Conservation priorities when species interact: the Noah's Ark Metaphor revisited

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Abstract

This note incorporates ecological interactions into the Noah's Arch problem [M.L. Weitzman, The Noah's Arch problem, Econometrica 66(6) (1998) 1279-1298]. In doing so, we arrive at a general model for ranking *in situ* conservation projects accounting for species interrelations and provide an operational cost-effectiveness method for the selection of best preserving diversity projects under a limited budget constraint.

Keywords: conservation priorities, ecological interactions, biodiversity, Weitzman ranking criterion.

JEL Classification: C6, Q5.

1 Introduction

Weitzman (1998) is a milestone in the economic theory of biodiversity. His "Noah's Arch problem" is not only a modeled metaphor that is helpful to organize thinking on how to face conservation trade-offs with finite resources. It also results in a practical cost-effectiveness methodology that can serve as inspiration to guide conservation policies. The idea is, for each species i, to collect information about: *i)* C_i, the cost of its protection, *ii)* ΔP_i, the increase of survival probability resulting from it, *iii)* U_i, the direct utility of how much we value the species, *iv)* D_i, its distinctiveness. From this information, each species is assigned a number R^i *via* the formula:

$$R^i = \frac{\Delta P_i}{C_i}\left(D_i + U_i\right) \ , \tag{1}$$

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which indicates its rank in conservation priorities. This ranking criterion has a theoretical foundation: it is rooted in a rigorous optimization model (Weitzman, 1998, Theorem 4, p. 1295).

While the criterion sheds light on real biodiversity issues and has actually been used in several applications[1], it is fair to say that it is more appropriate for *ex situ* conservation projects - say to build a gene bank or a zoo - rather than to manage a set of interacting species in their natural habitats. This is so because formula (1) uses no information of any kind about the web of life. Yet, in ecosystems, species interact. Some of them compete to share common resources, others develop synergies and mutually enhance each other or they simply pertain to the same trophic chain. Suppose, then, that the conservation authority has information about those ecological interactions, even if it is only under the rudimentary form of probability interdependencies. That is, it knows that a marginal increase of survival probability of species j will have an impact r_{ij} on the survival probability of species i. Could this information be used to qualify formula (1) and increase its relevance when it comes to *in situ* conservation trade-offs?

To our knowledge, three recent articles stress the need to account for ecological interactions in Weitzman's diversity concept. They have in common: *i*) to take into account the ecological interactions *via* interdependent survival probabilities in a simplified version of the Noah's Ark metaphor with two species (Baumgartner, 2004, Simanier 2008) or three species (van der Heide, van den Bergh and van Ierland, 2005), *ii*) to show that this consideration can reverse the conservation priorities.

The key of this note is to provide a general analysis of *in situ* conservation problems considering interdependent survival probabilities. Revisiting Weitzman's optimization problem, we extend his model in order to incorporate species interactions. Our principal output is to forward a general ranking formula that could be used as a rule of thumb for deciding *in situ* conservation priorities under a limited budget constraint.

The sketch of the paper is the following. Section 2 incorporates ecological interactions in Weitzman's parable of Noah's Arch, with any arbitrary number of species. The crux of the section is to provide with a new rule for establishing *in situ* conservation priorities through the expression (11) below that encompasses formula (1) as a special case. The link between this formula and Noah's optimal policy is explained. Section 3 illustrates the relevance of this new formula within a two-species example. We end this last section with a discussion on the possibility of ranking reversal in relation to three stylized kinds of ecological interactions: *predation*, *mutualism* and *competition.*

2 The Noah's Arch metaphor revisited

2.1 Introducing ecological interactions

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[1] see Eppink & van den Bergh (2007), in particular Section 3.1 on cost-effectiveness models and the various references therein

In the initial version of Weitzman's modeled allegory, Noah's decision problem is, for each species i, to choose a survival probability between a lower and an upper bound, $P_i \in \left[\underline{P}_i, \overline{P}_i\right]$, in order to maximize the sum of the *expected number of distinct genes:*

$$W\left(\{P_i\}_{i=1}^{k}\right),$$

and the *expected utility of the set of species:*

$$U\left(\{P_i\}_{i=1}^{k}\right) = \sum_{i=1}^{k} U_i * P_i \ .$$

Weitzman devotes much of his paper to define function $W\left(\{P_i\}_{i=1}^{k}\right)$ and to explain its link with the concept of information content (see his Theorem 1, p. 1284). We remain agnostic about the exact nature of this diversity function. Several functions exists and could be used. Those we study in the present paper are C^2 functions. Importantly, we consider the class of expected diversity functions with Hessian matrices that are *not* negative semi-definite. Weitzman's expected diversity function belongs to this class of functions. It encompasses - but is not limited to - functions W with a positive definite Hessian matrix, *i.e.* that are strictly convex functions.

Now let us take a step away from this initial metaphor, towards reality. Two modifications are brought into the formalism. First, rather than controlling directly the probability of survival P_i of each species $i = 1, ..., k$, Noah can exert a protection effort within an admissible range, $x_i \in [0, \overline{x}_i]$, which is interpreted as the controlled increase of survival probability P_i - say that x_i is the increase of survival probability for species i resulting from a protection effort, *e.g.* an investment in a vaccination campaign. It is important to distinguish the effort from the variation of survival probability because P_i is also determined by other factors, for there are ecological interactions among species. And this is where our second, most important, qualification appears: probabilities of survival are interdependent and Noah may have this information. Nowadays he can rely on the knowledge gained from the new and booming literature on *conservation biology*, as well as the two subfields on *species distribution models* and *population viability analysis*[2]. A group of experts can measure the marginal impact, say r_{ih}, that an increase in the probability of survival of a species h can have on the probability of survival of another species i. The experts can also appraise the impact of protection efforts on these probabilities. Assume, then, that a tractable approximation of all those pieces of information can be summarized by the system (2) of linear equations:

$$P_i = q_i + x_i +_{h \neq i} r_{ih} \ P_h \ , \quad q_i \in [0, 1[\ , \quad x_i \in [0, \overline{x}_i] \, . \tag{2}$$

The *admissible ranges of efforts*, $\times_{i=1}^{k} [0, \overline{x}_i]$, are those for which the solutions

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[2] See for instance Burgman, Ferson and Akcakaya (1993), Witting, Tomiuk & Loeschcke (2000), Guisan and Thuillier (2005), or Elith and Leathwick (2009) for a recent overview.

of the above system of equations can be interpreted as probabilities:

$$P_i \in \Pi_i = \left[\underline{\Pi}_i, \overline{\Pi}_i\right] \sqsubseteq [0,1]\,, \quad \forall i\ ,\ \forall\ x_i \in [0, \overline{x}_i]\ .$$

We denote $\underline{P}_i$ as the natural survival probability of species i, without any human intervention, $x_i = 0$. In the absence of natural interactions, which corresponds the case studied by Weitzman, we have $r_{ih} = 0, \forall i, \forall h$. A consequence is that in the most extreme case with no ecological interactions and no human intervention, species i has a probability of survival q_i, which could also be zero. The survival probabilities interval, without ecological interactions, would thus take values ranging from $\underline{P}_i = q_i$ to $\overline{P}_i = \underline{P}_i + \overline{x}_i$.

Noah also has to cope with a budget constraint:

$$\sum_{i=1}^{k} \frac{C_i}{\Delta P_i} * x_i \leq B\ , \tag{3}$$

where $\Delta P_i = \overline{\Pi}_i - \underline{\Pi}_i$ is the potential increase in survival probability, B is the total budget to be allocated to conservation - metaphorically, the size of the Arch - and $C_i/\Delta P_i$ is the cost per unit of increase of survival probability in the range $\overline{\Pi}_i - \underline{\Pi}_i$. An interesting remark is in order: except when ecological interactions are negligible, Noah can increase the probability of survival of any species i *via* two different channels: a direct one by increasing the protection effort x_i, at a cost $(C_i/\Delta P_i) * x_i$, and an indirect one through ecological interactions, due to the protection of another species j, with a cost $(C_j/\Delta P_j) * x_j$.

Noah's ark problem, when ecological interactions are taken into account, is then:

$$\max_{\{x_i\}_{i=1}^k \in\ \times_{i=1}^k [0, \overline{x}_i]} W\left(\{P_i\}_{i=1}^k\right) + U\left(\{P_i\}_{i=1}^k\right)\ , \tag{4}$$

subject to (2) and (3).

It will be convenient in the sequel to work with matrix expressions, written in bold characters. For any matrix $\mathbf{M}$, $\det(\mathbf{M})$ denotes its determinant, $\mathrm{adj}(\mathbf{M})$ its adjugate, $\mathbf{M}^\top$ its transpose. Besides, $\mathbf{I}^k$ is the $(k \times k)$ identity matrix, ι^k is the k dimensional column vector whose elements are all 1, and we recall the following definition of inequality between two k-dimensional vectors m and n: $m \leqq n$ if $m_i \leq n_i$, for all $i = 1, ..., k$.[3]

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[3] The other basic relationships between vectors are: *i)* $m = n$ if $m_i = n_i$, for all $i = 1, ..., k$, *ii)* $m < n$ if $m_i < n_i$, for all $i = 1, ..., k$, *iii)* $m \leq n$ if $m_i \leq n_i$, for all $i = 1, ..., k$, and $m \neq n$.

Let us define:

$$\begin{aligned}
\mathbf{Q} &\equiv \begin{bmatrix} q_1 \\ q_2 \\ \vdots \\ q_k \end{bmatrix}, \ \mathbf{R} \equiv \begin{bmatrix} 0 & r_{12} & ... & r_{1k} \\ r_{21} & 0 & ... & r_{2k} \\ ... & ... & \ddots & \vdots \\ r_{k1} & r_{k2} & ... & 0 \end{bmatrix}, \ \mathbf{P} \equiv \begin{bmatrix} P_1 \\ P_2 \\ \vdots \\ P_k \end{bmatrix}, \ \beta \equiv \begin{bmatrix} C_1/\Delta P_1 \\ C_2/\Delta P_2 \\ \vdots \\ C_k/\Delta P_k \end{bmatrix} \\
\overline{\mathbf{P}} &\equiv \begin{bmatrix} \overline{P}_1 \\ \overline{P}_2 \\ \vdots \\ \overline{P}_k \end{bmatrix}, \quad \underline{\mathbf{P}} \equiv \begin{bmatrix} \underline{P}_1 \\ \underline{P}_2 \\ \vdots \\ \underline{P}_k \end{bmatrix}, \quad \mathbf{X} \equiv \begin{bmatrix} x_1 \\ x_2 \\ \vdots \\ x_k \end{bmatrix}, \quad \overline{\mathbf{X}} \equiv \begin{bmatrix} \overline{x}_1 \\ \overline{x}_2 \\ \vdots \\ \overline{x}_k \end{bmatrix}.
\end{aligned}$$

In matrix form, the system (2) reads as:

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

If $\mathbf{I}^k - \mathbf{R}$ is invertible, solving this matrix equation one finds:

$$\mathbf{P} = \mathbf{\Lambda}\left(\mathbf{Q} + \mathbf{X}\right), \tag{5}$$

where $\mathbf{\Lambda} \equiv \left[\mathbf{I}^k - \mathbf{R}\right]^{-1}$.

Let $\mathcal{P}\left(\mathbf{X}\right) \equiv \mathbf{\Lambda}\left(\mathbf{Q} + \mathbf{X}\right)$ refer to the affine mapping from efforts to probabilities. Natural survival probabilities without protection policies are therefore:

$$\underline{\mathbf{P}} = \mathcal{P}\left(0 * \iota^{\mathbf{k}}\right) \ . \tag{6}$$

Without ecological interactions, $\mathbf{\Lambda}$ is the identity matrix, $\underline{\mathbf{P}} = \mathbf{Q}$ and $\overline{\mathbf{P}} = \underline{\mathbf{P}} + \overline{\mathbf{X}} = \mathbf{Q}+\overline{\mathbf{X}}$.

Now we can plug (5) into (4) to get rid of probabilities, and express Noah's problem only in terms of efforts. Define the two composite functions:

$$\begin{aligned}
W \circ \mathcal{P}\left(\mathbf{X}\right) &\equiv W\left(\mathcal{P}\left(\mathbf{X}\right)\right), \\
U \circ \mathcal{P}\left(\mathbf{X}\right) &\equiv U\left(\mathcal{P}\left(\mathbf{X}\right)\right).
\end{aligned}$$

Noah's problem expressed as a function of protection efforts $\mathbf{X}$ is then:

$$\max_{\mathbf{X}} W \circ \mathcal{P}\left(\mathbf{X}\right) + U \circ \mathcal{P}\left(\mathbf{X}\right), \tag{7}$$

subject to:

$$\begin{aligned}
\beta^{\top}\mathbf{X} &\leq B \ , \qquad (8) \\
0 * \iota^{\mathbf{k}} &\leqq \mathbf{X} \leqq \overline{\mathbf{X}} \ . \qquad (9)
\end{aligned}$$

Two questions arise: *i*) could anything general be said about the solution to problem (7), (8), (9)? And *ii*), taking a more practical stance, could we engineer a simple rule that approximates the general solution?

Regarding the first question, the key is to generalize a property already established in Weitzman (1998) who showed that the solution to Noah's problem when probabilities are independent lies on borders except for at most one decision variable. In other words, the optimal protection policy is *extreme*, in the sense of giving full protection to a subset of species, partial protection for at most one species, and exposing remaining species to the risk of minimal (or no) protection. But what if probabilities are interdependent?

Theorem 1 *Suppose* $\mathbf{I}^k - \mathbf{R}$ *is invertible. The solution to Noah's Arch problem with ecological interactions, defined by (7), (8) and (9), is an extreme policy.*

Proof. See Appendix A. ■

2.2 A myopic ranking rule for interacting species

Theorem 1 is a qualitative result, that does not indicate which species should be granted protection and why. This brings us to our second question; it would be welcome to have an explicit and easy-to-use approximation of the general solution. Facing the same problem, this is the practical point of view adopted by Weitzman (1998), which he describes as "the main theme" of his paper (p. 1294). His formula (1) offers a ranking that is not really a solution to the original problem, but rather a first order approximation of an optimal policy. In order to achieve this, he replaces the objective function by its linear approximation. He then obtains a classical linear programming problem, whose solution is to assign grades R_i given by formula (1) to species (those grades depend on the model parameters) and embark them in decreasing order of importance up to the point where the budget is exhausted. Those grades are exactly the practical ranking Noah is looking for.

We follow the same approach here, *i.e.* we linearize the objective function. The astute reader knows that, in general, such approximations can be seriously misleading (Baumol and Bushnell, 1967) and should not be followed blindly. Nevertheless, as proven in Theorem 2 below, there is something special about Noah's problem that makes this practice appropriate here, in a sense to be made precise.

Let us denote:

$$D_i \equiv \left.\frac{\partial W}{\partial P_i}\right|_{\mathbf{P}=\underline{\mathbf{P}}}, \quad U_i \equiv \left.\frac{\partial U}{\partial P_i}\right|_{\mathbf{P}=\underline{\mathbf{P}}},$$

and define the two matrices:

$$\mathbf{A} \equiv \begin{bmatrix} D_1 + U_1 \\ D_2 + U_2 \\ \vdots \\ D_k + U_k \end{bmatrix}, \quad \mathbf{\Upsilon} \equiv \mathbf{A}^\top \mathbf{\Lambda}.$$

From simple calculations, the linearized problem in matrix form turns out to be:

$$\max_{\mathbf{X}} \ \mathbf{\Upsilon X} + \text{ constant terms,} \tag{10}$$

subject to (8) and (9).

As can be observed in the above approximation of Noah's problem, the introduction of ecological interactions changes the "slope" of the objective function to be maximized, which is now $\boldsymbol{\Upsilon} \equiv \mathbf{A}^{\top}\boldsymbol{\Lambda}$ instead of just $\mathbf{A}^{\top}$. The crux, from the point of view of the present note, is to transform the information about ecological interactions conveyed by matrix $\mathbf{R}$, into operational data *via* the matrix $\boldsymbol{\Lambda}$:

$$\boldsymbol{\Lambda} = \left[\mathbf{I}^k - \mathbf{R}\right]^{-1} = \frac{1}{\det\left(\mathbf{I}^k - \mathbf{R}\right)} * \operatorname{adj}\left(\mathbf{I}^k - \mathbf{R}\right) \ .$$

When $\mathbf{I}^k - \mathbf{R}$ is invertible, the computation of the matrix $\boldsymbol{\Lambda}$ is easily made and if Λ_{ij} denotes a typical element of $\boldsymbol{\Lambda}$, then $\boldsymbol{\Upsilon}$ is a k-dimensional line vector of the type:

$$\boldsymbol{\Upsilon} = \left[\sum_{h=1}^{k}\left(D_h + U_h\right)\Lambda_{h1} \ , \ \sum_{h=1}^{k}\left(D_h + U_h\right)\Lambda_{h2} \ , \ \ldots, \ \sum_{h=1}^{k}\left(D_h + U_h\right)\Lambda_{hk}\right]$$

Let

$$\begin{aligned} \alpha_i &\equiv \sum_{h=1}^{k}\left(D_h + U_h\right)\Lambda_{hi} \ , \\ \beta_i &\equiv \frac{c_i}{\Delta P_i} \ , \end{aligned}$$

stand for the ith elements of, respectively, $\boldsymbol{\Upsilon}$ and β. We can now define the "benefit"-cost ratios $\overline{R}^i \equiv \alpha_i/\beta_i$, or with explicit reference to relevant information:

$$\overline{R}^i \equiv \frac{\Delta P_i}{C_i}\sum_{h=1}^{k}\left(D_h + U_h\right)\Lambda_{hi} \ , \qquad i = 1, \ldots, k. \tag{11}$$

As shown in Theorem 2 below, there is a sense in which expression (11) can be taken for the new practical formula sought to construct *in situ* conservation priorities. Observe that the number assigned to each species i does not depend merely on its own "benefits" but actually on overall "benefits" generated by species i on all the species, $\sum_{h=1}^{k}\left(D_h + U_h\right)\Lambda_{hi}$, via ecological interactions. Therefore, a species with a strong own interest can be overridden by another, endowed with a less direct interest, but whose importance is enhanced because of its ecological role. Of course, when there are no ecological interactions, $\boldsymbol{\Lambda}$ is the identity matrix, with $\Lambda_{ii} = 1, \Lambda_{hi} = 0, \forall h \neq i$, and (11) boils down to Weitzman's original system of grades for species i :

$$\overline{R}^i = R^i \equiv \frac{\Delta P_i}{C_i}\left(D_i + U_i\right) \ .$$

One can ask to what extent can we rely on formula (11) to build a hierarchy among species? Can conservation policy be based on such an approximation?

Baumol and Bushnell (1967) have famously attracted the attention on a number of potential flaws with linear approximations, two of them being of a great importance for the problem at hand: *i)* a linear approximation to a nonlinear program need not provide an answer better than a randomly chosen initial solution, *ii)* only if the objective function behaves monotonically in every variable within the admissible region can we be assured that a linear approximation will yield results which represent an improvement over the initial point. Clearly, Noah's objective function does not meet this last condition, for an increase of the effort x_i can improve the chances of species i at the expense of another species j (obviously so when i is a predator for j).

Still, we can prove the following Theorem which establishes a special interest to the use of a linear approximation in this decision problem:

Theorem 2 *Suppose* $\mathbf{I}^k - \mathbf{R}$ *is invertible. And suppose one selects a solution to the Noah's Arch Problem with ecological interactions to be of the following form: there exists a cutoff value* $\overline{R}^*$ *such that:*

- *if* $\overline{R}^i > \overline{R}^* \Longrightarrow x_i = \overline{x}_i$, *(species i is granted full protection),*
- *if* $\overline{R}^i < \overline{R}^* \Longrightarrow x_i = 0$, *(species i is granted zero protection).*

Let us call $\mathbf{X}^W$ *this policy and* $\mathbf{X}^*$ *the optimal solution approximated by* $\mathbf{X}^W$. *Then,*

i) $\mathbf{X}^W$ *offers an improvement compared to the absence of protection,*

ii) *the error introduced by* $\mathbf{X}^W$ *is no larger than* $K * \left(\overline{\mathbf{X}}^\intercal \iota^k\right)^2$, *where* $K = \max\left\{\partial^2 \left(W \circ \mathcal{P}\right) / \left(\partial x_i \partial x_j\right)\right\}$.

Proof. See Appendix B. ■

3 Final remarks

We close this note with a brief study of trade-offs alterations arising from the consideration of ecological interactions. This can be illustrated within a simple two-species example. Assume for simplicity that $|r_{12}| < 1, |r_{21}| < 1$. The system (2) becomes:

$$\begin{bmatrix} P_1 \\ P_2 \end{bmatrix} = \begin{bmatrix} q_1 \\ q_2 \end{bmatrix} + \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} + \begin{bmatrix} 0 & r_{12} \\ r_{21} & 0 \end{bmatrix} \begin{bmatrix} P_1 \\ P_2 \end{bmatrix} .$$

Here the matrix $I^k - R$ is invertible since $r_{12} r_{21} \neq 1$.

Solving the system of interactions:

$$\begin{aligned} P_1 &= \left(1 - r_{12} r_{21}\right)^{-1} \left(q_1 + r_{12} q_2 + x_1 + r_{12} x_2\right) , \\ P_2 &= \left(1 - r_{21} r_{12}\right)^{-1} \left(q_2 + r_{21} q_1 + x_2 + r_{21} x_1\right) . \end{aligned}$$

The grades also can be easily computed. They are:

$$\begin{aligned}\overline{R}^1 &= \frac{\Delta P_1}{c_1}\left[\frac{D_1+U_1}{1-r_{12}r_{21}}+\frac{r_{21}\left(D_2+U_2\right)}{1-r_{21}r_{12}}\right] \ , \\ \overline{R}^2 &= \frac{\Delta P_2}{c_2}\left[\frac{r_{12}\left(D_1+U_1\right)}{1-r_{12}r_{21}}+\frac{D_2+U_2}{1-r_{21}r_{12}}\right] \ .\end{aligned}$$

To further simplify, imagine that $c_1 = c_2 = c$, $\Delta P_1 = \Delta P_2 = \Delta P$. If ecological interactions are erroneously ignored, formally Noah assigns zero values by mistake to the system of interactions: $r_{12} = r_{21} = 0$. Suppose, without loss of generality, that on this erroneous basis the first species ranks higher:

$$R^1 = (D_1 + U_1) > R^2 = (D_2 + U_2) \ .$$

In other words $D_1 + U_1 = k * (D_2 + U_2)$, for some $k > 1$.

Two questions arise. Could this ranking be reversed once interactions are properly taken into account? And, if the answer is affirmative, why?

When the ranking is reversed:

$$\begin{aligned}\overline{R}^1 &< \overline{R}^2 \ , \\ &\Leftrightarrow \\ \frac{D_1+U_1}{1-r_{12}r_{21}}+\frac{r_{21}\left(D_2+U_2\right)}{1-r_{21}r_{12}} &< \frac{r_{12}\left(D_1+U_1\right)}{1-r_{12}r_{21}}+\frac{D_2+U_2}{1-r_{21}r_{12}} \ .\end{aligned}$$

Since $1 - r_{12}r_{21} > 0$, and using $D_1 + U_1 = k * (D_2 + U_2)$, the last inequality is equivalent to:

$$\begin{aligned}&\Leftrightarrow \quad k + r_{21} < kr_{12} + 1 \ , \\ &\Leftrightarrow \quad k < \frac{1-r_{21}}{1-r_{12}}. \quad \text{(since } |r_{12}| < 1\text{).}\end{aligned}$$

So, a ranking reversal occurs when:

$$1 < k < \frac{1-r_{21}}{1-r_{12}} \ .$$

In order to fix ideas, consider that k is arbitrarily close to one, *i.e.* the two species provide similar "benefits" and therefore a ranking reversal, if any, is due to the consideration of ecological interactions. Then note that for the above inequality to hold, necessarily $r_{12} > r_{21}$, which may occur in various interesting ecological configurations:

- **i)** *Predation*: species 1, a predator, feeds on species 2, its prey. So $r_{21} < 0$ whereas $r_{12} > 0$. Giving conservation priority to the prey is the most effective way to enjoy the benefits of both species.
- **ii)** *Mutualism*: for example plant-pollinator interactions, $r_{12}, r_{21} > 0$. The synergistic relation between those two species is best enhanced by promoting species 2, which has the largest collective marginal impact.

iii) *Competition*: two species have to share a common resource in the same living area that cannot fully support both populations, hence $r_{12}, r_{21} < 0$, so conservation efforts focus on species 2 because its marginal negative impact is lower.

References

[1] Baumgärtner, S., 2004. "Optimal investment in multi-species protection: interacting species and ecosystem health", *EcoHealth,* 1, 101–110.

[2] Baumol, W.J. & Bushnell, R.C., 1967. "Error Produced by Linearization in Mathematical Programming", *Econometrica*, 35(3/4), 447-471.

[3] Burgman, M.A., Ferson S. & Akcakaya HR, 1993. Risk Assessment in Conservation Biology, London: Chapman and Hall, pp 44–83

[4] Elith, J. & Leathwick J.R., 2009. "Species distribution models: ecological explanation and prediction across space and time", *Annual Review of Ecology, Evolution, and Systematics,* 40, 677–697.

[5] 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," *Ecological Economics*, 61(2-3), 284-293.

[6] Guisan, A. & Thuiller, W., 2005. "Predicting species distribution: offering more than simple habitat models". *Ecology Letters*, 8: 993–1009.

[7] 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". *Ecological Economics* 55, 218–223.

[8] Rockafellar, R. T., 1997. "Convex analysis". *Princeton landmarks in mathematics* (Reprint of the 1979 Princeton mathematical series 28 ed.). Princeton, NJ: Princeton University Press.

[9] Simianer, H., 2008. "Accounting for non-independence of extinction probabilities in the derivation of conservation priorities based on Weitzman's diversity concept". *Conservation Genetics*, 9(1), 171-179.

[10] Solow A., Polasky S. & Broadus J., 1993. "On the measurement of biological diversity". *Journal of Environmental Economics and Management*, 24, 60–68.

[11] Weitzman, M.L., 1998. "The Noah's Ark Problem", *Econometrica*, 66(6), 1279-1298.

[12] Witting, L., Tomiuk, J. & Loeschcke, V., 2000. "Modelling the optimal conservation of interacting species". *Ecological Modelling*, 125, 123–143.

Appendix

A Proof of Theorem 1

The proof rests on two pieces of information:

i) Noahs' problem is to maximize a continuous function over a compact set, therefore by Weiestrass *extreme value theorem* there exists a solution.

ii) The Hessian matrix of $W \circ \mathcal{P}(\mathbf{X}) + U \circ \mathcal{P}(\mathbf{X})$ is *not* negative semi-definite, a statement we shall prove below.

Item ii) violates the necessary second order condition for interior solutions to Noah's problem and, in combination with item i), leads to conclude the existence of a solution on the boundary of the efforts set, as claimed by Theorem 1.

In order to reach this conclusion, it remains to prove item ii). Since $U \circ \mathcal{P}(\mathbf{X})$ is linear, the difficulty is to ensure that the Hessian matrix of $W \circ \mathcal{P}(\mathbf{X})$ is not negative semi-definite. Recall that $\mathcal{P}(\mathbf{X})$ is a k-dimensional vector with typical element $\mathcal{P}_h(\mathbf{X})$, $h = 1, ..., k$, and let $J_{\mathcal{P}}(\mathbf{X})$ stand for the *Jacobian* matrix:

$$J_{\mathcal{P}}(\mathbf{X}) \equiv \begin{bmatrix} \frac{\partial \mathcal{P}_1(\mathbf{X})}{\partial x_1} & \frac{\partial \mathcal{P}_1(\mathbf{X})}{\partial x_2} & \cdots & \frac{\partial \mathcal{P}_1(\mathbf{X})}{\partial x_k} \\ \frac{\partial \mathcal{P}_2(\mathbf{X})}{\partial x_1} & \frac{\partial \mathcal{P}_2(\mathbf{X})}{\partial x_2} & \cdots & \frac{\partial \mathcal{P}_2(\mathbf{X})}{\partial x_k} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\partial \mathcal{P}_k(\mathbf{X})}{\partial x_1} & \frac{\partial \mathcal{P}_k(\mathbf{X})}{\partial x_2} & \cdots & \frac{\partial \mathcal{P}_k(\mathbf{X})}{\partial x_k} \end{bmatrix} .$$

Note that, since each function $\mathcal{P}_h(\mathbf{X})$ is linear, the Jacobian matrix is made of invariant numbers, so we need not mention the application point $\mathbf{X}$ and we can simply refer to the matrix $J_{\mathcal{P}}$.

Denote $\nabla^2 W \circ \mathcal{P}(\mathbf{X})$ the *Hessian* matrix of $W \circ \mathcal{P}(\mathbf{X})$, a $k * k$ matrix with typical elements $\partial^2 (W \circ \mathcal{P}) / (\partial x_i \partial x_j)$. From meticulous derivations of the composite function $W \circ \mathcal{P}(\mathbf{X})$, and after simplifications allowed by the linearity of the mapping $\mathcal{P}(\mathbf{X})$, one obtains:

$$\nabla^2 W \circ \mathcal{P}(\mathbf{X}) \equiv J_{\mathcal{P}}^{\top} * \nabla^2 W(\mathbf{X}) * J_{\mathcal{P}} .$$

If $\nabla^2 W \circ \mathcal{P}(\mathbf{X})$ is negative semi-definite, then for any nonzero vector $m \in \mathbb{R}^k$ we must have:

$$m^{\top} * \nabla^2 W \circ \mathcal{P}(\mathbf{X}) * m = m^{\top} * J_{\mathcal{P}}^{\top} * \nabla^2 W(\mathbf{X}) * J_{\mathcal{P}} * m \leq 0 .$$

Notice that $J_{\mathcal{P}} * m$ is simply a nonzero $(k * 1)$ vector, which we may simply call n. Hence we can rewrite the above inequality as:

$$n^{\top} * \nabla^2 W(\mathbf{X}) * n \leq 0 \ ,$$

which would mean that $\nabla^2 W(\mathbf{X})$ is negative semi-definite, a possibility that has been ruled out by assumption. QED.

B Proof of Theorem 2

Item i). The solution proposed in Theorem 2 is inspired from gradient methods used to find optimal solutions based on the property of iterative improvements, like the famous Frank-Wolfe algorithm. The first step of those algorithms is to substitute to the objective function its first order Taylor approximation $Z(\mathbf{X})$ computed at an admissible vector $\mathbf{X}^0$ (here at the zero protection vector $\mathbf{X}^0 = 0 * \iota^k$). Let us note $\nabla W \circ \mathcal{P}$ the Gradient, a $k * 1$ vector with typical elements $\partial (W \circ \mathcal{P}) / \partial x_i$, that corresponds actually to the vector $\boldsymbol{\Upsilon} \equiv \mathbf{A}^{\top} \boldsymbol{\Lambda}$ given in the text.

Using those notations:

$$Z(\mathbf{X}) \simeq W \circ \mathcal{P}\left(0 * \iota^k\right) + \nabla W \circ \mathcal{P}\left(0 * \iota^k\right)^{\top}\left(\mathbf{X} - 0 * \iota^k\right).$$

A first step of a gradient algorithm would $\max_{\mathbf{X}} Z(\mathbf{X})$ subject to the relevant constraints. Since in $Z(\mathbf{X})$ only the term $\nabla W \circ \mathcal{P}\left(0 * \iota^k\right)^{\top} \mathbf{X} = \boldsymbol{\Upsilon}\mathbf{X}$ varies, this step is equivalent to maximize (10) subject to (8) and (9). And the policy $\mathbf{X}^W$ presented in the Theorem 2 is exactly the maximizer of this linear programming problem.

By definition of $\mathbf{X}^W$, we must have:

$$Z\left(\mathbf{X}^W\right) \geq Z\left(0 * \iota^k\right) \ .$$

$$\iff \quad \nabla W \circ \mathcal{P}\left(0 * \iota^k\right)^{\top}\left(\mathbf{X}^W - 0 * \iota^k\right) \geq \nabla W \circ \mathcal{P}\left(0 * \iota^k\right)^{\top}\left(0 * \iota^k - 0 * \iota^k\right) = 0, \tag{12}$$

so the vector $\mathbf{X}^W - 0 * \iota^k$ is an ascent direction for $W \circ \mathcal{P}$. Although this means that the approximation $Z(\mathbf{X})$ is non decreasing along this direction, it is not guaranteed that the non linear objective will behave similarly, *i.e.* we cannot yet conclude $W \circ \mathcal{P}\left(\mathbf{X}^W\right) \geq W \circ \mathcal{P}\left(0 * \iota^k\right)$.

By convexity of function $W \circ \mathcal{P}$ we can write:

$$W \circ \mathcal{P}\left(\mathbf{X}^W\right) - W \circ \mathcal{P}\left(0 * \iota^k\right) \geq \nabla W \circ \mathcal{P}\left(0 * \iota^k\right)^{\top}\left(\mathbf{X}^W - 0 * \iota^k\right),$$

and since we have established in (12):

$$\nabla W \circ \mathcal{P}\left(0 * \iota^k\right)^{\top}\left(\mathbf{X}^W - 0 * \iota^k\right) \geq 0,$$

we are led to conclude:

$$W \circ \mathcal{P}\left(\mathbf{X}^W\right) - W \circ \mathcal{P}\left(0 * \iota^k\right) \geq 0.$$

Item ii). Recall that $\nabla^2 W \circ \mathcal{P}$ stands for the Hessian matrix of $W \circ \mathcal{P}$. Using Taylor expansions, one can write:

$$W \circ \mathcal{P}\left(\mathbf{X}^*\right) = W \circ \mathcal{P}\left(0 * \iota^k\right) + \nabla W \circ \mathcal{P}\left(0 * \iota^k\right)^\top \mathbf{X}^* + \frac{1}{2!}\left(\mathbf{X}^*\right)^\intercal \ \nabla^2 W \circ \mathcal{P}\left(\mathbf{Z}^*\right)\ \mathbf{X}^* \ ,$$

for some admissible vector $\mathbf{Z}^*$, and

$$W \circ \mathcal{P}\left(\mathbf{X}^W\right) = W \circ \mathcal{P}\left(0 * \iota^k\right) + \nabla W \circ \mathcal{P}\left(0 * \iota^k\right)^\top \mathbf{X}^W + \frac{1}{2!}\left(\mathbf{X}^W\right)^\intercal \ \nabla^2 W \circ \mathcal{P}\left(\mathbf{Z}^w\right)\ \mathbf{X}^W,$$

for some admissible vector $\mathbf{Z}^w$.Therefore

$$\begin{aligned} W \circ \mathcal{P}\left(\mathbf{X}^*\right) - W \circ \mathcal{P}\left(\mathbf{X}^W\right) &= \nabla W \circ \mathcal{P}\left(0 * \iota^k\right)^\top \left(\mathbf{X}^* - \mathbf{X}^W\right) + \frac{1}{2!}\left(\mathbf{X}^*\right)^\intercal \ \nabla^2 W \circ \mathcal{P}\left(\mathbf{Z}^*\right)\ \mathbf{X}^* \\ &\quad - \frac{1}{2!}\left(\mathbf{X}^W\right)^\intercal \ \nabla^2 W \circ \mathcal{P}\left(\mathbf{Z}^w\right)\ \mathbf{X}^W \ . \end{aligned}$$

But, by definition of $\mathbf{X}^W$

$$\nabla W \circ \mathcal{P}\left(0 * \iota^k\right)^\top \left(\mathbf{X}^* - \mathbf{X}^W\right) \leq 0 \ ,$$

so

$$\begin{aligned} W \circ \mathcal{P}\left(\mathbf{X}^*\right) - W \circ \mathcal{P}\left(\mathbf{X}^W\right) &\leq \frac{1}{2!}\left(\mathbf{X}^*\right)^\intercal \ \nabla^2 W \circ \mathcal{P}\left(\mathbf{Z}^*\right)\ \mathbf{X}^* - \frac{1}{2!}\left(\mathbf{X}^W\right)^\intercal \ \nabla^2 W \circ \mathcal{P}\left(\mathbf{Z}^w\right)\ \mathbf{X}^W \\ &\leq \frac{K}{2!}\left[\left(\mathbf{X}^*\right)^\intercal \ \iota^k\right]^2 - \frac{K}{2!}\left[\left(\mathbf{X}^W\right)^\intercal \ \iota^k\right]^2 \leq K\left(\overline{\mathbf{X}}^\intercal \iota^k\right)^2, \end{aligned}$$

where $K = \max\left\{\partial^2\left(W \circ \mathcal{P}\right) / \left(\partial x_i \partial x_j\right)\right\}$.