the weakest species
564 (Proposition 1). As soon as $r_{21} \neq r_{12}$, these results must be qualified. They now become more complex
565 functions of not only the q_i s, but also the r_{ij} s. In order to grasp these qualifications, imagine that
566 species 1 is the strongest species ($q_1 > q_2$). We know from Proposition 1 that, when $r_{21} = r_{12} = r$, the
567 Weitzman index (respectively Rao index) suggests that species 1 (resp. species 2) should be protected.
568 Now, imagine that $r_{21} = 0 < r_{12}$. On this basis alone, if q_1 and q_2 were identical, both Weitzman and
569 Rao would prioritize species 2 (see Proposition 3). However, if $q_1 > q_2$, from expressions (59) and
570 (60) Rao clearly recommends species 2, whereas Weitzman's conclusion is ambiguous. Eventually the
571 conclusion reveals a trade-off between two opposite effects, and this trade-off depends, among other
572 things, on the importance of J and the number of common "genes" between species 1 and 2. Under
573 different circumstances, Rao's ranking can also be ambiguous. Assume that $r_{21} = 0 < r_{12}$ and $q_1 < q_2$.
574 In this case, Weitzman clearly prioritizes species 2. Rao's ranking, on the other hand, embodies two
575 opposing logics, one in favor of species 2 (the more ecologically beneficial), and the other in favor of
576 species 1 (the weakest species). The final choice will reveal Rao's trade-off between these opposing forces.
577 As can be deduced from expression (60), contrary to Weitzman's trade-off, Rao's conclusion does not
578 depend on J .

579

580 E IUCN species extinction status

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

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

Table 2: IUCN species extinction status. Sources: <http://www.iucnredlist.org/> and Mooers et al. (2008)

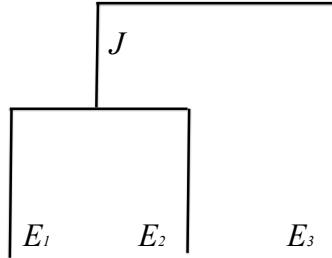


Figure 1: Three species phylogenetic tree

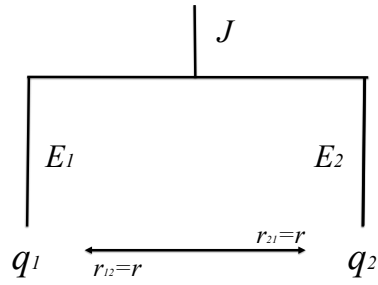


Figure 2: Two-species ultrametric tree with $J > 0$

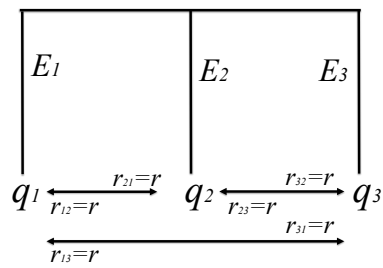


Figure 3: Three-species ultrametric case with $J = 0$

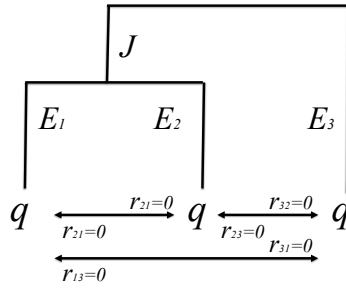


Figure 4: Three-species ultrametric case with $J > 0$

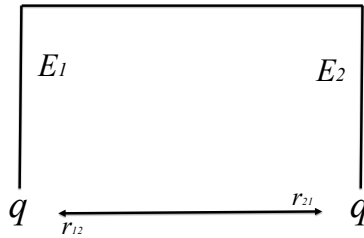


Figure 5: Two-species ultrametric case with $J = 0$

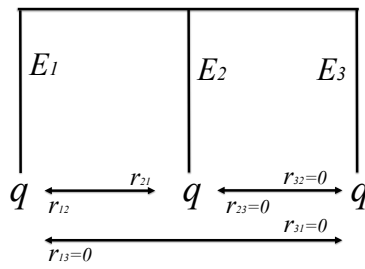


Figure 6: Three-species ultrametric case with $J = 0$

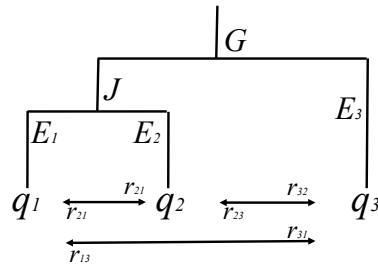


Figure 7: Three-species ultrametric case with $J > 0$ and $G > 0$

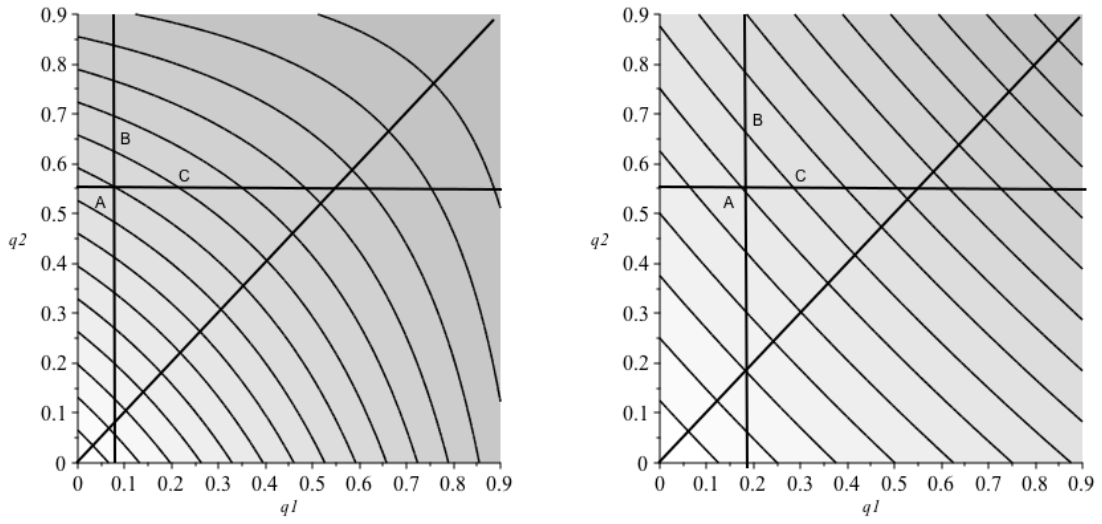


Figure 8: Isoquants : Weitzman (left), Rao (right)

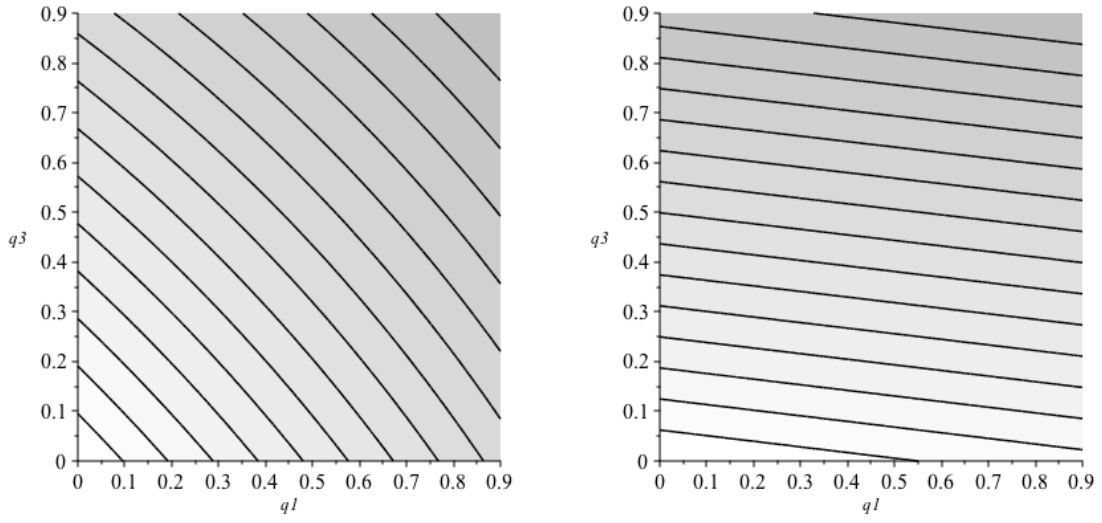


Figure 9: Weitzman's criterion Isoquants : $q_2 = 0.01$ (left), $q_2 = 0.99$ (right)

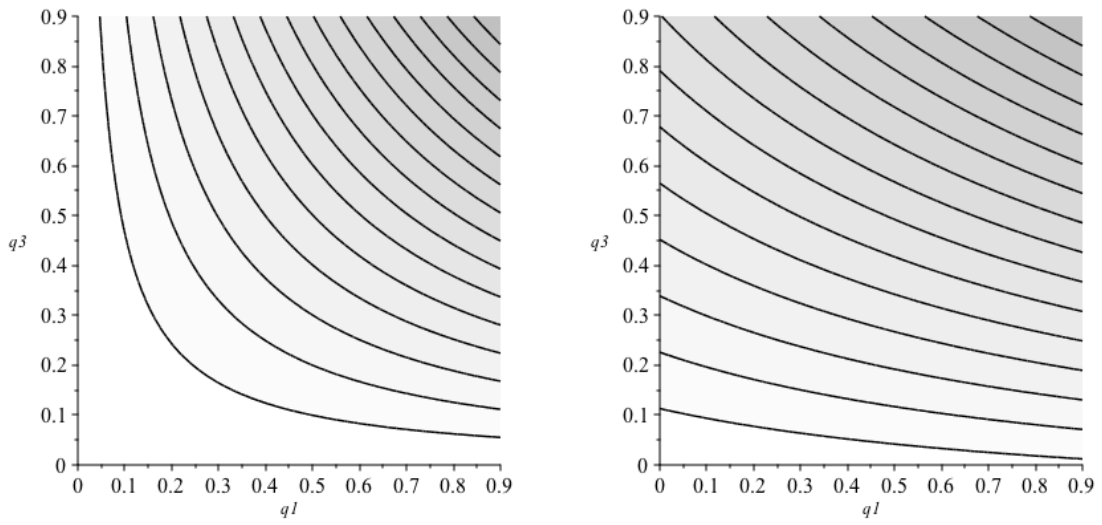


Figure 10: Rao's criterion Isoquants : $q_2 = 0.01$ (left), $q_2 = 0.99$ (right)

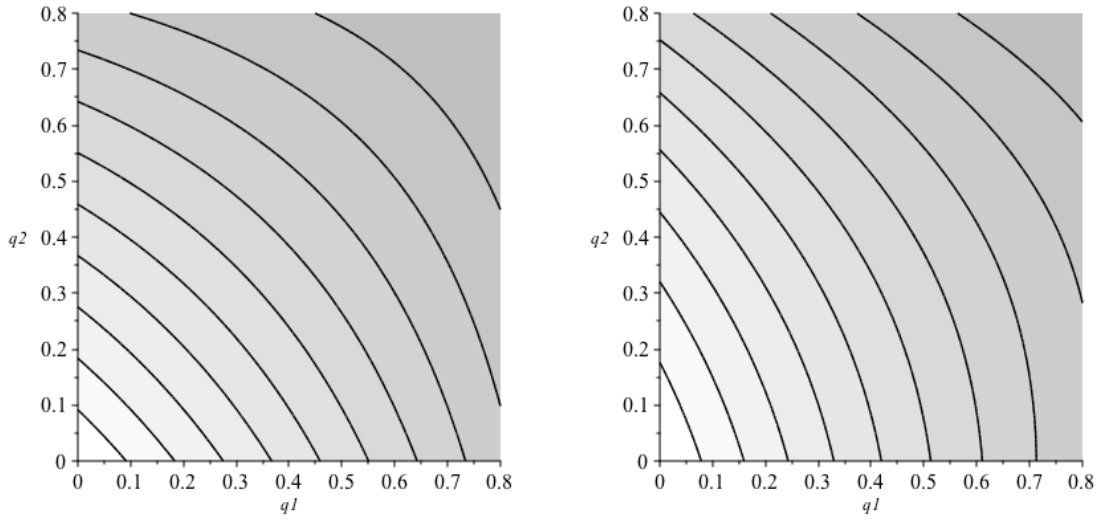


Figure 11: Weitzman's criterion Isoquants : no interaction case (left), predator-prey case (right)

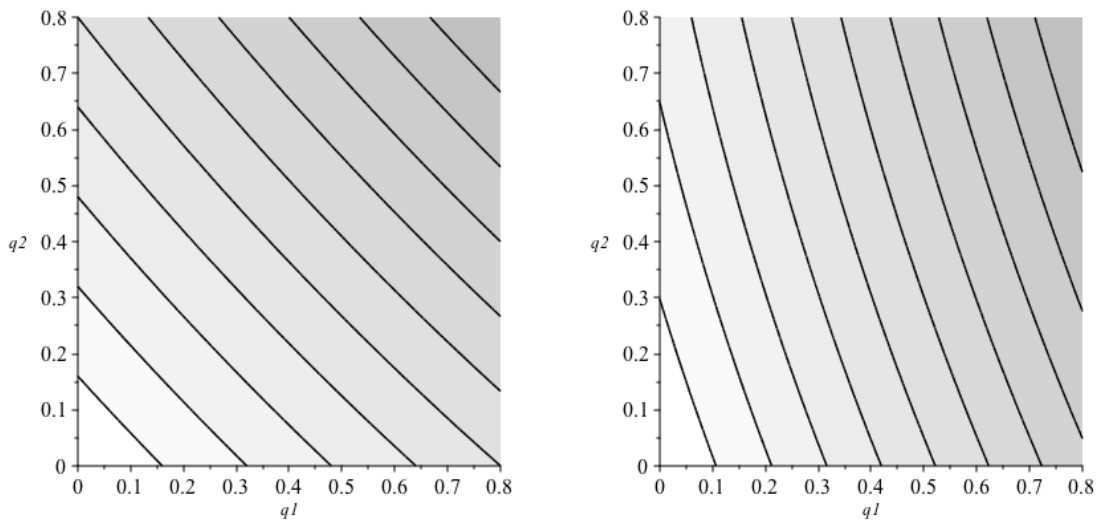


Figure 12: Rao's criterion Isoquants : no interaction case (left), predator-prey case (right)

588 **Notes**

589 ¹see <https://www.environment.gov.au/>

590 ²Regarding species prioritization and related debates about conservation choices, the reader may refer to
 591 Wilson et al. (2011), Joseph et al. (2011), Carwardine et al. (2012), Schultz et al. (2013), Courtois et al. (2014,
 592 2018), Bennett et al. (2014), Frew et al. (2016), Gerber (2016), or Lacona et al. (2017), among others.
 593

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

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

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

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

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

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

614 ⁹Note that one must ensure that the result is between 0 and 1. Two possible strategies can satisfy this
615 requirement: 1) assuming that estimates of the model parameters in real-world scenarios naturally guarantee this
616 condition, 2) identifying an upper bound for conservation efforts that guarantees this property. An algorithm
617 exists for this purpose. It is available from the authors on request.

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

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

624 ¹²Ultrametrism here means that $E_1 + J = E_2 + J$

625 ¹³Computation sheets are available upon request.

626 ¹⁴Note that as we focus here on the choice of investing either in species 1 or 2 and because we do not consider
627 yet any interactions, the survival probability of species 3 does not affect the ranking - we could assume q_3 to be
628 any value between 0 and 1.

629 ¹⁵Weitzman criterion is almost indifferent between preserving the two species as G is small making efforts
630 almost perfectly substitutable.

631 ¹⁶Note that the system of interdependent probabilities (2) cannot be solved when $r = 1/2$.

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