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Vers une gestion in situ des diversités biologiques

Chloé Mulier

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Chloé Mulier. Vers une gestion in situ des diversités biologiques. Economies et finances. Université Montpellier, 2015. Français. NNT : 2015MONTD057 . tel-01653077

HAL Id: tel-01653077

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THÈSE

Pour obtenir le grade de
Docteur

Délivré par l'**Université de Montpellier**

Préparée au sein de l'école doctorale d'Economie et de
Gestion (EDEG)

Et de l'unité de recherche LAMETA

Spécialité : **ECONOMIE**

Présentée par **Chloé MULIER**

**TOWARDS IN-SITU MANAGEMENT OF
BIOLOGICAL DIVERSITIES**

**VERS UNE GESTION IN-SITU DES
DIVERSITES BIOLOGIQUES**

Soutenue le 16 Décembre 2015 devant le jury composé de

| | |
|---|-----------------------|
| M. Luc DOYEN, Directeur de recherche CNRS, UMR GREThA, Bordeaux | Rapporteur |
| M. Jean-Christophe PEREAU, Professeur Université de Bordeaux, UMR GREThA, Bordeaux | Rapporteur |
| M. Stefan BAUMGÄRTNER, Professeur-docteur, Chaire « Environmental economics and Resource Management, Université de Fribourg, Fribourg | Examineur |
| M. Christopher COSTELLO, Professeur Bren School of Environmental Science and Management, UC Santa Barbara. | Examineur |
| Mme. Estelle GOZLAN, Chargée de recherche INRA, UMR Economie Publique INRA-Agroparistech, Paris | Examinatrice |
| M. Pierre COURTOIS, Chargé de recherche INRA, UMR LAMETA, Montpellier | Co-directeur de thèse |
| M. Charles FIGUIERES, Directeur de recherche INRA, UMR LAMETA, Montpellier | Directeur de thèse |



Dans ces eaux des Antilles, à dix mètres au-dessous de la surface des flots, (...) que de produits intéressants j'eus à signaler sur mes notes quotidiennes! (...) Par nuées, apparaissent des surmulets, corsetés de raies d'or de la tête à la queue; (...) des pomacanthés dorés, (...) habillés de velours et de soie, passaient devant nos yeux comme des seigneurs de Véronèse; (...) et des sélènes argentées, dignes de leur nom, se levaient sur l'horizon des eaux comme autant de lunes aux reflets blanchâtres.

Jules Verne, *Vingt mille lieues sous les mers*

Titre Vers une gestion *in situ* des diversités biologiques

Résumé La diversité biologique constitue l'un des piliers du fonctionnement des écosystèmes, et un potentiel pour l'adaptation et l'évolution de la vie dans le contexte du changement climatique. Les espèces constituant cette biodiversité sont étroitement connectées de différentes façons. Une diminution de cette biodiversité peut déclencher des effets de cascade et des conséquences largement imprévisibles, bien au delà de la seule réduction apparente du nombre ou de la distribution des espèces. La grande complexité de l'organisation écologique est très souvent un cauchemar pour la prise de décision. Les difficultés commencent avec le choix d'une mesure adéquate de la biodiversité. Une telle mesure est cependant une étape nécessaire si nous voulons prioriser nos actions de gestion de la biodiversité, afin de préserver le plus de diversité possible avec des ressources limitées. Bien que cette thèse ne prétende pas produire des réponses complètes à ces problèmes complexes, elle offre quelques points de réflexion pour la gestion de la biodiversité. Elle se compose de quatre chapitres. Le premier chapitre soulève la question de la gestion d'une biodiversité mélangée, au sein de laquelle des espèces invasives peuvent également s'inviter. Ce chapitre souligne les interconnexions entre la sévérité des impacts des invasions biologiques et le contexte dans lequel cette invasion intervient. Considérant les impacts des invasions comme "ambivalents" — i.e. pouvant être positifs, négatifs, ou neutres pour le système dans lequel l'invasion s'installe — nous proposons une typologie afin d'évaluer l'ambivalence des impacts, sur la base de l'identification des sources potentielles de variabilité des impacts. Pour le second chapitre, nous nous concentrons sur la mesure de la biodiversité lorsque l'on tient compte des interactions entre espèces, de façon à produire une version de la métaphore de l'Arche de Noé (Weitzman, 1998) mieux adaptée aux problèmes de conservation *in situ*. Nous montrons tout d'abord que, lorsque l'on tient compte d'interactions écologiques, le problème défini par Weitzman demeure une solution extrême; et deuxièmement, qu'un renversement de la hiérarchie des espèces préservées est possible et entièrement déterminée par la catégorie des interactions. Dans le troisième chapitre, nous utilisons le cadre de coût-bénéfice *in-situ* développé dans le chapitre 2 afin de comparer les résultats de priorisation de deux indices de biodiversité, Weitzman et Rao. Ces deux indices combinent différemment l'information sur les probabilités autonomes de survie des espèces, les interactions écologiques et la dissimilitude entre espèces afin de mesurer la biodiversité. Nous analysons des plans simples de protection de la biodiversité pour chaque indice, et démêlons le rôle

joué par les différents éléments d'information nécessaires au calcul du ranking par l'indicateur, dans un écosystème à trois espèces. Nous montrons que chaque indice réalise un compromis qui lui est propre entre ces éléments d'information, et que l'introduction d'interactions écologiques entre plus de deux espèces mène à des conclusions plus complexes. Les interactions écologiques donnent ainsi une information additionnelle importante afin de déterminer les objectifs de conservation. Notre dernier chapitre est une adaptation du cadre d'optimisation défini précédemment. Il élabore une règle de décision myope afin de déterminer quelles invasions doivent être contrôlées en priorité, en tenant compte des coûts de gestion relatifs et les impacts trophiques en cascade. Nous discutons le gradient de la fonction d'objectif composé d'une fonction de diversité W et d'une fonction d'utilité U , afin de déterminer si nous devrions conserver plusieurs ou seulement quelques espèces sous une contrainte de budget.

Mots-clés Gestion, priorisation, biodiversité, indices, espèces invasives

Title Towards *in situ* management of biological diversities

Abstract Biological diversity constitutes one of the major pattern of ecosystem functioning, and a potential for adaptation and evolution of life in the context of climate change. As species are in many ways tightly interconnected, biodiversity loss can trigger large cascade effects and might lead to largely unpredictable consequences, reaching far beyond the visible reduction in the number or distribution of species. The high complexity of ecological organization is often a nightmare for decision-making, starting from accurately measuring biodiversity. This is however a necessary step to take if we want to prioritize action in biodiversity management, in order to preserve as much diversity as possible under limited resources. Though this thesis does not pretend to provide complete answers to those quite complex issues, it provides some reflection points for biodiversity management. It is composed of four chapters. The first chapter raises the issue of dealing with a mixed biodiversity, in which invasive species can be guests. It highlights the interconnections between the severity of the impacts of biological invasions and the contexts in which this invasion occurs. Considering invasion impacts as inherently "ambivalent" — i.e. good, bad or neutral for the system in which it arrives — we propose a typology to assess ambivalence in impact, based on the identification of potential sources of impact variability. For the second chapter, we focus on the measurement of biodiversity when accounting for species interactions, which we incorporates into the Noah's Arch problem developed by Weitzman (1998). We then derive a general model for ranking *in situ* conservation projects. We show firstly that, when accounting for ecological interactions, the problem defined by Weitzman is still an extreme solution, and secondly, that a ranking reversal is possible and completely defined by the interaction categories. In the third chapter, we use the *in situ* cost-benefit framework developed in Chapter 2 to compare the outcomes of two biodiversity indices, Weitzman's and Rao's. Those two indexes combine information about species survival probability, ecological interaction and distinctiveness in a different way to measure biodiversity; We analyze simple biodiversity protection plans for each index, and disentangle the role played by the different data requirement in the rankings, in a three species ecosystem. We show that such pieces of information will come as a trade-off when considered simultaneously in the measure, and that the introduction of ecological interactions among more than two species lead to more complex conclusions. Ecological interactions thus give important additional information to determine conservation objectives. Our last chapter is an adaptation of the previously defined

optimization framework for the prioritization of invasive species management. It elaborates a myopic rule to determine which invasions must be controlled in priority, taking into account relative management costs and trophic cascades impacts. We discuss the gradient of the objective function composed of a diversity function W and a utility function U , to see whether we should retain several or only a few species for management under a budget constraint.

Keywords Management, prioritization, biodiversity, indices, invasive species

L'Université de Montpellier 1 n'entend donner aucune approbation ni improbation aux opinions émises dans cette thèse. Celles-ci doivent être considérées comme propres à leur auteur.

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REMERCIEMENTS

Je tiens avant tout à remercier chaleureusement mon directeur de thèse, Charles Figuières. Son écoute, sa confiance et son soutien sans faille m'ont aidé à passer des caps dans ma réflexion et mener mes idées au bout avec conviction et rigueur. Un grand merci également à mon co-directeur de thèse, Pierre Courtois, pour nos discussions et nos réflexions enthousiastes qui m'ont permis d'avancer à grands pas, tout en me permettant d'apprendre de mes erreurs ! Merci aussi à Jean Michel Salles, mon maître de thèse, pour sa compréhension et pour m'avoir encouragée à vivre cette belle expérience de thèse.

Merci également aux membres du jury, Stefan Baumgärtner, Christopher Costello, Luc Doyen, Estelle Gozlan et Jean-Christophe Pereau d'avoir pris le temps de lire et d'évaluer cette thèse.

Tous mes remerciements vont également à Jacques Tassin, écologue au CIRAD, pour ses conseils et son aide précieuse sur la question des espèces invasives. Merci également à Marie Laure Navas et David Mouillot pour les entrevues qu'ils m'ont accordées et nos échanges sur l'utilisation des indicateurs de biodiversité en écologie et en économie.

Le soutien et la convivialité des personnes du LAMETA ont également énormément compté lors de ces années ; Notamment lors de mon départ en tournée et de ma réintégration au laboratoire après huit mois passés sur les routes. J'ai eu le sentiment de n'avoir jamais quitté le bâtiment 26 ! Merci à Mabel pour son sourire et ses paroles rassurantes, à Laurent pour les délires musicaux, les tournois de babyfoots et les meilleures brazzucades de l'Ouest, Cédric pour sa disponibilité et son esprit sportif à toute épreuve, à Jean Walter pour les swings endiablés ; à Caro pour ses séances de Tai chi pour éviter le syndrome de

la tortue, et toute l'équipe de la doc pour leur bonne humeur !

Je dois beaucoup à tous les doctorants et amis qui m'ont entourés pendant ces cinq années : Rachida pour son indéfectible soutien et sa clairvoyance ; Clémentine pour m'avoir aidée à garder mon âme d'enfant ; Jean-Baptiste et Jean-Marc pour leur grain de folie communicatif ; Marine et Chris pour toutes les douleurs et les joies partagées sur les routes du cirque ; Coralie pour nos expériences équestres ; Pauline pour nos épiques soirées et notre belle virée à Malte ; Sophie et Florent pour nos randos gustatives et nos soirées au coin du feu ; Vanja pour avoir partagé avec moi les moments de doute et de joie ; Fanny et Vincent, Amandine et Symphorien pour cette belle amitié tout au long de la thèse, malgré la distance et les obligations parentales ! Pour Anne, Amor et leurs enfants pour m'avoir accueilli tant de fois au ranch, et pour m'avoir remis le pied à l'étrier... Un grand merci ! Mais aussi Guillaume, Philippe, Laura, Maxime, Léa, Julia, Mathieu, Laure, et tous les autres pour tous ces bons souvenirs au LAMETA.

Merci infiniment à mes parents de m'avoir soutenue dans les moments de doute : leur fierté est ma plus grande joie ; à ma petite soeur Marion et à Seb pour tous ces moments de complicité rafraîchissants. Merci à ma grand-mère pour nos échanges et l'exemple de liberté qu'elle représente pour moi. Merci à ma tante, mais aussi à Marie Jo et Dominique de m'avoir accueilli dans leur havre de paix lors des moments difficiles de la tournée.

Je ne pourrais assez remercier Guillaume, pour m'avoir poussée à vivre mes rêves les plus fous, et à écouter mon coeur et mes passions. Son optimisme et son amour m'ont portée et soutenue même dans les moments les plus difficiles.

Merci aux chevaux, qui m'en apprennent chaque jour davantage sur moi-même.

"Un artiste n'est pas un ouvrier du divertissement qui compte ses heures ;

il se consume au feu de sa passion."

Jérôme Garcin

GENERAL INTRODUCTION

GENERAL INTRODUCTION



The stunning beauty of life on earth has always fascinated human beings. The most primitive forms of art are mostly related to plants or animals, while the development of human societies completely relies on such diversity. Travelers and writers as John Muir or Jules Verne magnified its beauty and sometimes incredible eccentricity. "Nature" was progressively studied from the perspective of "biological diversity" and "natural diversity" (Dasmann, 1968), leading to the abbreviation "biodiversity", in the preamble of the national forum on Biological Diversity organized by the National Research Council (NRC) in Washington in 1986. Biodiversity conservation constitutes a considerable challenge ahead of us, and probably one of our greatest and most urgent responsibility towards future generations and our own. In his book *Biodiversity*, Wilson (1988) launched a vibrant denunciation of the accelerating loss of species in response to human population and economic development pressures. The following years saw the emergence of an extensive literature, especially in ecology, on the role of biodiversity in providing livelihoods for human beings. (e.g. Vitousek et al, 1997; Chapin et al., 2000; Cardinale et al., 2012). More than 22% of mammals, 13% of birds, 21% of reptilians and over 50% of plants currently studied by the IUCN are considered as endangered (IUCN, 2015).

0.1 BIODIVERSITY DEFINITIONS AND CHALLENGES

Biodiversity is generally defined as the variety of life, including variation among genes, species, and functional traits (Cardinale et al., 2012). If it seems obvious that a clear and exhaustive definition is almost impossible for such a broad term, it is however possible to gain information about the complexity of existing biodiversity by decomposing it in several components. Biologists often use an operational decomposition into the genetic, taxonomic and ecosystemic levels of diversity (Marty, Vivien, Lepart, & Larrere, 2009). But many other definition levels may be considered, for example populations, species, family, order, genus, phylum, etc. (Groombridge, 1992). If such decomposition is crucial in order to define biological diversity, the role and meaning of this biodiversity is far more complex than isolated numbers on a scale.

The preamble of the CBD¹ (CBD & UNEP, 2004) gives the following definition : “*the variability among living organisms from all sources, including inter alia, terrestrial, marine and other aquatic ecosystems, and the ecological complexes of which these are a part*”. But even this broad definition lacks to refer to the ecological processes controlling the fluxes of energy, nutrients and organic matter through the environment, which are central for a working definition of biodiversity (Cardinale et al., 2012). Ecosystem functioning underlies directly or indirectly the provision of specific services, which may or may not lead to benefits for human well-being. When studying biodiversity, it is therefore crucial to determine what to measure in biodiversity, and how this may impact human well-being through the provision of main functions and services. This is well summarized in the scheme below developed by Haines-Young & Potschin (2009), in which biodiversity appears at the crossroads of many important concepts from both economic and ecological points of view.

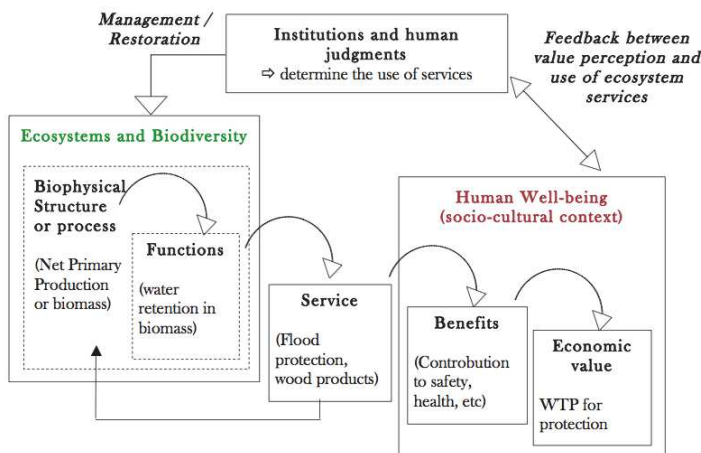


FIGURE 1 – Adapted from Young and Potschin, 2009

Therefore, when designing a management policy, we have to account not only for the ecological components of biodiversity, but also for potential services gained from biodiversity and associated economic benefits.

In their 2012's paper, Cardinale et al. reviewed twenty years of research on the link between biodiversity and ecosystem functioning. Although the impact of human-induced biodiversity loss on ecosystem functioning is subject to an intense debate in the ecology community (Hooper et al., 2005), Cardinale et al. (2012) highlighted five important consensus statement on that matter². On the one hand, more diverse system are supposed to lead to (1) larger efficiency of ecological communities ; (2) increased stability of ecosystem functions through time ; (3) increased ecosystem productivity, through the presence of key species implying the existence of numerous collateral species ; and amplified resource capture through the presence of a larger array of functional traits among organisms. On

1. Convention on Biodiversity. The CBD is one of the three international treaties ratified at the Earth Summit in 1992, at the United Nations Conference on Environment and Development.

2. Those consensus points were more or less the actualized version of Hooper et al. (2005) on the subject.

the other hand systems incurring a loss of diversity (4) experiment non-linear and more than proportional impacts; (5) another emerging consensus is that diversity loss across trophic levels lead to stronger impacts on ecosystem function than diversity loss within trophic levels.

From those consensus points, we can draw two important remarks as a starting point of this thesis and an attempt of justification for public policy. First, biodiversity is one of the principal pattern of ecosystem functioning and constitutes a potential for evolution and adaptation capacities of living species to a context of climate change. It should be considered as a certain form of life organization, including potential direct and indirect interactions between species. Biodiversity loss may thus have largely unpredictable consequences reaching far beyond the visible reduction of existing species, which may trigger more important cascade effects through those interdependencies. Second, if biological diversity can be associated to undeniable existence value, some use values can also be derived from the services delivered by a working biodiversity. Therefore, public policies regarding biodiversity must aim at preserving biodiversity as an existence value but also as a use value. Indeed, the improvement of biodiversity situation and the maintenance of ecosystem services would deliver widespread benefits, contributing to global human well-being (Leadley, 2010, Larigauderie et al., 2012).

From those remarks, two major challenges can be deduced for public policy on biodiversity. First, to know what is the exact goal of this policy. What is the objective we are aiming for? The question is not new and historically, we observed a shift from "nature" protection towards a more general goal of active biodiversity management (Blandin, 2007). The debate opposing the traveler and writer John Muir to the forest engineer Gifford Pinchot about the true objective of biodiversity conservation at the beginning of the 20th century is representative of the dichotomy between a "wild" versus a "managed" conception of nature. For Muir, wilderness reflects the "perfection of God's Creation" that must be preserved integrally in its most original form, whereas Pinchot believed in responsible stewardship as the sustainable use of natural resources, which supports human well being. Although this latter view progressively gained ground with the birth of the International Union for the Conservation of Nature (IUCN) in 1948 giving its credentials to a utilitarian view of ecosystem services, the existence value of biodiversity remains a key political goal and is often defined as the key justification of conservation policies.

A second challenge – related to the first – is the prioritization of preservation action, which appears as necessary in a context of shrinking conservation funds worldwide. After defining a goal, the allocation of efforts is to be performed in order to reach this goal in the most cost-efficient manner. The recent 12th Meeting of the Conference of Parties to the Convention on Biological diversity, held in October 2014, stressed the urgent need to increase mobilization of financial resources at international and domestic levels from a large variety of sources, including major productive sectors (Chiarolla, Lapeyre, & Treyer, 2014). In order to get this funding on political agendas, information on the "rate of return" of investing funds to conservation, along with careful definition and prioritization

of conservation targets is crucially needed (Pearce, 2005, Wilson et al., 2006 ; Brooks et al., 2006).

0.2 FROM BIODIVERSITY CONSERVATION TO BIODIVERSITY MANAGEMENT

Ecological studies have been mostly studying the objects of biological diversity, whereas economic studies have progressively investigated this field of research to answer the question of managing resources under a limited budget constraint. The etymology of both disciplines "ecology" and "economics" comes from the same ancient greek root *oikos*, meaning "house" or "habitat". Ecology is the "science" of the house (*oikos - logos*) and aims therefore to study the physical existence conditions of organisms. Economics are the "rules" or "administration" of the house (*oikos - nomia*) and is thus primarily dedicated to studying the organization of society. Consequently, economics analyzes the design of public policies and their properties. In this way, economics studies the policies aimed at shaping the physical environment, such as biodiversity management.

Debates arise in each discipline regarding both the rationale behind biodiversity management as a goal - being understood that this goal can be crucial or instrumental (e.g. to better achieve the objective of social welfare predominant among economists) - as well as the most effective way to reach that goal. If biodiversity has long been the hallmark of ecologists or evolutionists, why should economists study biodiversity? First, because biodiversity contributes to life on earth and to the functioning of ecosystems, providing human being with incommensurable services and allowing the existence of (some) economic sectors. Second, because the world is facing an acceleration of biodiversity loss, mostly caused by the erratic development of our economic system. Third, biodiversity loss shows strong economic implications, for which economists may contribute to elaborate solutions.

Asked from the different standpoint of conservationists and economists, the question of biodiversity preservation seems rather similar : assume we can agree on the crucial objective to preserve as much biological diversity as possible. The formulation "as much as possible" is often driven by economic constraints such as opportunity costs of not degrading this diversity in the best case and the direct cost of protecting an already endangered diversity in the worst case. Costs of preservation, whether measured in monetary units or along psychological, or ethical dimensions are therefore very important to consider.

In order to reach solutions of preservation, it is important to measure and collect information on this diversity. If we want to preserve as much diversity as possible under limited resources, we have to determine where is the most important part of diversity. Consequently, we should be able to find ways to measure it (Vane-Wright, Humphries, & Williams, 1991). To evaluate harmful impacts on the diversity of a region, or to estimate which regions currently has the highest diversity, we need means to classify and compare those data. Statistical functions called "indices" can help to provide numerical values of diversity or "measures" of diversity, a commonly shared characteristic of any data set. A way to measure diversity is to study the relative abundance of different ca-

categories in a set (or species in an ecosystem for biodiversity conservation), which is very close from measuring the richness and evenness of the categories in the set. (e.g. Berger-Parker index, Shannon-Wiener index or Simpson index). They differ in their sensitivity to rare categories of species, and both entail a common limit, which is to consider all categories (or species) as similar. An important sub-class of indices, advocated in Wood (2000) is based on data about pairwise dissimilarities between species. Indeed, for a consistent measure of biodiversity, it is also crucial to be able to measure divergence among categories. Those differences can be defined using dissimilarities measured as Euclidian metrics, or ultrametric distances, which will be defined later on. The choice of distances defines the unit of diversity we are looking at, for example genes or physical characteristics. They have therefore a crucial importance for conservation, and may well influence conservation priorities.

As noticed by Aulong, Erdlenbruch and Figuières (2005) and Baumgärtner (2007), measuring biodiversity requires prior value judgments on the character and purpose attributed to biodiversity. For most economists, biodiversity must be preserved as a social value, for instance increasing freedom of choice from a given set of natural resources, or leading to more welfare to society. Measuring biodiversity is therefore about evaluating and ranking the options offered by different biodiversity configurations. Ecological dimensions are rarely accounted for when deciding over the ranking of different biodiversity sets. On the other hand, ecologists endorse a more conservative view of species diversity and consider its contribution to long term functioning of ecosystems. Baumgärtner (2007) proposes a dichotomy between "conservative" indices accounting for biodiversity as a condition to ecosystem functioning, and "liberal" indices in which biodiversity is a resource pool from which economic agents can choose the most preferred option. Whilst the "conservative" view includes mostly species richness and abundances in the measures, the "liberal" view put the emphasis on species features and dissimilarity. A famous representative of the "liberal" view described by Baumgärtner is the diversity index developed by Weitzman (1992).

Although a large battery of indices is already used in the literature, little was done to actually compare biodiversity objective functions retained in those indices. However, the choice of such an objective function may have significant impact on optimization outcomes and thus on eventual conservation choice. Weitzman was among the first³ to tackle the question of effectiveness of conservation policies. In his Noah's ark metaphor, he describes a world in which Noah should protect species from the flooding, while being constrained by the size of his ark. He thus derives a cost-effective criterion helping Noah to rank species in order to choose which species must be boarded first, i.e. which species will contribute the most to biodiversity. This cost-effective method uses a certain biodiversity function, based on aggregated pairwise distances between species, to be maximized sub-

3. There is a range of other important and related papers, among which Vane-Wright, Humphries and Williams (1991), Crozier (1992), Faith (1992), Weitzman (1992), Solow, Polasky and Broadus (1993), Bossert, Pattanaik and Xu (2003)

ject to a budget constraint. Somewhat different biodiversity indices could however be used under this methodology. Whatever the retained biodiversity index, this initial Noah's ark methodology can also be met with skepticism, because it does not account for ecological interactions. Put differently, it does not tackle *in situ* conservation issues (Mainwaring, 2001 ; Weikard, 2002). In successive papers, Baumgärtner (2004), Van der Heide et al (2006) and Simanier (2008) already noticed that accounting for species interactions may reverse Weitzman's conservation ranking, and even suggested to turn to other types of indices in order to rank biodiversity conservation issues. In this thesis, we propose to look at the characteristics of the diversity measure developed by Rao (1982), also called Rao's quadratic entropy. We submit it to the same treatment than Weitzman's index, introducing ecological interactions into the index. This measure is increasingly used in ecology since the mid of the 90's. This measure is mathematically defined as the expected dissimilarity between two entities randomly drawn from a collection, and accounts simultaneously for both abundances and dissimilarity measures ; yet, its behaviour in the maximum varies depending on the mathematical properties of the dissimilarity matrix used (Pavoine, 2005). Indeed, this index can be maximized by a reduced richness of measured categories. In other words, its maximization can be obtained from different combinations of categories frequencies, some of which can entail zeros for certain categories. (Shimatani, 2001, Izsák & Szeidl, 2002, Champely & Chessel, 2002, Pavoine, Ollier, & Pontier, 2005). This characteristic led Pavoine et al (2005), to rename this category of index as an index of species "originality", rather than diversity. Both Rao's entropy and Weitzman's index have strong axiomatic characterization, which establishes their transparency as diversity measures (Bossert, Pattanaik and Xu 2002, Rao 1986).

Baumgärtner (2007) stresses that no existing index currently allows prioritization on the basis of species richness, abundances and dissimilarities. Species richness, evenness, and divergence all have a crucial role in describing and measuring biodiversity, but melting those dimensions into a single index might be difficult and counterproductive in terms of interpretation. It is however useful to compare how two indices stemming from different schools of thought can perform to measure a given diversity of species. If the selection procedures of those indices are now well-known and studied from an axiomatic point of view (Bossert, Pattanaik, & Xu, 2002,), little has been done so far to compare their outcomes in terms of diversity prioritization. Gerber (2011) provides a comparison of four indices (Weitzman (1992), Solow et al (1993), Hill (2001) and Gerber (2011)). This comparison is however not made in a context of *in situ* protection plans, i.e. accounting for potential ecological interactions, and Rao's index has been ignored, despite its importance in ecology and biology.

0.3 THE ISSUE OF BIOLOGICAL INVASIONS : QUESTIONING EQUILIBRIUM AND A CHALLENGE FOR BIODIVERSITY CONSERVATION

In situ conservation implies to account for species interdependencies, such as predator-prey relationship, competition, parasitism or mutualism. Most interactions occur between and within trophic levels, and many of them are still largely unknown. If species interact inside ecosystems, they may also interact across them, as a consequence of species movements and biological invasions. The issue of invasive species raises some interrogations about our previous definitions of biodiversity, and the related goal of biodiversity maximization to set conservation objectives. This maximization is constrained by two major dimensions : first, the limited amounts of resources allocated to biodiversity conservation ; second, the shape and characteristics of the retained diversity function. However in some cases, choices to be made implies complicated consequences when invasive species are considered. The ethical implications are obvious, and often raised from a strictly anthropocentric point of view : Can we talk about a "valuable" versus a "useless" or even "noxious" diversity ? The huge debate following the paper of Davis et al (2011) in the ecological community on the issue of biological invasions, also known as the second cause of biodiversity loss by the IUCN, revealed the important implications of such interrogations. At the heart of this discussion, is the notion of ecological equilibrium.

Biological invasion literature often describes human activity as primarily responsible for the introduction and spreading of invasive species, leading to a disruption of an ideal natural state. This influx of invasive species has long been considered to be the source of "imbalances" in the "natural equilibrium" (Elton, 1958). Several authors rapidly acknowledged their lack of confidence in the concept of a fixed equilibrium : "*this "equilibrium of nature" [...] is an excessively dynamic concept which never maintains itself but moves constantly*" (Gabrielson, 1950, cited in Blandin, 2009). The primary "Balance of Nature" concept was gradually replaced by a more technical vision of ecosystem stability wherein equilibrium is seen as a collection of species perfectly adapted to each other and interacting in such a way as to maintain certain equilibrium characteristics. Evolution as such is understood to be the process of establishing these optimally co-adapted species. Perturbations to this system – including biological invasions – are negatively viewed and considered obstacles to eventual stability.

However, some authors have considered that these new situations are not necessarily imbalances of some previous ecosystem state, but rather a transitional and punctual equilibrium toward a new ecosystem state. Perturbations are increasingly seen as structuring ecological systems (Loucks 1970, Pickett & White, 1986 ; White, 1979). For Ricklefs (1987), local diversity is determined by both local processes within the biological community and global processes (such as speciation and dispersion, climate or geography). Following the work of MacArthur & Wilson (1967), Ricklefs was one of the first to consider that species immigration from other zones could act to structure local diversity, counterbalancing the effect of the diversity reduction induced by selection pressure. However, quite interes-

tingly, human action as a driver of species migration was occulted from these studies.⁴ Hobbs et al. (2006) developed a strategy for the management of what they call "novel ecosystems", analyzing new species combinations brought about by human activity and global environmental changes. This recent but still controversial approach places human perturbations as a central element within evolutionary ecology and emphasizes the idea of successional pathways of ecosystem developments, which potentially includes invasive species. (Hobbs et al., 2006).

Despite this recent evolution of approaches in invasion ecology, many papers still implicitly refer to an original and unspoiled state of nature wherein human beings are considered external, perturbing elements. Responding to this trend, the 19 ecologists voiced their concern in the recent publication by Davis et al. (2011), claiming the impracticability of ecosystem restoration as returning to some "rightful" historical state. They advocate for policy and management decisions to take into account the potential positive effects of many non-native species. Sousa et al (2011) related biological invasions to cases of increased ecosystem functioning.

As a consequence, policy and management objectives have to adapt to those new paradigms, using both ecological and economic findings. According to Shogren et al (2006), economists traditionally focus on socio-economic factors of invasion and their implications, while many ecologists do not consider how human action influence their study system. As identified by Settle, Crocker, & Shogren (2002), the two disciplines present however some convergence points in their methods, since they both are dealing with limits and scarcity : while ecology deals with resource availability, light, or energy constraints, economics deals with either budget or welfare constraints. Ecological research can contribute to the elaboration of diverse conservation scenarios and measure the impacts of policy alternatives on ecosystems. In choosing among those alternatives, social sciences such as economics have a role to play in understanding the socio-cultural and economic impacts of ecosystem dynamics and designing policies aimed at guiding ecological processes in the appropriate direction.

In economics, the aim of policy-making is generally to reach a well-specified and stationary goal. Considering invasion as a public bad to be prevented or eradicated, the equilibrium objective in many economic studies are generally aiming for the pre-existing ecosystem state, prior invasion. Accordingly, ecosystem transformations resulting from anthropogenic actions are for the most part considered necessarily detrimental. The categorization of a species as good, bad, or ambivalent is far from a trivial distinction. The usual assumption is that a first-best scenario regarding invasive species consists of isolating the pest and halting its proliferation. As such, most of the literature concentrates on prevention and control, and little attention is generally paid to management problems facing ambivalent, or mixed, impacts.

4. Note that this is still the case in current biogeographic models - e.g. neutral theory (Hubbell, 2001).

0.4 OUTLINE OF THE THESIS

Biodiversity measurement is crucial in order to prioritize species for conservation, or several preservation options. This measurement is not only a function of the traditional richness, evenness, and divergence, but also depends on many ecological factors such as ecological interactions, or the role of species in the ecosystem. Can we account for those ecological realities in order to provide accurate information for species selection? This thesis consists of four different chapters.

The first chapter raises the issue of dealing with invasive species, a considerable a challenge for biodiversity conservation. The complexity to manage those species is related to their inherently ambivalent character, i.e. not unequivocally good or bad, but depends mostly on the characteristics of the system in which it arrives. We define the notion of impact ambivalence and propose a methodology to assess ambivalence in impact using a typology, based on the identification of potential sources of impact variability : the variability of impacts across space, across time, and across stakeholders. In the light of this typology, we review the state of the art in impact assessment and propose a grid to assess ambivalence. This essay raises two key insights for the rest of the thesis : first, a modification of the ecological, but also the socio-economical context may modify management priorities ; and second, as most invasions are likely to produce both positive and negative impacts, the subjective aggregation of these impacts is often the only method allowing decision makers to rank the severity of biological invasions. This characteristic of the management process highlights the need for transparency in the choice of one management strategy over another.

The second chapter raises two major questions. If some measured categories of biodiversity may present potentially negative or positive impact, through its ecological and socio-economic context, how should it be measured? Facing the complexity of finding clear-cut management solutions for invasive "biodiversity", we have to go back at the roots of biodiversity measurement. What happens to the conservation policies outcomes if we account for interactions between species? This essay incorporates ecological interactions into the Noah's ark problem (Weitzman, 1998), and derives a general model for ranking *in situ* conservation projects. It provides an operational cost-effective method based on Weitzman's framework for the selection of best preserving diversity projects under a limited budget constraint. It results in two principal outcomes : first, with ecological interactions, the Noah's ark problem defined by Weitzman is still an extreme solution, i.e. the optimal protection policy gives full protection to a subset of species, partial protection for at most one species, and exposes the remaining species to the risk of no protection. Second, the ranking reversal is possible and completely defined by the categories of interactions. A small application to a two species case allows us to illustrate our results in basic situations of predation, mutualism, and competition.

Now, is Weitzman's index an appropriate diversity function? There exists plenty of other proposals in the literature, notably in the ecological literature. In the third chapter,

we chose to compare the outcomes of our previous *in situ* Weitzman's criterion, to another index applying the same *in situ* conditions : Rao's index of diversity or quadratic entropy. We analyze simple biodiversity protection plans for each index, and disentangle the role played by the different data requirement in the rankings in a three species ecosystem. This chapter delivers three important conclusions : (i) two indexes stemming from different academic backgrounds combine information about species survival probability, ecological interaction and distinctiveness in a different way to measure biodiversity ; (ii) such pieces of information will come as a trade-off when considered simultaneously in the measure ; (iii) the introduction of ecological interactions among more than two species lead to complex conclusions. Thus, the introduction of ecological interactions in each of those two frameworks seem to be an important additional information in order to determine conservation objectives.

Our last chapter is an adaptation of the previously defined optimization framework for the prioritization of invasive species management. This prioritization tool allows to determine which invasions must be controlled in priority, taking into account relative management costs and impacts of interactions across and within trophic levels. A key output of the paper is the design of a myopic rule, which may be used by a manager in order to efficiently allocate his budget to limit ecosystem disruptions. In order to determine whether we should retain for management several species or only a few under a budget constraint, we discuss the gradient of the objective function composed of the diversity function W and the utility function U , which can be set as concave or non-concave.

Therefore, this thesis offers several contributions :

- A methodological and interdisciplinary contribution, on understanding the context of invasion through the elaboration of a typology of invasion impacts
- Two theoretical contributions to the indicators literature.
- An extension of those theoretical contributions applied to our initial problem, the management of Non-Indigenous Species, which will be the object of future applications.

I

THE AMBIVALENCE OF BIOLOGICAL
INVASIONS IMPACTS : THE GOOD, THE
BAD, AND THE NEUTRAL

THE AMBIVALENCE OF BIOLOGICAL INVASIONS IMPACTS : THE GOOD, THE BAD, AND THE NEUTRAL

1

1.1 ABSTRACT

The nature and range of impacts associated with biological invasions – be they economic, social-cultural, or ecological – depend on many factors, including the location of the invasion in space and time, as well as the local perceptions attached to it. As these contextual factors vary, invasion-related impacts may switch from being positive to neutral or even negative. The ambivalent nature of these impacts makes impact assessment a difficult task and calls for an assessment methodology that enables policy makers to identify sources of impact variability. In this paper, we define the notion of impact ambivalence and propose a typology based on the identification of potential sources of impact variability. We distinguish between three types of ambivalence : the variability of impacts across space, across time, and across stakeholders. We then discuss impact assessment and biological invasion management in light of this typology. We review the state of the art in impact assessment and propose a grid to assess ambivalence. We focus on the socio-economic characteristics that make ecosystems resilient and conclude by making several key insights regarding impact assessment and management methods.

1.2 INTRODUCTION

Following the seminal paper of Sagoff (2005) that questioned whether biological invasions in fact threaten the natural environment, an intense debate over the impact of invasive species emerged in ecology (e.g. Simberloff, 2005, 2009; Simberloff et al., 2013; Evans et al. 2008; Davis et al. 2011). While scientists may disagree over the principal message they wish to communicate to the scientific community and to policy-makers – one party emphasizing the threat that these invasions pose and the corresponding need for vigilance, and the other dismissing it – they all agree on two major points : (1) not all non-native invasive species (NIS) are necessarily harmful, and (2) due to the scarcity of management resources, managers should prioritize their actions according to a ranking of the impacts associated with problematic NIS.

Identifying which invasions should be controlled first is far from a trivial matter. A NIS may negatively affect the economy or the biodiversity in one ecosystem, but not in another. Within a single ecosystem, a NIS may positively impact the economy, but negatively impact biodiversity, or vice versa. A NIS may also generate a positive economic impact for one group of stakeholders but a negative impact for another. In a similar manner, a NIS may have a positive ecological impact on one native species but a negative impact on another. Additionally, whether a NIS has a positive or negative impact in any of these domains depends on its timing and geographical spread. In contrast to a standard public bad such as pollution or greenhouse gas emissions, the impacts associated with biological invasions cannot be considered an unequivocal bad. Instead, the value of an invasion of this sort depends on a variety of contextual factors, including the perspective of the evaluating party.

For this reason, we reject in this paper the impact based interpretation of the Convention on Biodiversity (CBD article 8h), according to which an invasive species is an alien species whose introduction and spread threatens ecosystems, habitats, and biological diversity. Instead, we consider biological invasions in the context of more inclusive and

nuanced ecological and biogeographical considerations, and define an invasive species as a non-native species that settles and spreads in an ecosystem in which it previously did not exist (see Humair et al. 2014, Richardson et al. 2011, Blackburn et al. 2011 and the references therein for extended discussions on what constitutes a NIS).

Management strategy, and prioritisation strategy in particular, is rooted in an assessment of impacts that is explicitly concerned with context and perspectives (Kueffer et al. 2007). In particular, the relation between contextual elements and the resulting variability of impacts is a crucial consideration in the management of biological invasions. Previous research on NIS has attempted to separately generalise the traits of problematic invaders and the characteristics of vulnerable habitats (Drake et al., 1989, Kolar and Lodge 2001). This approach has allowed for the development of heuristics used to predict the invasiveness of a species and the vulnerability of native habitats to these species. Yet, as noted by Kueffer and Hirsch Hadorn (2008) and Kueffer and Daehler (2009), no integrative framework currently exists that enables decision-makers to understand the interactions between species, the socio-ecological environment, and human actions.

This paper seeks to better understand how the same NIS may switch from the status of a public good to the status of a public bad. We distinguish between three categories of impacts resulting from NIS and propose a typology of the ambivalence of impacts on the basis of a set of examples. Ambivalence is measured on three distinct scales : the spatial scale, the time scale, and the socio-economic scale. The impact of a NIS at each of these scales may change direction, and we seek to examine the factors responsible for such changes. Complementing the literature on ecological characteristics, we examine the socio-economic characteristics that contribute to the vulnerability and resilience of coupled social and ecological ecosystems. We then derive insights for management and explain how impact assessment could make use of this typology and of the assessment grid we develop in order to identify effective management priorities.

The paper is organized as follows. First, we define impacts and the notion of impact

ambivalence and propose a typology of impact variability. Second, we discuss the use of an assessment grid based on this typology. Next, we examine the socio-economic characteristics that make socio-ecological systems resilient to NIS and focus on the characteristics of these systems that are prone to producing impact ambivalence. We conclude with a discussion of implications for management strategies and insights regarding the advancement of this interdisciplinary field.

1.3 DEFINING IMPACT AMBIVALENCE

Before discussing each form of ambivalence on the basis of several examples, it is useful to define precisely what we mean by space, time, and stakeholders. Space refers to the geographic location where the invasion occurs. Because our analysis aims at accounting for economic, socio-cultural, and ecological impacts, the notion of a purely biological ecosystem is too narrow as a measure of location. Instead, we consider a larger notion of an ecosystem, integrating in our definition both the natural processes as well as anthropogenic inputs that comprise the economic and social networks of the system at hand. This is what we hereafter refer to as a 'socio-ecosystem' (Gunderson and Holling, 2002), which is the scale at which we study invasions. Time refers to the commencement and duration of the impacts associated with an invasion. Time is a useful proxy not only for the magnitude of the invasion, but also for the adaptive capacity of the socio-ecosystem to handle the negative impacts incurred by a non-native species. The term stakeholders refers to the different human groups impacted by the invasion. Each of these groups may be socially, economically, and/or ecologically impacted. Stakeholders can be, for example, farmers who suffer economic impacts from an invasion ; tourists whose recreational activities may be affected ; or even any member of the socio-ecosystem who may attribute a positive or negative non-use value to a non-native species.

1.3.1 A typology of ambivalence

Ambivalence across space Concentrating first on the **spatial dimension**, which serves as the major source of impact ambivalence, we observe very different impacts from one socio-ecosystem to another. With respect to economic impacts, two geographically separated systems may experience significant differences in the degree of impacts felt by biological invasions due to differences in the structure of the economic organizations in each system. The overall impact of an invasion will be more significant in an economy that directly depends on the natural resources affected relative to an economy that is less reliant on these natural resources. For example, an invasion by an aquatic plant such as the water hyacinth (*Eichhornia crassipes*) would have a colossal negative impact on African fishing communities that are exclusively dependent on river resources, such as around the Lake Naivasha, in Kenya, as the plant covers the water and inhibits boat travel. Conversely, the water hyacinth can be used as an effective solution for wastewater treatment (Malik 2007), and has been proved to be a good forage for pigs in many parts of the world (Little ECS, 1968, Waithaka, 2013), and thus could conceivably provide some economic benefits as a NIS in this area. In Florida, the Brazilian pepper tree (*Schinus terebinthifolius*) is of no economic interest and is perceived as an environmental weed, whereas rural people living on Reunion Island harvest the same species for consumption and sale (Tassin et al., 2006). In economic systems that do not rely heavily on natural resources, the direct economic impacts of invasion by an aquatic plant would be lower than it is in the cases above. One example could be invasion by the rampant primrose willow (*Ludwigia peploides*), which results in impacts that are more environmental or social than economic (Kull et al., 2014).

The social and cultural dimensions of invasions are crucial aspects of the evaluation of impacts. The socio-cultural impacts associated with NIS may vary significantly depending on the socio-ecosystem. Whether a NIS is perceived in a positive or negative light depends on local attitudes towards nature and the implicit choices made by society based on their relationship with the natural landscape. Several NIS tend to be viewed

positively in some societies and negatively in others, which lead to very different ways in which each society perceives and confronts the impacts associated with these species. For instance, Australian Aborigines often resist programs designed to eradicate feral species, believing that the worth of a species lies in its ability to flourish in an environment and not in its claim to being an original inhabitant (Warren, 2007). In occidental countries, the same species may be perceived favorably by the general public but disliked by farmers, independently of the impacts associated with the species. This is typically the case of the coypu (*Myocastor coypus*) in France (Mougenot and Roussel, 2006). A grim example of this type of preference are the bioxenophobic attitudes held by the Nazis, who promoted the utilization of exclusively native plants in horticultural landscapes (Wolschke-Bulmahn, 1996).

Finally, **ecological impacts** may also differ significantly across contexts depending on the ecosystem or range of ecosystems in which a NIS settles, first due to the geographical, topological, climatic characteristics of the ecosystem, but also due to the pre-existing species found in each ecosystem. Some introduced species can remain very localized, while others may spread and become very common. The Eurasian milfoil (*Myriophyllum spicatum*), for instance, has shown high rates of propagation in some areas, and declining populations in others (Perry and Deller, 1996). The nature of the ecological impact associated with a NIS may also depend on the spatial scale we examine. The effect of invasive plants on pollination processes depends on the spatial scale of the invasion, which may be negative if only local native plants are affected, but become positive at a landscape scale (Bjerknes et al., 2007).

Ambivalence across time Within the same socio-ecosystem, the variability of impacts may be measured at different points in time. The impact of an invasion is correlated with the range of the invasion, but also to the adaptive capacity of the socio-ecosystem to cope with the invasion.

While economic impacts may be non-existent at the beginning of an invasion, they

can gain importance over time. Conversely, impacts may be negative at a certain point in time but become positive as the society economically adapts to the new situation through the invention of new regulating technique or adoption of new economic outlets used to regulate the invasion. For example, in the highlands of Madagascar, the invasive mimosa (*Acacia dealbata*) has been deeply integrated into some agricultural systems. Once considered a weed, it has become a useful and celebrated shrub in this region (Kull et al., 2007).

Similarly, a supposed NIS may become naturalized over time and eventually accepted as no longer problematic. The perception of an invasion may change over time and over generations as a species may become more and more integrated in local landscapes and the social habits that engage these landscapes. When the little owl (*Athena noctua*) was introduced in Great Britain during the 1930's, it was considered a serious threat towards native species and was therefore nearly exterminated. Since that time, its cultural value has been reversed such that the owl has now become a favourite bird among local ornithologists (Rotherham, 2012). The perception of the black cherry (*Prunus serotina*) in Europe has also undergone changes over time, as it was at first strongly resisted and later widely accepted (Starfinger et al., 2003). Moreover, some plant invasions are so ancient that local people consider the species as native instead of introduced. Furthermore, the technical ability of societies to address the proliferation of NIS develops over time, as well. This is important to note given that biological control plans are generally accomplished over long periods of time.

Finally, the environment itself may also adapt to a NIS over time, such that impacts that occur at the beginning of invasion may evolve, for example, as the density of invasion increases. In New Zealand, the European shrub gorse (*Ulex europaeus*) is more adapted to ecological disturbances than the native myrtaceous manuka (*Leptospermum scoparium*), and provides valuable substitute habitat for native invertebrates (Harris et al., 2004). In northern New South Wales, Australia, several native pigeons rely on the fruit of camphor

laurel (*Cinnamomum camphora*) as their principal food during certain periods of the year (Date et al., 1996). Furthermore, some invasions may have positive outcomes under a certain density, especially in degraded habitats. It is commonly recognized, for instance, that bird reproduction rates are not altered by low and moderate invasions of non-native plants, but are reduced in highly invaded habitats (Grant et al., 2004 ; Ma et al., 2011). Finally, as ecosystems are constantly in various states of transformation, the impact of a NIS may change over time due to a modification in the nature of the relationships between native species or to the spontaneous introduction of another NIS. These transformations may allow certain species to compete more efficiently with the invader and regulate the overall provision level of the ecosystem or, alternatively, to aggravate the problem and instigate a cascade of ecosystem disruptions. On Reunion Island for example, the introduced *Clidemia hirta* both provides fruit for native birds and alters the physiognomy of native vegetation. The subsequent introduction of *Pycnonotus jocosus* has reinforced the dispersal capacity of *C. hirta* on the upward side of the island ; but it has also been observed to be an active predator of weevils, which can themselves attack native plants (Mandon-Dalger et al., 2004).

Ambivalence across stakeholders According to characteristics of the particular socio-ecosystem under consideration, anthropological, ecological, and economic impacts may burden some stakeholders more than others.

From the **economic standpoint**, stakeholders may be differentiated by sector, by industry, or by firm. According to these differences, they may have different levels of resilience to an invasion, and thus exhibit varying levels of interest in the invasion itself. For instance, while the allergenic annual ragweed (*Ambrosia artemisiifolia*) is a scourge for public health services and for allergic individuals, it is virtually ignored by every others (Solmon et al., 2014). Another example is given by weeds, which represent a significant nuisance to many agricultural crops. Within the agricultural sector, each crop generally encounters particular invaders. On Reunion Island, the red-whiskered bulbul (*Pycnonotus jocosus*) is

problematic for the owners of fruit orchards, but not for those working in other agricultural sectors (Amiot et al., 2007).

Socio-cultural or psychological impacts may also vary across stakeholders, depending on their capacity to deal with the NIS, the aesthetic and recreational importance they place on the impacted landscape, and the role that native species or communities of species play in their livelihoods and every day lives. For instance, plans to eradicate feral domestic mammals (e.g. camels in Australia, deer in New Caledonia, gray squirrels in Europe) often encounter opposition from a segment of the public, while being approved of by the rest (Simberloff et al., 2013). Sensitivity to NIS may also differ within a single family depending on aesthetic values, education, personal experience, and individual interests.

The set of ecological impacts within a socio-ecosystem may also vary widely. In many circumstances, the introduction of a NIS positively impacts one native species but negatively impacts another. One example among many is the ecological impact of the red swamp crayfish (*Procambarus Clarkii*) in the Camargue socio-ecosystem in southern France. The rapid propagation of this crayfish in lagoons significantly impacted the ecosystem by transforming the nature of species interdependence in the affected habitat. The crayfish caused a decline in the population of aquatic vegetation (macrophytes), as well as a decline in the population of native crayfish through the introduction of a parasitic mycosis (*Aphanomyces astaci*). However, it positively impacted several populations of native birds including the Glossy Ibis (*Plegadis falcinellus*), Eurasian Spoonbill (*Patalea Leucorodia*), and Western Cattle Egret (*Bubulcus Ibis*) (Kayser et al. 2008). Thus, ecologists who place importance on native biodiversity may view this invasion negatively, whereas ornithologists may well perceive it positively. Taking into account the fact that stakeholders can be impacted socially, economically, as well as ecologically, and the fact that NIS cause impacts that may be positive in one domain but negative in another, the probability that an invasion creates both winners and losers is often very high.

1.4 ASSESSING THE AMBIVALENCE OF IMPACTS

Assessment of impacts is particularly problematic in the context of a precautionary management approach that builds on an ability to predict potential future impacts. Risk assessment approaches were launched in the late 1990's with the purpose of ranking impacts and prioritizing management actions to address the worst invasions. In particular, risk assessment tools have been designed in order to assess the riskiness of an invasion according to the context of the country in which it occurs, e.g. Australia (Pheloung et al., 1999), Pacific islands (Daehler, 2004) and South Africa (Roura-Pascual et al., 2010). The focus of these studies is on the vulnerability of ecosystems to invasion, and although Roura-Pascual et al. (2010) also mention social context and stakeholders, ecological context remains their central feature.

Ecological typologies have been produced to complement these approaches, such as the habitat classification framework for decision makers (Kueffer and Daehler, 2009) or typologies of species characteristics that predispose them to becoming invasive (Foxcraft et al. 2007). Socio-economic characteristics of socio-ecosystems have recently received increased attention, with studies assessing management priorities on the basis of deliberative multicriteria evaluation techniques (Cook and Proctor, 2007; Monteroso et al., 2010) and scenario scoring approaches (Nentwig et al., 2010; Kumschick et al., 2012). The idea of these approaches is to enable stakeholders to rank invasion scenarios that describe the socio-ecological impacts of a NIS as exhaustively as possible. These scenarios are at the cornerstone of the assessment process and should therefore account for ambivalence in impacts.

1.4.1 Making use of a typology of ambivalence

As noted by Kumschick et al. (2012), a main limitation of scoring approaches and other prioritization tools is their strict focus on the unwanted changes that arise from invasions. Studies rarely take into account the positive changes that might result from

| IMPACTS CATEGORIES \ FOCUS SCALE | SPATIAL SCALE | TIME SCALE | STAKEHOLDERS SCALE |
|----------------------------------|---|---|---|
| ECONOMIC | <i>Eichhornia crassipes</i> : impact on fishing in South Africa/used as forage in Madagascar | <i>Brazilian Pepper tree</i> : from weed to harvested species on the Reunion Island | <i>Pycnonotus jocosus</i> : impact on fruit orchards but not on other types of agricultural crops |
| SOCIO-CULTURAL | <i>Myocastor coypus</i> : positive perception by the general public, negative by farmers | <i>Acacia dealbata</i> : from weed to celebrated shrub in Madagascar <i>Athena noctua</i> : from threat to symbol in Great Britain | <i>Ambrosia Artemisiifolia</i> : allergenic impact on some individuals but not on others |
| ECOLOGICAL | <i>Myriophyllum spicatum</i> : depending on ecological conditions ; abundant in some zones/rare in others | <i>Ulex europaeus</i> : from invasive to valuable substitutive habitat for native invertebrates, across time, with increased density | <i>Procambarus Clarkii</i> : negative impact on aquatic species / positive impact on birds |

TABLE 1.1 – Identification of species likely to exhibit impact ambivalence, examples

species introductions (Wainger and King, 2001), such as increasing population densities of threatened native species (Schlaepfer et al., 2011 ; Schlaepfer et al., 2012) or economic benefits (Leung et al., 2012).

An important step in impact assessment in general and in scenario building in particular is to examine whether the impact of a NIS is likely to be ambivalent. The typology presented above is useful in achieving this task as it decomposes the types of ambivalence according to the categories of impacts. It can be summarized in a 3X3 matrix, which we illustrate in the above Table 1.1 with several different species cited as examples in the description of our typology.

The purpose of using this typology matrix is to identify the potential sources of impact ambivalence within a given socio-ecosystem. For each NIS identified, we seek to

distinguish the three categories of impacts and to examine whether each category is likely to exhibit ambivalence according to the spatial scale, the timeframe, and the stakeholders involved. Once a list of NIS that are likely to cause ambivalent impacts is created using this matrix, the next step in scenario building is to assess the likelihood of impact ambivalence according to the ecological and socio-economic characteristics of the socio-ecosystem. These characteristics are indeed the key factors required when quantifying the propensity for ambivalence and assessing the resilience of a socio-ecosystem to a NIS.

Socio-ecosystem characteristics Social factors interact in complex ways to initiate and sustain different facets of biological invasions (Kueffer and Hirsch Hadorn, 2008), and several studies have highlighted the role of economic factors in the introduction and spread of the impacts resulting from non-native species (Spangenberg 2007; Binimelis et al., 2007; Rodriguez-Labajos et al., 2009; Kueffer et al., 2010; Pysek et al., 2010; Jeschke and Genovesi, 2011). Kumschick et al. (2012) discuss the ‘circumstances of the infestation’ as important in informing the choice of which species should be actively managed. Because conservation budgets are limited, even if a NIS is unequivocally more harmful than any other, management may well target another NIS that is cheaper to control in order to maximise the benefit/cost ratio of the action taken. The contextual factors of the scenario as well as the methods available to mitigate negative impacts are likely to modify these ratios and should be carefully taken into consideration when assessing impact scenarios and priorities. Three elements of the socio-economic context are particularly relevant in understanding why a socio-ecosystem is more vulnerable to one NIS over another : (1) the socio-economic organization of the system, (2) the availability of technologies for prevention and control, (3) socio-cultural perceptions toward the NIS.

Each of these contextual elements are zone specific and rely on a large set of qualitative and quantitative characteristics, such as the wealth and density of the population, the predominant type of economic activity, the degree of urbanization and dependency on natural resources, and even the cultural acceptability of the NIS in the eyes of the

stakeholders. In addition to influencing the vulnerability/resilience of a socio-ecosystem to a NIS, these socio-economic characteristics are vectors of impact ambivalence, as they interact to determine the adaptive capacities of the socio-ecosystem.

Many studies have attempted to understand the ecological traits that contribute to making some ecosystems more vulnerable (respectively resilient) than others (e.g. the habitat classification of Kueffer and Daehler (2009)). Identifying the socio-economic criteria that make socio-ecosystems vulnerable/resilient to one NIS or another attracted less attention.. Notable exceptions are the work of Binimelis et al. (2007), Rodriguez-Labajos et al. (2009) or Rodriguez-Labajos (2014). This later work distinguishes risk, uncertainty, and ignorance factors making socio-ecosystem vulnerable to invasions, and examines feasible prevention and adaptation strategies for the management of NIS (i.e. case study on the management of the zebra mussel in the Ebro region). As a preliminary step toward the prioritization of management activities, we propose using similar socio-economic information in order to screen which NIS are likely to be the most problematic.

Socio-economic characteristics can hardly be considered independently from one another. For example, even if a socio-ecosystem with an important primary sector is usually more vulnerable to a pest like water primrose (*Ludwigia peploides*) relative to a socio-ecosystem with an important tertiary sector, then differences in wealth, technologies, or even leisure activity between the two socio-ecosystems may result in the second system effectively being more vulnerable than the first. Notably, it is the complementarity between socio-economic characteristics that determines a socio-ecosystem's resilience to NIS. As a consequence, modifying only one socio-economic characteristic may or may not produce ambivalence in impacts. Moreover, as highlighted in several illustrations in our typology, a socio-ecosystem with a set of socio-economic characteristics may be vulnerable to one category of NIS but adaptable to another, while the reverse may be true in a different socio-ecosystem characterized by different contextual factors. A non-exhaustive list

| IMPACTS CATEGORIES SOCIO- ECOSYSTEM CHARACTERISTICS | ECONOMIC | SOCIO-CULTURAL | ECOLOGICAL |
|---|---|--|---|
| SOCIO-ECONOMIC ORGANIZATION | Economic sectors (primary, secondary, tertiary), economic activity, dependency on natural resources, urbanization, population density, wealth | Wealth, cultural identity, immigration, inequalities, education, rurality | Economic sectors, population density, land use and interference of socio-economic organization on habitats, recreational activities |
| TECHNOLOGIES | Availability, affordability, and efficiency of impact mitigation techniques, RD, adaptive capacities | Availability, affordability and efficiency of traditional practices to mitigate impacts | Availability, affordability and efficiency of control techniques, RD, adaptive capacities |
| SOCIO-CULTURAL PERCEPTIONS | Exposure to invasions, responsibility in the invasion process, age of the invasion | 'Observability' of the NIS, media coverage, degree of 'sympathy' of the species, status as a flagship species, cultural relationship to Nature | Population awareness of ecosystem services |

TABLE 1.2 – Description of socio-ecosystem characteristics relatively to the three main impact categories

of characteristics relevant to the understanding of the socio-economic variables making ambivalence likely is presented in Table 1.2.

Although we are unable to deduce from this table a straight classification of which socio-economic environments are more vulnerable or resilient to a NIS than others, gathering this information is nonetheless a key step for understanding and assessing cases of ambivalence and the relative impacts of NIS. Socio-ecosystems may well cope with some categories of invasives but not with others, and only a careful examination of the economic sectors at risk, the available mitigation technologies, and the adaptive capacities and

willingness of stakeholders to accommodate a NIS into their landscape will allow us to screen which biological invasions should be management priorities.

1.5 CONCLUSION

The principal achievements of this paper are to (i) contribute to the understanding of the impacts associated with biological invasions by defining a typology of ambivalence ; (ii) highlight the challenges posed by the socio-ecological context of biological invasions ; (iii) propose a methodology to assess ambivalence in impact assessments. Two key insights regarding the management of NIS can be distilled from this work. The first is that a modification of the ecological, but also of the socio-economical context, may modify management priorities. Only an exhaustive understanding of the context and of the adaptive capacities of the socio-ecosystem will enable decision makers to prioritize management actions efficiently. The second insight is that NIS impacts are highly heterogeneous and disparate. Only a few non-native species will become invasive and among these, impacts will be negative only under specific ecological and socio-economic contexts. Most invasions are likely to produce both positive and negative impacts, and subjective aggregation of these impacts is often the only method that allows decision makers to rank the severity of biological invasions. This characteristic of the management process highlights the need for transparency in the choice of one management strategy over another.

II

CONSERVATION PRIORITIES WHEN SPECIES INTERACT : THE NOAH'S ARK METAPHOR REVISITED

CONSERVATION PRIORITIES WHEN SPECIES INTERACT : THE NOAH'S ARK METAPHOR REVISITED

2.1 ABSTRACT

This note incorporates ecological interactions into the Noah's Ark problem. 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.

2.2 INTRODUCTION

Weitzman (1998) is a milestone in the economic theory of biodiversity. His Noah's Ark 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 :

$$R^i = \frac{\Delta P_i}{C_i} (D_i + U_i), \quad (2.1)$$

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).

This criterion sheds light on real biodiversity issues and has actually been used in several applications. Some of these have led to changes in allocation of conservation funding (e.g., in New Zealand, Joseph et al. 2008), and variants have been used to allocate surveillance effort over space (e.g. Hauser & McCarthy, 2009). Other applications are quoted in (Eppink et al., 2007). But it is fair to say that this approach 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 (2.1) 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 survival 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 (2.1) 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 (Baumgärtner 2004, Simanier 2008) or three species (Van der Heide, 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 Ark, 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 (2.12) below that encompasses formula (2.1) 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 check the robustness of our formula and end the paper with a discussion on the possibility of ranking reversal in relation to three stylized kinds of ecological interactions : *predation*, *mutualism* and *competition*.

2.3 ANALYSIS

The "Noah's Ark Problem" is a parable intended to be a kind of canonical form representing how best to preserve biodiversity under a limited budget constraint. 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, $P_i \in [\underline{P}_i, \bar{P}_i]$, in order to maximize the sum of the *expected diversity function* :

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

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 defining the expected diversity function $W\left(\{P_i\}_{i=1}^k\right)$ and to explaining its link with the concept of information content (see his Theorem 1, p. 1284). This function could take various specific forms, depending on the way dissimilarity is conceptualized. A precise example, from Weitzman (1998) , is discussed in Section 4. In order for our results to remain as general as possible, we simply

consider in this paper the class of C^2 functions, *i.e.* whose first and second order derivative both exist and are continuous.

And we assume they admit Hessian matrices that are *nowhere* negative semi-definite, *i.e.* there is no admissible $\{P_i\}_{i=1}^k$ such that the Hessian of $W(\{P_i\}_{i=1}^k)$ is negative semi-definite at $\{P_i\}_{i=1}^k$. Weitzman's expected diversity function belongs to this class. 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 $i = 1, \dots, k$, Noah can exert a protection effort within an admissible range, $x_i \in [0, \bar{x}_i]$, 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, the provision of supplementary food, the protection and enhancement of habitat (Garnett & Crowley, 2000). It is important to distinguish the effort from the change in the 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 the nature of those interactions are known. Nowadays, Noah can rely on the knowledge gained from the new and booming conservation biology literature on *species distribution models* and *population viability analysis*. See for instance Burgman et al. (1993), Witting et al. (2000), Guisan & Thuiller (2005), or Elith & Leathwick (2009) for a recent overview. Note that this literature does not take into account directly of species interactions ; it just provides estimates of probabilities in space and time. From there, although applied econometric problems will have to be overcome, correlations between probabilities could be estimated.

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 spe-

cies i . The experts can also appraise the impact of protection efforts on these probabilities. Assume, then, that the relationships between extinction risks are linear. Put differently, a tractable approximation of all those pieces of information can be summarized by the system (2.2) of linear equations :

$$P_i = q_i + x_i + \sum_{h \neq i} r_{ih} P_h, \quad q_i \in [0, 1[, \quad x_i \in [0, \bar{x}_i]. \quad (2.2)$$

There are biological and economic factors that determines eligible efforts. Formally, *admissible* ranges of efforts are $\times_{i=1}^k [0, \bar{x}_i]$. Implicitly, additional efforts beyond the threshold \bar{x}_i have no effect on the survival probabilities. And we assume :

$$P_i \in \Pi_i = [\underline{\Pi}_i, \bar{\Pi}_i] \subseteq [0, 1], \quad \forall i, \quad \forall x_i \in [0, \bar{x}_i].$$

Because probabilities are conceived as the solution to a system of simultaneous equations, identifying the admissible range of efforts is not an easy work. Each single bound cannot be found in isolation from the other bounds ; they all have to be considered simultaneously. Fortunately it is possible to get around this issue. In Appendix A we propose an algorithm that provides the admissible ranges of efforts. We denote \underline{P}_i as the survival probability of species i without any conservation efforts, $x_i = 0, \underline{P}_i \geq \underline{\Pi}_i$. In the absence of natural interactions, which corresponds to the case studied by Weitzman, we have $r_{ih} = 0, \forall i, \forall h$. A consequence is that in the very particular case with no ecological interactions and no conservation efforts, species i has a probability of survival q_i . The survival probabilities interval, without ecological interactions, would thus take values ranging from $\underline{P}_i = q_i$ to $\bar{P}_i = \underline{P}_i + \bar{x}_i$.

Noah also has to cope with a budget constraint :

$$\sum_{i=1}^k \beta_i * x_i \leq B. \quad (2.3)$$

where B is the total budget to be allocated to conservation - metaphorically, the size of the Ark - and β_i is the cost per unit of effort to preserve species i .

It is worthwhile making three remarks about this budget constraint. Firstly, it is assumed that changes in extinction probability are a linear function of expenditure. This

may be inconsistent in real world applications where the marginal expense needed to reduce extinction risks is increasing. For example, McCarthy et al. (2008) documents that the marginal preservation cost of threatened Australian birds increases when probability of extinction approaches zero. Weitzman rightly defends this linearity assumption as an acceptable approximation when the variation of probability falls in a sufficiently narrow range. But clearly, if costs are non linear and convex functions of efforts, an important qualitative result of our paper could change (Theorem 2.1 below may not hold any longer). Secondly, as a formal matter one could retrieve Weitzman's model with a simple change of variable, $\beta_i \equiv C_i / \Delta P_i$ where C_i is the cost per unit of increase of survival probability in the range $\Delta P_i = \bar{\Pi}_i - \underline{\Pi}_i$. Thirdly, 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 $\beta_i * x_i$, and an indirect one through ecological interactions, due to the protection of another species j , with a cost $\beta_j * x_j$.

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

$$\max_{\{x_i\}_{i=1}^k \in \times_{i=1}^k [0, \bar{x}_i]} W \left(\{P_i\}_{i=1}^k \right) + U \left(\{P_i\}_{i=1}^k \right), \quad (2.4)$$

subject to (2.2) and (2.3).

It will be convenient subsequently to work with matrix or vector expressions, written in bold characters. For any matrix \mathbf{M} , let \mathbf{M}^\top denote its transpose. Further, \mathbf{I}^k is the $(k \times k)$ identity matrix, $\mathbf{1}^k$ is the k dimensional column vector whose elements are all 1, and we recall the following definition of inequality between two k -dimensional vectors \mathbf{m} and \mathbf{n} with components m_i and n_i respectively : $\mathbf{m} \leq \mathbf{n}$ if $m_i \leq n_i$, for all $i = 1, \dots, k$. The other basic relationships between vectors are : i) $\mathbf{m} = \mathbf{n}$ if $m_i = n_i$, for all $i = 1, \dots, k$, ii) $\mathbf{m} < \mathbf{n}$ if $m_i < n_i$, for all $i = 1, \dots, k$, iii) $\mathbf{m} \leq \mathbf{n}$ if $m_i \leq n_i$, for all $i = 1, \dots, k$, and $\mathbf{m} \neq \mathbf{n}$. We also need basic matrix operations, "+", "-" and "*", that refer to, respectively the addition, the subtraction and the multiplication.

Let us define :

$$\begin{aligned}
 \mathbf{Q} &\equiv \begin{bmatrix} q_1 \\ q_2 \\ \vdots \\ q_k \end{bmatrix}, \quad \mathbf{R} \equiv \begin{bmatrix} 0 & r_{12} & \dots & r_{1k} \\ r_{21} & 0 & \dots & r_{2k} \\ \dots & \dots & \ddots & \dots \\ r_{k1} & r_{k2} & \dots & 0 \end{bmatrix}, \quad \mathbf{P} \equiv \begin{bmatrix} P_1 \\ P_2 \\ \vdots \\ P_k \end{bmatrix}, \quad \boldsymbol{\beta} \equiv \begin{bmatrix} \beta_1 \\ \beta_2 \\ \vdots \\ \beta_k \end{bmatrix} \\
 \bar{\mathbf{P}} &\equiv \begin{bmatrix} \bar{P}_1 \\ \bar{P}_2 \\ \vdots \\ \bar{P}_k \end{bmatrix}, \quad \underline{\mathbf{P}} \equiv \begin{bmatrix} \underline{P}_1 \\ \underline{P}_2 \\ \vdots \\ \underline{P}_k \end{bmatrix}, \quad \mathbf{X} \equiv \begin{bmatrix} x_1 \\ x_2 \\ \vdots \\ x_k \end{bmatrix}, \quad \bar{\mathbf{X}} \equiv \begin{bmatrix} \bar{x}_1 \\ \bar{x}_2 \\ \vdots \\ \bar{x}_k \end{bmatrix}
 \end{aligned}$$

In matrix form, the system (2.2) reads as :

$$\mathbf{P} = \mathbf{Q} + \mathbf{X} + \mathbf{R} * \mathbf{P}. \quad (2.5)$$

Throughout this article, we will assume :

Assumption 2.1 (INV) *The matrix $\mathbf{I}^k - \mathbf{R}$ is invertible.*

Under Assumption (INV), the system (3.2) can be solved to give :

$$\mathbf{P} = \boldsymbol{\Lambda} * (\mathbf{Q} + \mathbf{X}), \quad (2.6)$$

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

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

$$\underline{\mathbf{P}} = \mathcal{P}(0 * \iota^k), \quad (2.7)$$

where $0 * \iota^k$ is a vector made of k zeroes. Without ecological interactions, $\boldsymbol{\Lambda}$ is the identity matrix, $\underline{\mathbf{P}} = \mathbf{Q}$ and $\bar{\mathbf{P}} = \underline{\mathbf{P}} + \bar{\mathbf{X}} = \mathbf{Q} + \bar{\mathbf{X}}$.

Now we can plug (3.3) into (2.4) to get rid of probabilities, and express Noah's problem only in terms of efforts. Define the two *composite* functions, which here are mappings from

the values taken by function $\mathcal{P}(\mathbf{X})$ to the set of real numbers :

$$W \circ \mathcal{P}(\mathbf{X}) \equiv W(\mathcal{P}(\mathbf{X})),$$

$$U \circ \mathcal{P}(\mathbf{X}) \equiv U(\mathcal{P}(\mathbf{X})).$$

Under Assumption (INV), to each vector \mathbf{X} corresponds a unique vector $\mathbf{P} = \mathcal{P}(\mathbf{X})$. Therefore we can define Noah's problem with ecological interactions, the constrained maximization of a function of protection efforts \mathbf{X} :

$$\max_{\mathbf{X}} W \circ \mathcal{P}(\mathbf{X}) + U \circ \mathcal{P}(\mathbf{X}), \quad (2.8)$$

subject to :

$$\beta^\top * \mathbf{X} \leq B, \quad (2.9)$$

$$0 * \iota^k \leq \mathbf{X} \leq \bar{\mathbf{X}}. \quad (2.10)$$

2.4 RESULTS

Two questions arise : *i*) could anything general be said about the solution to the problem expressed by (2.8), (2.9), (2.10)? And *ii*), taking a more practical stance, could we engineer a simple rule that approximates the general solution?

2.4.1 Noah's policy is extreme

Weitzman (1998) showed that the solution to Noah's problem lies on the boundary of the efforts set. As the set of constraints is made of linear constraints, the boundary involves corners, e.g. $x_i = 0$ or $x_i = \bar{x}_i$, and possibly a segment between two corners, therefore with $x_i \in [0, \bar{x}_i]$ for at most one species. This can be defined as an *extreme policy*. In words, the optimal protection policy gives full protection to a subset of species, partial protection for at most one species, and exposes the remaining species to the risk of no protection.

But what if probabilities are interdependent? We show that when species interact, the optimal solution is also extreme.

Theorem 2.1 *The solution to Noah's Ark problem with ecological interactions, defined by (2.8), (2.9) and (2.10), is an extreme policy.*

Proof. The proof rests on two pieces of information :

- i) Noah's 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.

In order to prove item ii), because $U \circ \mathcal{P}(\mathbf{X})$ is linear, we just have 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 $\mathcal{P}_h(\mathbf{X})$, $h = 1, \dots, k$, and let $J_{\mathcal{P}}(\mathbf{X})$ stand for the *Jacobian* matrix :

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

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 :

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

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 :

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

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 :

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

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

2.4.2 A ranking rule for interacting species

Theorem 2.1 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 (2.1) 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 (2.1) to species (those grades depend on the model parameters) and order 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** (see Baumol & Bushnell, 1967) and should not be followed blindly. Nevertheless, as proven in Theorem 2.2 below, there is something special about Noah's problem that makes this practice appropriate here.

Let us denote :

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

and define the two matrices :

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

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

$$\max_{\mathbf{X}} \mathbf{Y} * \mathbf{X} + \text{constant terms}, \quad (2.11)$$

subject to (2.9) and (2.10).

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 $\mathbf{Y} \equiv \mathbf{A}^\top * \mathbf{\Lambda}$ 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 $\mathbf{\Lambda} = [\mathbf{I}^k - \mathbf{R}]^{-1}$. Given that $\mathbf{I}^k - \mathbf{R}$ is invertible, the computation of the matrix $\mathbf{\Lambda}$ is easily made and if Λ_{ij} denotes a typical element of $\mathbf{\Lambda}$, then \mathbf{Y} is a k -dimensional line vector of the type :

$$\mathbf{Y} = [\alpha_1, \alpha_2, \dots, \alpha_k],$$

where

$$\alpha_i \equiv \sum_{h=1}^k (D_h + U_h) \Lambda_{hi}.$$

We can now define the "benefit"-cost ratios $\bar{R}^i \equiv \alpha_i / \beta_i$, or with explicit reference to relevant information :

$$\bar{R}^i \equiv \frac{\Delta P_i}{C_i} \sum_{h=1}^k (D_h + U_h) \Lambda_{hi}, \quad i = 1, \dots, k. \quad (2.12)$$

As it is well-known, the argmax to the linear programming problem (2.11) is to fully protect the species with the highest grade \bar{R}^i , then the species with the second highest grade, and so on and so forth, up to the point where the budget is exhausted. It means that there exists a threshold value \bar{R}^* such that all species i with $\bar{R}^i < \bar{R}^*$ are not embarked in the Ark, whereas those with grade larger than the threshold are all fully protected, except for at most one species with grade exactly equal the cutoff value \bar{R}^* that is only partially protected. Let us call \mathbf{X}^W this policy, which can be described formally as follows :

$$\left\{ \begin{array}{lll}
 \text{if } \bar{R}^i < \bar{R}^* , & \text{species } i \text{ is granted zero protection,} & \implies x_i = 0 , \\
 \text{if } \bar{R}^i > \bar{R}^* , & \text{species } i \text{ is granted full protection,} & \implies x_i = \bar{x}_i , \\
 \text{if } \bar{R}^i = \bar{R}^* , & \text{species } i \text{ is granted full protection} & \\
 & \text{if there is enough budget,} & \implies x_i = \bar{x}_i , \\
 & \text{otherwise the remaining budget} & \implies x_i \in]0, \bar{x}_i[. \\
 & \text{funds its partial protection,} &
 \end{array} \right. \quad (2.13)$$

As shown in Theorem 2.2 below, \mathbf{X}^W is a first order approximation of the optimal solution to Noah's Ark problem with ecological interactions. Put differently, there is a sense in which expression (2.12) 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, $\sum_{h=1}^k (D_h + U_h) \Lambda_{hi}$, 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, Λ is the identity matrix, with $\Lambda_{ii} = 1, \Lambda_{hi} = 0, \forall h \neq i$, and (2.12) boils down to Weitzman's original system of grades for species i :

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

One can ask to what extent can we rely on formula (2.12) to build a hierarchy among species? Can a 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 important for the problem at hand : *i*) a linear approximation to a nonlinear program need not provide an answer better than a randomly chosen admissible answer, *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 point where the linearization is made. 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 2.2 Consider the Noah's Ark Problem with ecological interactions, defined by (2.8), (2.9) and (2.10), and call \mathbf{X}^* its optimal solution. Then,

- i) the approximation of \mathbf{X}^* by \mathbf{X}^W , indicated in (2.13), offers an **improvement compared to the absence of protection**,
- ii) the approximation error, $W \circ \mathcal{P}(\mathbf{X}^*) - W \circ \mathcal{P}(\mathbf{X}^W)$, is no larger than $K * (\bar{\mathbf{X}}^\top \mathbf{t}^k)^2$, where $K = \max \{ \partial^2 (W \circ \mathcal{P}) / (\partial x_i \partial x_j) \}$.

Proof. Item i). The solution proposed in Theorem 2.2 is inspired from gradient methods used to find optimal solutions based on the property of iterative improvements, like the famous Frank-Wolfe algorithm.

A first step is to replace the objective function by its first order Taylor approximation $Z(\mathbf{X})$ computed at an admissible vector \mathbf{X}^0 (here at the zero protection vector $\mathbf{X}^0 = 0 * \mathbf{t}^k$). Let us note $\nabla W \circ \mathcal{P}$ the Gradient, a $k * 1$ vector with typical elements $\partial (W \circ \mathcal{P}) / \partial x_i$, which corresponds actually to the vector $\mathbf{Y} \equiv \mathbf{A}^\top * \mathbf{\Lambda}$ given in the text.

Using those notations :

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

A second step is to find \mathbf{X} that maximizes $Z(\mathbf{X})$ subject to the relevant constraints. Since in $Z(\mathbf{X})$ only the term $\nabla W \circ \mathcal{P}(0 * \mathbf{t}^k)^\top * \mathbf{X}$ varies, this step is equivalent to maximize (2.11) subject to (2.9) and (2.10). And the policy \mathbf{X}^W presented in the Theorem 2.2 is exactly the maximizer of this linear programming problem.

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

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

$$\iff \nabla W \circ \mathcal{P}(0 * \mathbf{t}^k)^\top * (\mathbf{X}^W - 0 * \mathbf{t}^k) \geq \nabla W \circ \mathcal{P}(0 * \mathbf{t}^k)^\top * (0 * \mathbf{t}^k - 0 * \mathbf{t}^k) = 0, \quad (2.14)$$

so the vector $\mathbf{X}^W - 0 * \mathbf{t}^k$ 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 $W \circ \mathcal{P}(\mathbf{X}^W) \geq W \circ \mathcal{P}(0 * \mathbf{t}^k)$.

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

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

and since we have established in (2.14) :

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

we are led to conclude :

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

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 :

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

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

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

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

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

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

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

so

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

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

The upper bound K for the approximation error mentioned in the above theorem is of course related to the non-linearity of $W \circ \mathcal{P}$, formally captured by the second order derivatives $\partial^2 (W \circ \mathcal{P}) / (\partial x_i \partial x_j)$. As a matter of interpretation, we can say that the stronger the curvature of W (the stronger preference for diversity if W is convex) the larger this upper bound.

2.5 A TWO-SPECIES EXAMPLE : ILLUSTRATION AND DISCUSSION

We close this note with an illustration using a simple two-species example. Let us first study to which extent the consideration of ecological interactions can alter priorities.

Assume for simplicity that $|r_{12}| < 1, |r_{21}| < 1$. The system (2.2) 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 :

$$P_1 = \frac{q_1 + r_{12}q_2 + x_1 + r_{12}x_2}{1 - r_{12}r_{21}} , \quad (2.15)$$

$$P_2 = \frac{q_2 + r_{21}q_1 + x_2 + r_{21}x_1}{1 - r_{21}r_{12}} . \quad (2.16)$$

The grades also can be easily computed. They are :

$$\begin{aligned} \bar{R}^1 &= \frac{\Delta P_1}{C_1} \left[\frac{D_1 + U_1}{1 - r_{12}r_{21}} + \frac{r_{21}(D_2 + U_2)}{1 - r_{21}r_{12}} \right] , \\ \bar{R}^2 &= \frac{\Delta P_2}{C_2} \left[\frac{r_{12}(D_1 + U_1)}{1 - r_{12}r_{21}} + \frac{D_2 + U_2}{1 - r_{21}r_{12}} \right] . \end{aligned}$$

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 :

$$\bar{R}^1 < \bar{R}^2,$$

\Leftrightarrow

$$\frac{D_1 + U_1}{1 - r_{12}r_{21}} + \frac{r_{21}(D_2 + U_2)}{1 - r_{21}r_{12}} < \frac{r_{12}(D_1 + U_1)}{1 - r_{12}r_{21}} + \frac{D_2 + U_2}{1 - r_{21}r_{12}}.$$

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

$$\Leftrightarrow k + r_{21} < kr_{12} + 1,$$

$$\Leftrightarrow k < \frac{1 - r_{21}}{1 - r_{12}}. \quad (\text{since } |r_{12}| < 1).$$

So, a ranking reversal occurs when :

$$1 < k < \frac{1 - r_{21}}{1 - r_{12}}. \quad (2.17)$$

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.

Let us now examine the robustness of our results by specifying an expected diversity function. Denote G the number of genes jointly owned by the two species whereas M_i is

the total number of genes owned by species i . Assume, as in Weitzman (1998, (expression (5)) that the expected (genetic) diversity function takes the following functional form :

$$\begin{aligned} W(P_1, P_2) &= P_1 P_2 (M_1 + M_2 - G) + P_1 (1 - P_2) M_1 \\ &\quad + P_2 (1 - P_1) M_2 + (1 - P_1) (1 - P_2) 0 \\ &= M_1 P_1 + M_2 P_2 - G P_1 P_2. \end{aligned}$$

Considering relations (2.15) and (2.16) between efforts and probabilities, we obtain :

$$W \circ \mathcal{P}(x_1, x_2) = M_1 \mathcal{P}_1(x_1, x_2) + M_2 \mathcal{P}_2(x_1, x_2) - G \mathcal{P}_1(x_1, x_2) \mathcal{P}_2(x_1, x_2) .$$

Two questions arise. **Can we compare the true solution and the approximate solution?** **And can we estimate the error due to the approximation of the optimal solution?** From Theorem 2.2, the upper bound on the error due to the approximation can be computed from the Hessian $\nabla^2 W \circ \mathcal{P}(\mathbf{X})$. In this two-species example, it is easy to derive the following formulae :

$$\begin{aligned} \partial^2 (W \circ \mathcal{P}) / (\partial x_1 \partial x_2) &= \partial^2 (W \circ \mathcal{P}) / (\partial x_2 \partial x_1) = -\frac{(1 + r_{12} r_{21})}{(1 - r_{12} r_{21})^2} G , \\ \partial^2 (W \circ \mathcal{P}) / (\partial x_1)^2 &= -\frac{2r_{21}}{(1 - r_{12} r_{21})^2} G , \quad \partial^2 (W \circ \mathcal{P}) / (\partial x_2)^2 = -\frac{2r_{12}}{(1 - r_{12} r_{21})^2} G . \end{aligned}$$

So the upper bound K on the approximation error, indicated in Theorem 2.2, is :

$$K = (1 - r_{12} r_{21})^{-2} * G * \max \{ -2r_{21}, -(1 + r_{12} r_{21}), -2r_{12} \} , \quad (2.18)$$

a value which depends only on the number of genes owned jointly by the two species, G , and on the ecological interaction terms, r_{ji} .

Of course, this is only an upper bound. In some cases, the approximation could also give the exact solution. To illustrate this, assume as before that $C_1 = C_2 = C$, $\Delta P_1 = \Delta P_2 = \Delta P$, that utilities are identical, $U_1 = U_2 = U = 0$, and the upper bounds on efforts are the same for the two species, $\bar{x}_1 = \bar{x}_2 = \bar{x}$. Assume also that the total budget can cover the protection cost of only one species, $B = \bar{x} * C / \Delta P$. Noah then has to choose among two extreme policies, the first one ($x_1 = 0; x_2 = \bar{x}$) that provides the following expected

diversity :

$$W(0, \bar{x}) = M_1 \frac{q_1 + r_{12}q_2 + r_{12}\bar{x}}{1 - r_{12}r_{21}} + M_2 \frac{q_2 + r_{21}q_1 + \bar{x}}{1 - r_{12}r_{21}} - G \frac{(q_1 + r_{12}q_2 + r_{12}\bar{x})(q_2 + r_{21}q_1 + \bar{x})}{(1 - r_{12}r_{21})^2},$$

and the second one ($x_1 = \bar{x}; x_2 = 0$) with expected diversity :

$$W(\bar{x}, 0) = M_1 \frac{q_1 + r_{12}q_2 + \bar{x}}{1 - r_{12}r_{21}} + M_2 \frac{q_2 + r_{21}q_1 + r_{21}\bar{x}}{1 - r_{12}r_{21}} - G \frac{(q_1 + r_{12}q_2 + \bar{x})(q_2 + r_{21}q_1 + r_{21}\bar{x})}{(1 - r_{12}r_{21})^2}.$$

It is optimal to protect species 2 if :

$$W(0, \bar{x}) > W(\bar{x}, 0)$$

$$\Leftrightarrow$$

$$(1 - r_{12}r_{21}) [M_2 (1 - r_{21}) - M_1 (1 - r_{12})] > G [(1 - r_{21}) (q_1 - q_2 + r_{12}q_2 - r_{21}q_1) + (r_{12} - r_{21}) \bar{x}].$$

In the particular case where $G = 0$, then $M_i = \partial W / \partial P_i = D_i$, and the above condition boils down to a very simple expression :

$$W(0, \bar{x}) > W(\bar{x}, 0) \Leftrightarrow \frac{M_1}{M_2} = \frac{D_1}{D_2} < \frac{1 - r_{21}}{1 - r_{12}},$$

a condition which is also necessary for the approximated solution to select species 2 (remember condition (2.17)). It comes as no surprise that the optimal solution and its approximation coincide, since when $G = 0$ the upper bound on the approximation error is zero, as can be seen from expression (2.18).

III

**WEITZMAN'S VERSUS RAO'S
CRITERION : A TALE OF TWO
DIVERSITIES**

WEITZMAN'S VERSUS RAO'S CRITERION : A TALE OF TWO DIVERSITIES

3

3.1 ABSTRACT

This paper analyses simple biodiversity protection plans, using alternatively Weitzman's and Rao's criteria, two biodiversity indices stemming from different disciplines. Both indices combine differently and rest on pieces of information about (1) species survival probability, (2) some measure of dissimilarity between species. Adding another layer of information about (3) the ecological interactions between species, we modelize interdependent survival probabilities in a three species ecosystem. Using this information, we arrive at what we call *in situ* versions of those criteria, which eventually are functions of protection efforts only. We show that choosing a particular *in situ* criterion has policy implications, for they sometimes deliver diverging protection recommendations. We disentangle the role played by the different data requirements in the rankings, which allows us to highlight their major characteristics and differences as biodiversity measures.

3.2 INTRODUCTION

The science of biodiversity conservation has grown rapidly in recent decades. Important progress has been made on two interconnected fronts. On the one hand, reflection has advanced on definitions and measures of biodiversity to produce what could be called a "biodiversity index theory" (for general overviews, see Mangurran, 2004, Baumgärtner, 2004, Aulong, Figuières and Erdlenbruch, 2005, 2008). On the other hand – and building

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

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

Using the framework developed by Courtois et al (2014) with ecological interactions for *in situ* cost-benefit analysis, the originality of the present paper is to scrutinize the consequences of using two diversity indices : Weitzman (1992)'s index, which is popular in several literatures including economics, and Rao (1982)'s index, mostly used in ecology and biology, but largely ignored by economists. Will both indices lead to the same policy? They both account simultaneously for survival probabilities and dissimilarity measures.

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

Rao's index is defined as the expected dissimilarity between two entities randomly drawn from a collection, whereas Weitzman's index, in the specific context we will analyze, is the expected length of the evolutionary tree associated to the collection. The axiomatic properties of both indices has been elicited (Rao, 1986, Bossert, Pattanaik and Xu, 2002), which gives them some transparency as measures of diversity.

Since our goal is to unravel and understand basic issues, we will simplify the study whenever possible. Attention is restricted to a three-species ecosystem² with ecological interactions. Weitzman's and Rao's indices are used for the comparison of particularly simple preservation policies, where the manager of a natural park has enough budget to care about at most one single species. Which one should he choose, given the direct or indirect advantages — through interactions — provided by this species?

The second section of this paper models the type of *in situ* prioritization problems we are dealing with. After describing the characteristics of our three species ecosystem, we define how both indices generally combine this information and how they may be used for ranking species for *in situ* conservation. The third section aims at disentangling the role of the different aspects that compose the indicators, namely (i) the autonomous survival probabilities, (ii) the dissimilarities, (iii) the coefficients of ecological interactions. We end this paper with a discussion of the limits and perspectives of this approach.

3.3 A CLASS OF *in situ* PRIORITIZATION PROBLEMS

Consider an ecosystem with three species. To each species i , $i = 1, 2, 3$, is attached a survival probability P_i that depends partly, because of ecological interactions³, on the survival probabilities of the two other species P_j , with $j \neq i$, and on the protection effort it receives, $x_i \in \{0, \bar{x}\}$. The efforts considered in this paper are as simple as possible,

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

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

of a binary nature, *i.e.* a species is protected ($x_i = \bar{x}$) or not ($x_i = 0$); and the entire available budget is just enough to cover the protection of one species, no more, no less. Protection plans for two or three species at the same time are not affordable. Without being too specific for the moment – more details will be given in the following sections – if \mathbf{X} stands for a 3-dimensional vector of efforts, with components x_i , and \mathbf{P} is the vector of interdependent survival probabilities, with components P_i , then the link between efforts and probabilities is a 3-dimensional vector of functions $\mathbf{P}(\mathbf{X})$.

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

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

3.3.1 Interdependent survival probabilities of species

In the absence of ecological interactions and protection policies, each species i has an *autonomous survival probability* $q_i \in [0, 1]$, with $i = 1, 2, 3$. In order to take into account the ecological interactions and the protection efforts put in place, those raw data have to be modified to arrive at *interdependent survival probabilities*, denoted $P_i \in [\underline{P}_i, \bar{P}_i]$, $i = 1, 2, 3$. We assume these probabilities are linear functions of the protection efforts x_i , $i = 1, 2, 3$ measured in terms of probability variations, and of numbers $r_{ij} \equiv \partial P_i / \partial x_j$, $i \neq j$

representing the marginal ecological impact of species j on the survival probability of species i . We assume $|r_{ij}| < 1$, *i.e.* a variation in probability P_j has a less than proportional impact on P_i . Overall, the system of interdependent probabilities of survival for three species is as follows :

$$\begin{cases} P_1 = q_1 + x_1 + r_{12}P_2 + r_{13}P_3 \\ P_2 = q_2 + x_2 + r_{21}P_1 + r_{23}P_3 \\ P_3 = q_3 + x_3 + r_{31}P_1 + r_{32}P_2 \end{cases} \quad (3.1)$$

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

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

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

In matrix form, the system (3.1) of probabilities reads as :

$$\mathbf{P} = \mathbf{Q} + \mathbf{X} + \mathbf{R} * \mathbf{P} \quad (3.2)$$

Under the following assumption :

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

the system (3.2) can be solved⁴ to give :

$$\mathbf{P} = [\mathbf{I} - \mathbf{R}]^{-1} * (\mathbf{Q} + \mathbf{X}). \quad (3.3)$$

4. This is a sufficient condition for solvability. The necessary condition is :

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

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

$$\underline{\mathbf{P}} = \mathcal{P}(0 * \iota) \quad (3.4)$$

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

3.3.2 Species dissimilarities

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

We will assume that distances among species are ultrametric. There are two reasons to focus on the ultrametric case.

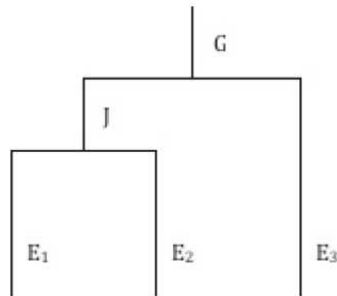
Firstly, when applied to a non ultrametric framework Rao's index may lead to unpalatable diversity rankings, where only few species are retained for conservation. In an extreme example, with one variable measured as source of distinctiveness among species, quadratic entropy is equal to the variance and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

Secondly, Weitzman (1992) constructed his diversity function using a complex iterative process. But this calculation boils down to the simple computation of the expected length of the evolutionary tree when distances are ultrametric. In addition, Solow and Polasky (1994) shows that apart from ultrametric distances, Weitzman's index is not strictly monotone relatively to distances used. Indeed, in a three species case (which is the case developed in this paper), Weitzman's measure of diversity is equivalent to the sum of the largest and the smallest distance. It is thus insensitive to any modification of the intermediary distance (Pavoine et al, 2005). The ultrametric property is possessed by all dissimilarities which can be directly associated with rooted trees in which all the end nodes are equidistant from the root of the tree (Van de Peer, 2003). Ultrametric distances provides an interesting framework for comparing both indices outcomes while keeping matters as simple as possible, especially as we introduce potential interactions among species of this tree.

In the three species case, ultrametric dissimilarities translate into a phylogenetic tree representation with proportional branches as shown in Figure 3.1 below, and where :

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

FIGURE 3.1 – An ultrametric tree with three species



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

$$M_1 = E_1 + J + G ,$$

$$M_2 = E_2 + J + G ,$$

$$M_3 = E_3 + G .$$

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

$$d_{12} = d_{21} = E_1 = E_2 = E ,$$

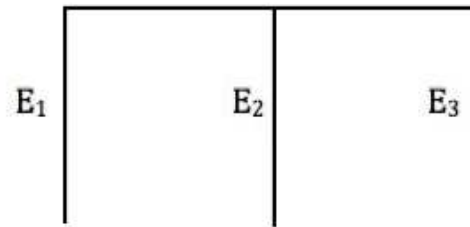
$$d_{13} = d_{31} = d_{23} = d_{32} = E_2 + J = E_1 + J = E_3$$

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

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

When $J = 0$ there are no common genes between species 1 and 2. Thus we get back to a case very similar to the two-species case, in which the tree representation is as in Figure 3.2.

In this setting where $J = 0$, ecological interactions and survival probabilities are the only parameters discriminating the three species. Indeed, the three species are here perfectly substitutable from the point of view of their dissimilarities. As J raises away from 0,

FIGURE 3.2 – An ultrametric tree with three species and $J = 0$ 

we are able to represent the role of dissimilarity among species for both indicators since $E_1 = E_2 \neq E_3$.

3.3.3 Definitions of *in situ* indices for biodiversity

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

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

a particular element of this parameters space.

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

- If no species disappears, an event that occurs with probability $P_1 P_2 P_3$, the length of the total tree, or the total number of different books if the three libraries are available, is $E_1 + E_2 + J + E_3 + G$,
- if only species 1 survives, an event occurring with probability $(1 - P_2)(1 - P_3)P_1$, the length of the tree is $E_1 + J + G$,
- if only species 1 and 2 survives, an event with probability $P_1 P_2 (1 - P_3)$, the length of the tree is $E_1 + E_2 + J + G$,

- and so on...

Therefore, the expected length of the tree is :

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

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

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

Since the goal is to rank protection priorities while taking into account ecological interactions, the above index has to be modified in order to incorporate the later information. We obtain the desired qualification by plugging the relation $\mathcal{P}(\mathbf{X})$ between efforts and probabilities into $W(\mathbf{P})$. This results in what may be further called *Weitzman's in situ biodiversity index* :

$$\begin{aligned}
\mathcal{W}(\mathbf{X}) &\equiv W \circ \mathcal{P}(\mathbf{X}) , \\
&= [P_1(\mathbf{X}) + P_2(\mathbf{X}) + P_3(\mathbf{X})] (E + J) - P_1(\mathbf{X}) P_2(\mathbf{X}) J . \quad (3.5)
\end{aligned}$$

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

$$\mathcal{W}_e(\mathbf{X}) = \mathbf{X}^T * \mathbf{A}_e^W * \mathbf{X} + \mathbf{X}^T * \mathbf{B}_e^W + c^W , \quad (3.6)$$

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

In this formula, \mathbf{A}_e^w and \mathbf{B}_e^w are, respectively, a matrix and a vector whose components are complex combinations of parameters included in the element $e \in \Omega$. Details are given

in Appendix C. Note that if the vector e changes, so does expression (3.6). Hence we explicitly mention this dependence *via* subscripts, as in the notations $\mathcal{W}_e, \mathbf{A}_e^W, \mathbf{B}_e^W$.

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

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

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

$$\mathcal{R}(\mathbf{X}) \equiv R(\mathcal{P}(\mathbf{X})) = 2 \left[\begin{array}{c} (P_1(\mathbf{X}) P_2(\mathbf{X}) + P_1(\mathbf{X}) P_3(\mathbf{X}) + P_2(\mathbf{X}) P_3(\mathbf{X})) E \\ + (P_1(\mathbf{X}) + P_2(\mathbf{X})) P_3(\mathbf{X}) J \end{array} \right] . \quad (3.7)$$

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

$$\mathcal{R}_e(\mathbf{X}) = \mathbf{X}^T * \mathbf{A}_e^R * \mathbf{X} + \mathbf{X}^T * \mathbf{B}_e^R + c^R , \quad (3.8)$$

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

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

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

— Project 1 :

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

— Project 2 :

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

— Project 3 :

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

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

$$\mathcal{W}_e(\mathbf{X}_1) \geq \max \{ \mathcal{W}_e(\mathbf{X}_2), \mathcal{W}_e(\mathbf{X}_3) \} . \quad (3.9)$$

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

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

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

$$\mathcal{R}_e(\mathbf{X}_1) \geq \max \{ \mathcal{R}_e(\mathbf{X}_2), \mathcal{R}_e(\mathbf{X}_3) \} , \quad (3.10)$$

or equivalently :

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

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

3.4 DISENTANGLING THE UNDERLYING LOGICS OF IN-SITU PRIORITIES

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

From a technical point of view, the entire difficulty boils down to the computation of differences such as :

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

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

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

3.4.1 When the indices disagree

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

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

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

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

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

$$\mathcal{W}_{e_q}(\mathbf{X}_1) - \mathcal{W}_{e_q}(\mathbf{X}_2) = \frac{J\bar{x}}{(1+r)^2} (q_1 - q_2), \quad (3.11)$$

$$\mathcal{R}_{e_q}(\mathbf{X}_1) - \mathcal{R}_{e_q}(\mathbf{X}_2) = \frac{2E\bar{x}}{(1+r)^2} (q_2 - q_1). \quad (3.12)$$

So, Weitzman's ranking of the two policies is sensitive to J – featuring indifference when $J = 0$ – whereas Rao's ranking is not. Assuming $J > 0$, from (3.11) and (3.12) we can deduce :

Proposition 3.1 *Let the class of conservation problems be given by the list of parameters e_q and let $J > 0$. In this case, the two diversity indices deliver opposite rankings :*

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

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

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

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

Ecological interactions have little importance in this first example, since both species are placed in an identical ecological role. Results are simply consistent with the logics embodied in the indicators alone. Weitzman seeks the longest expected tree and only one species can be protected. If either species 1 or species 2 goes extinct, E "books" are lost but $E + J$ are safe. It is wise then to affect protection resources on the species which is initially the most safe, unless $J = 0$ because in this case, clearly, Weitzman's criterion is indifferent regarding which species should be afforded protection efforts. For Rao, however, the question is : how to choose the combination of probabilities leading to the highest expected dissimilarity ? Put more precisely, in this two-species problem Rao seeks the largest product $P_1(\mathbf{X}) P_3(\mathbf{X})$. This is best achieved when the policy helps the weakest species.

3.4.1.2 Robustness : three species

Those results are somehow robust to the introduction of a third and similar species into the framework, provided that the only source of heterogeneity among species is still their autonomous survival probability. To achieve this, we must keep the same distances between species 1, 2 and 3, and thus $J = 0$ (otherwise, heterogeneity also goes through dissimilarities) and $G = 0$, and where q_3 can take any arbitrary value. That is, we have to consider a slightly different list of parameters $e'_{q'}$ and perform again all the computations. It turns out that :

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

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

$$\begin{aligned}\mathcal{R}_{e'_q}(\mathbf{X}_1) - \mathcal{R}_{e'_q}(\mathbf{X}_2) &= \frac{2E\bar{x}}{(r+1)^2} (q_2 - q_1) , \\ \mathcal{R}_{e'_q}(\mathbf{X}_1) - \mathcal{R}_{e'_q}(\mathbf{X}_3) &= \frac{2E\bar{x}}{(r+1)^2} (q_3 - q_1) , \\ \mathcal{R}_{e'_q}(\mathbf{X}_2) - \mathcal{R}_{e'_q}(\mathbf{X}_3) &= \frac{2E\bar{x}}{(r+1)^2} (q_3 - q_2) ,\end{aligned}$$

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

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

3.4.2 When the indices agree

3.4.2.1 The influence of dissimilarity ($E_3 \neq E_1 = E_2$)

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

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

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

Key pieces of information are :

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

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

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

$$\mathcal{R}_{e_j}(\mathbf{X}_3) - \mathcal{R}_{e_j}(\mathbf{X}_1) = \mathcal{R}_{e_j}(\mathbf{X}_3) - \mathcal{R}_{e_j}(\mathbf{X}_2) = 2Jq\bar{x} > 0.$$

And a conclusion immediately appears :

Proposition 3.2 *Let the class of conservation problems be given by the list of parameters e_j . In this three-species ecosystem where dissimilarities are the only source of heterogeneity among species, the two diversity indices deliver the same rankings :*

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

This result is intuitive. If only species 1 (or 2) disappears, there remains $2(E + J)$ “books”. But if species 3 only disappears, the number of safe “books” falls down to a lower $2E + J$. However, in Section 3.5.1 it is proved that the property emphasized in Proposition 3.2 is fragile, more precisely it holds only when ecological interactions are not too strong (even if all those ecological interactions are not a source of heterogeneity).

3.4.2.2 The influence of ecological interactions

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

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

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

The computation of the biodiversity criterions reveals :

$$\begin{aligned} \mathcal{W}_{e_{R2}}(\mathbf{X}_1) - \mathcal{W}_{e_{R2}}(\mathbf{X}_2) &= \frac{E\bar{x}}{1 - r_{12}r_{21}}(r_{21} - r_{12}), \\ \mathcal{R}_{e_{R2}}(\mathbf{X}_1) - \mathcal{R}_{e_{R2}}(\mathbf{X}_2) &= \frac{2E\bar{x}(2q + x)}{(1 - r_{12}r_{21})^2}(r_{21} - r_{12}). \end{aligned}$$

Thus, we can establish :

Proposition 3.3 *Let the class of conservation problems be given by the list of parameters e_{R2} . The two criteria deliver the same ranking of policies \mathbf{X}_1 and \mathbf{X}_2 . They recommend to preserve the species with the largest marginal benefit on the survival of the other species :*

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

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

i) Predation : species 2, a predator, feeds on species 1, its prey. By definition we have

$r_{21} > 0$ and $r_{12} < 0$. Both criteria recommend to preserve the prey - here species 1 - since its interaction coefficient is larger ($r_{21} > 0 > r_{12}$).

ii) Mutualism : species 1 and 2 impact positively on each other. By definition we have

$r_{12} > 0$ and $r_{21} > 0$. Both criteria recommend to preserve the species with the largest marginal benefit on the survival probability of the other species.

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

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

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

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

And relative performances of policies are measured by :

$$\mathcal{W}_{e_{R3}}(\mathbf{X}_1) - \mathcal{W}_{e_{R3}}(\mathbf{X}_2) = E\bar{x}(r_{21} + r_{31}), \quad (3.13)$$

$$\mathcal{W}_{e_{R3}}(\mathbf{X}_1) - \mathcal{W}_{e_{R3}}(\mathbf{X}_3) = E\bar{x}(r_{21} + r_{31}), \quad (3.14)$$

$$\mathcal{W}_{e_{R3}}(\mathbf{X}_2) - \mathcal{W}_{e_{R3}}(\mathbf{X}_3) = 0, \quad (3.15)$$

$$\mathcal{R}_{e_{R3}}(\mathbf{X}_1) - \mathcal{R}_{e_{R3}}(\mathbf{X}_2) = 2E\bar{x} \begin{bmatrix} r_{21}r_{31}(2q+x) + r_{21}(3q+x) \\ +r_{31}(2q+x) \end{bmatrix}, \quad (3.16)$$

$$\mathcal{R}_{e_{R3}}(\mathbf{X}_1) - \mathcal{R}_{e_{R3}}(\mathbf{X}_3) = 2E\bar{x} \begin{bmatrix} r_{21}r_{31}(2q+x) + r_{21}(2q+x) \\ +r_{31}(3q+x) \end{bmatrix}, \quad (3.17)$$

$$\mathcal{R}_{e_{R3}}(\mathbf{X}_2) - \mathcal{R}_{e_{R3}}(\mathbf{X}_3) = 2E\bar{x}q(r_{31} - r_{21}). \quad (3.18)$$

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

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

The above expressions (3.13) and (3.14) show that this is true iff $r_{21} + r_{31} > 0$, that is if the cumulated impact of species 1 on the survival probability of the two other species is larger than the cumulated impact of these species on all other species (which is null here as we assume $r_{12} = r_{13} = r_{23} = r_{32} = 0$). This result somehow confirms Proposition 3.3 as it recommends to put conservation efforts on the species which is the more beneficial (or the less detrimental) to the survival of the species composing the ecosystem.

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

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

>From expressions (3.16) and (3.17), this is true iff $r_{21}r_{31}(2q+x) + r_{31}(2q+x) + r_{21}(3q+x) > 0$ and $r_{21}r_{31}(2q+x) + r_{21}(2q+x) + r_{31}(3q+x) > 0$. In case species 1 impacts positively species 2 and 3, preservation effort is put on species 1. Otherwise, interpreting the criterion is more tricky as one of the above inequality may not hold. In such a case, effort is then put on the species which is the more (negatively) impacted by species 1. We find again a confirmation of the result forwarded by Proposition 3.3.

However, the decision rule depicted here is not anymore a simple additive formula but a combination of additive and multiplicative components ($r_{21}r_{31}$) making interpretation fastidious. Adding interrelations or species in the analysis increases complexity as it increases complementarities and multiplicative effects.

3.5 INTERACTIONS BETWEEN EFFECTS

3.5.1 Autonomous survival probabilities and dissimilarities

Now let us have a look at the combination of autonomous survival probabilities and dissimilarity. Consider a slight departure of parameters configuration e_q of Section 3.4.1.1. In the new list of parameters e_{qJ} , the unique difference comes from parameter J which is not null anymore, $J > 0$, and $r_{ij} = r$, when $i \neq j$. The vector \mathbf{Q} and the matrix \mathbf{R} are :

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

And the relative performance of policies can be deduced from :

$$\mathcal{W}_{e_{qJ}}(\mathbf{X}_1) - \mathcal{W}_{e_{qJ}}(\mathbf{X}_2) = \frac{J\bar{x}}{(1+r)^2} (q_1 - q_2), \quad (3.19)$$

$$\mathcal{W}_{e_{qJ}}(\mathbf{X}_1) - \mathcal{W}_{e_{qJ}}(\mathbf{X}_3) = \frac{J\bar{x} [r(q_1 + q_3 + x) + q_2(1-r)]}{(1+r)^2(2r-1)}, \quad (3.20)$$

$$\mathcal{W}_{e_{qJ}}(\mathbf{X}_2) - \mathcal{W}_{e_{qJ}}(\mathbf{X}_3) = \frac{J\bar{x} [r(q_2 + q_3 + x) + q_1(1-r)]}{(1+r)^2(2r-1)}, \quad (3.21)$$

$$\mathcal{R}_{e_{qJ}}(\mathbf{X}_1) - \mathcal{R}_{e_{qJ}}(\mathbf{X}_2) = \frac{2E\bar{x}}{(1+r)^2} (q_2 - q_1), \quad (3.22)$$

$$\begin{aligned} \mathcal{R}_{e_{qJ}}(\mathbf{X}_1) - \mathcal{R}_{e_{qJ}}(\mathbf{X}_3) &= \frac{2J\bar{x} [r(3q_3 - q_1 - q_2) + rx - (q_3 - q_1 - q_2)]}{(1+r)^2(2r-1)} \\ &+ \frac{2E\bar{x}}{(1+r)^2} (q_3 - q_1), \end{aligned} \quad (3.23)$$

$$\begin{aligned} \mathcal{R}_{e_{qJ}}(\mathbf{X}_2) - \mathcal{R}_{e_{qJ}}(\mathbf{X}_3) &= \frac{2J\bar{x} [r(3q_3 - q_1 - q_2) + rx - (q_3 - q_1 - q_2)]}{(r+1)^2(2r-1)} \\ &+ \frac{2E\bar{x}}{(1+r)^2} (q_3 - q_2). \end{aligned} \quad (3.24)$$

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

The conclusions are more subtle when the third species is at stake, and they depend on the importance of ecological interactions : Weitzman prefers species 3 only if $r < 1/2$ ⁵. In other words, dissimilarity prevails when ecological interactions are not too strong. And the conclusion is even more complex when it comes to Rao's index. Whatever the choice, it is reversed when r crosses the value $1/2$.

Now, as a particular case let the autonomous probabilities of survival be all identical. The relative performances of policies (3.19) to (3.24) simplify to :

$$\mathcal{W}_{e'_{qj}}(\mathbf{X}_1) - \mathcal{W}_{e'_{qj}}(\mathbf{X}_2) = 0, \quad (3.25)$$

$$\mathcal{W}_{e'_{qj}}(\mathbf{X}_1) - \mathcal{W}_{e'_{qj}}(\mathbf{X}_3) = \frac{J\bar{x} [r(q+x) + q]}{(1+r)^2(2r-1)}, \quad (3.26)$$

$$\mathcal{W}_{e'_{qj}}(\mathbf{X}_2) - \mathcal{W}_{e'_{qj}}(\mathbf{X}_3) = \frac{J\bar{x} [r(q+x) + q]}{(1+r)^2(2r-1)}, \quad (3.27)$$

$$\mathcal{R}_{e'_{qj}}(\mathbf{X}_1) - \mathcal{R}_{e'_{qj}}(\mathbf{X}_2) = 0, \quad (3.28)$$

$$\mathcal{R}_{e'_{qj}}(\mathbf{X}_1) - \mathcal{R}_{e'_{qj}}(\mathbf{X}_3) = \frac{2J\bar{x} [r(q+x) + q]}{(1+r)^2(2r-1)}, \quad (3.29)$$

$$\mathcal{R}_{e'_{qj}}(\mathbf{X}_2) - \mathcal{R}_{e'_{qj}}(\mathbf{X}_3) = \frac{2J\bar{x} [r(q+x) + q]}{(1+r)^2(2r-1)}. \quad (3.30)$$

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

3.5.2 Ecological interactions and dissimilarities

Now, combine the heterogeneity of ecological interactions and dissimilarities. Consider a parameters configuration e_{RJ} in which $J > 0$, and $r_{ij} = 0$, except for r_{12} and r_{21} that can

⁵ The value $r = 1/2$ is forbidden. For this particular value, the system of interdependent probabilities (3.2) cannot be solved.

be arbitrarily chosen. The vector \mathbf{Q} and the matrix \mathbf{R} are :

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

And the relative performance of policies can be deduced from :

$$\mathcal{W}_{e_{RJ}}(\mathbf{X}_1) - \mathcal{W}_{e_{RJ}}(\mathbf{X}_2) = \bar{x} \frac{(E+J)(1-r_{12}r_{21}) - J(2q+x)}{(1-r_{12}r_{21})^2} (r_{21} - r_{12}), \quad (3.31)$$

$$\mathcal{W}_{e_{RJ}}(\mathbf{X}_1) - \mathcal{W}_{e_{RJ}}(\mathbf{X}_3) = \bar{x}(E+J) \frac{(1+r_{12}-r_{12}r_{21}-r_{12}^2r_{21})r_{21}}{(1-r_{12}r_{21})^2} \quad (3.32)$$

$$- \bar{x}J \frac{(r_{12}q+2q+x)r_{21}+q}{(1-r_{12}r_{21})^2}, \quad (3.33)$$

$$\mathcal{W}_{e_{RJ}}(\mathbf{X}_2) - \mathcal{W}_{e_{RJ}}(\mathbf{X}_3) = \bar{x}(E+J) \frac{(1+r_{21}-r_{12}r_{21}-r_{12}r_{21}^2)r_{12}}{(1-r_{12}r_{21})^2} \quad (3.34)$$

$$- \bar{x}J \frac{(r_{21}q+2q+x)r_{12}+q}{(1-r_{12}r_{21})^2}, \quad (3.35)$$

$$\mathcal{R}_{e_{RJ}}(\mathbf{X}_1) - \mathcal{R}_{e_{RJ}}(\mathbf{X}_2) = \frac{2E\bar{x}(2q+\bar{x})}{(1-r_{12}r_{21})^2} (r_{21} - r_{12}), \quad (3.36)$$

$$\mathcal{R}_{e_{RJ}}(\mathbf{X}_1) - \mathcal{R}_{e_{RJ}}(\mathbf{X}_3) = 2\bar{x}(E+J) \frac{q(r_{12}r_{21}^2 + r_{12}^2r_{21} + 2r_{12}r_{21} - r_{12} - 1)}{(1-r_{12}r_{21})^2} \quad (3.37)$$

$$+ 2\bar{x} \frac{Er_{21}(qr_{12} + q + \bar{x}) - Jq(1+r_{21})}{(1-r_{12}r_{21})^2}, \quad (3.38)$$

$$\mathcal{R}_{e_{RJ}}(\mathbf{X}_2) - \mathcal{R}_{e_{RJ}}(\mathbf{X}_3) = 2\bar{x}(E+J) \frac{q[r_{12}r_{21}^2 + r_{12}^2r_{21} + 2r_{12}r_{21} - r_{21} - 1]}{(1-r_{12}r_{21})^2} \quad (3.39)$$

$$+ 2\bar{x} \frac{Er_{12}(qr_{21} + q + \bar{x}) - Jq(1+r_{12})}{(1-r_{12}r_{21})^2}. \quad (3.40)$$

When the comparison only involves species 1 and 2, that are perfectly substitutable from the point of view of their dissimilarities, and for low values of J the conclusion is clear-cut : both indices favor the species with the largest ecological impact. When species 3 is at stake, conclusions are ambiguous. In order to fix ideas, assume that all ecological impacts are non-negative ($r_{12} \geq 0, r_{21} \geq 0$). Then, for example, Both Weitzman and Rao prefer species 3 over species 1 (or species 2) when the ecological impact of the latter is sufficiently weak. But indices may also diverge. For instance, when the autonomous survival probability q is sufficiently close to 0, Rao clearly drops species 3 in favor of any

of the other two. A conclusion that cannot be drawn from Weitzman's index under the same condition on q .

3.5.3 Autonomous survival probabilities and ecological interactions

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

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

Computations for rankings of species 1 and 2 arrive at :

$$\begin{aligned} \mathcal{W}_{e_{qR}}(\mathbf{X}_1) - \mathcal{W}_{e_{qR}}(\mathbf{X}_2) &= J \frac{\bar{x}(1+r_{12}r_{21})}{(1-r_{12}r_{21})^2} (q_1 - q_2) \\ &+ J \frac{2\bar{x}}{(1-r_{12}r_{21})^2} (q_2r_{12} - q_1r_{21}) \\ &+ \frac{\bar{x}[(E+J)(1-r_{12}r_{21}) - Jx]}{(1-r_{12}r_{21})^2} (r_{21} - r_{12}), \end{aligned} \quad (3.41)$$

$$\begin{aligned} \mathcal{R}_{e_{qR}}(\mathbf{X}_1) - \mathcal{R}_{e_{qR}}(\mathbf{X}_2) &= \frac{2E\bar{x}(1+r_{12}r_{21})}{(1-r_{12}r_{21})^2} (q_2 - q_1) \\ &- \frac{4E\bar{x}}{(1-r_{12}r_{21})^2} (q_2r_{12} - q_1r_{21}) \\ &+ \frac{2E\bar{x}^2}{(1-r_{12}r_{21})^2} (r_{21} - r_{12}). \end{aligned} \quad (3.42)$$

Of course, when $r_{21} = r_{12} = r$, one finds again the results of Section 3.4.1.1. Recall that Weitzman selects the strongest species - with the largest q_i - for protection, whereas Rao prefers the weakest species (Proposition 3.1).

As soon as $r_{21} \neq r_{12}$, these results have to be qualified. They are now more complex functions of, not only the q_i s, but also the r_{ij} s. In order to grasp these qualifications, pretend that species 1 is the strongest ($q_1 > q_2$). We know from Proposition 3.1 that, when $r_{21} = r_{12} = r$, Weitzman (respectively Rao) suggests species 1 (resp. species 2) should be protected. Now, imagine that $r_{21} = 0 < r_{12}$. On this basis alone, if q_1 and q_2 were

identical, both Weitzman and Rao would prefer species 2 (see Proposition 3.3). But if $q_1 > q_2$, from expressions (3.41) and (3.42) Rao clearly prefers species 2, whereas Weitzman's conclusion is ambiguous. Eventually its answer reveals a trade-off between two opposite effects, and this trade-off depends, among other things, on the importance of J , the number of common "genes" between species 1 and 2.

Under different circumstances, Rao's ranking can also be ambiguous. Assume that $r_{21} = 0 < r_{12}$ and $q_1 < q_2$. Then Weitzman clearly prefers species 2. But Rao's ranking embodies two opposite logics, one in favor of species 2 (the more ecologically beneficial), and the other in favor of species 1 (the weakest species). The final choice will reveal Rao's trade-off between those two opposite forces. And, as can be deduced from expression (3.42), contrary to Weitzman's trade-off it does not depend on J .

3.6 CONCLUSION

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

There are three important outcomes :

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

2. When ecological interactions matters for the ranking, the favored species is the one that sustains the best ecological chain. In general, the introduction of ecological interactions among more than two species can lead to complex conclusions.
3. When the three drivers are combined, the policy advocated by each index reveals a specific trade-off between Q , R and J .

Given their inherent construction, each biodiversity index is a measure of a certain vision of biodiversity. It is interesting to know that, other things equal, there is a tendency for Weitzman's index to favor robust species, whereas Rao's index cares more about fragile species. From a practical point of view, an interesting follow-up to this research would be to consider any number of species, among which only a subset can be offered protection. The analytical understanding of the rankings will be lost, but this step does not seem to pose any computer problems.

IV

MANAGING BIOLOGICAL INVASIONS : HOW TO SET PRIORITIES

MANAGING BIOLOGICAL INVASIONS : HOW TO SET PRIORITIES

4

4.1 ABSTRACT

The increase in the number of biological invasions is of growing concern for the status of biodiversity worldwide. Their impact on the environment and the economy are rapidly growing, conferring a status of public bad to many invasive species in several part of the world. Because resources are limited, the funds available for the management of problematic biological invasions need to be allocated in the most efficient way. Applying a cost/benefit approach incorporating species utility, distinctiveness, robustness of species and their interactions, this paper provides with an operational optimal method for setting management priorities of invasive species, under a limited budget constraint.

4.2 INTRODUCTION

The number as well as the damages caused by biological invasions are tremendously increasing (Perrings et al., 2010, Vilà et al., 2011, Essl et al., 2011). Recent studies made an important contribution to classify their impacts (Blackburn et al., 2014, Jeschke et al., 2014), providing an extensive list of environmental as well as economic damages that ought to be taken into account. One of the most worrisome feature of invasive species is their impact on biodiversity. They are an important cause of extinction, therefore being categorized as one of the major threat to biodiversity (Bax et al., 2003, Clavero and Garciaberthou, 2005, McNeely, 2001, Molnar et al., 2008, Vilà et al., 2011).

Although many biological invasions are likely to be harmful, we are left with an uncomfortable choice to make : which of those species should be targeted first for mitigation or eradication actions ? How should we spend a limited budget to address the problem of invasion management ? The questioning underlying this issue is a prioritization one. Budget being limited, we must unfortunately set priorities in our effort to control invasions, since we do not have enough resources to mitigate all of them at the same time. Every single undesirable species cannot be dealt with, therefore urging for the use of a framework to help us set priorities.

As developed earlier in this thesis, many dimensions influences the severity of biological invasion impacts, and therefore the potential management priorities. In our first chapter, we described a method insisting on the importance of disentangling the different component of impacts. This methodology was a first step in informing prioritization. It helps to determine the most important levers before choosing the relevant prioritization methodology, such as the application of a scoring method.

Prioritization literature is indeed mostly based on scoring approaches. Basically, scoring implies giving marks to invasive species on the basis of a set of criteria previously determined. The species with the lowest (or highest, depending on the methodology used) overall score are considered the priority. Non exhaustively, Batianoff and Butler (2002, 2003) scored expert opinions on species "invasiveness", and then compared the obtained ranking list to impact scores. Thorp and Lynch (2000) added different criteria such as potential for spread and sociological values to rank weeds. More recently, Kumschick and Nentwig (2010) and Kumschick et al. (2012) developed frameworks to prioritize action on alien species according to their impacts. They incorporated experts opinions as well as the diverging interests of the various stakeholders, therefore a good capture of the political and social issues underlying prioritization in invasive management.

If scoring is a convenient approach in order to produce a ranking, these methods were developed outside of any formal optimization framework, and this occurred to their

expense. Three important flaws can be noted : i) the costs of management are rarely explicitly taken into account, while we observe paradoxically important heterogeneity in species management costs, ii) scoring different dimension of the impacted system yields to difficulties in scoring aggregation in order to define the objective of management policies, iii) interactions among species are, at best, superficially accounted for. This last point can be seriously misleading and for example, Zavaleta et al. (2001) showed that eluding trophic cascades reflexions while removing an invasive species could lead to major unexpected changes to other ecosystem components, potentially creating unwanted secondary impacts.

The seminal papers of Solow et al. (1993) and Weitzman (1998) are two milestones in the cost-benefit analysis of conservation policy, which resulted in a practical methodology to prioritize conservation choices based on a rigorous optimization model. The idea is to assess cost-benefit ratios of conservation for each species, which can next be ranked in order to set priorities. Several attempts to prioritize species conservation were made following this work, some of which have led to real changes in the allocation of conservation funding (Joseph et al., 2008, McCarthy et al., 2008). Variants of this prioritization approach have been used to allocate surveillance effort over space (Hauser and McCarthy, 2009).¹. Such a methodology provides us with a formal framework to think about prioritization and could be applied to manage biological invasions.

From a conservation point of view, biological invasion management aims at maximizing biodiversity and ecosystem services and it is to be performed in a cost-efficient way. A particularly problematic flaw with regard to Weitzman's approach is that it fails to account for species interrelations. Disruptions from invasions are mainly due to the dynamics of spread and its negative impact on native species. Interrelation network and the dynamics of reproduction is thus at the cornerstone of the optimization framework. Courtois et al. (2014) revisited Weitzman's optimization problem and extended his model in order to incorporate species interactions. Basing on this approach, our principal output

1. Other applications are quoted in Eppink and van der Bergh (2007).

in this chapter is to provide a **general ranking formula that could be used as a rule of thumb in order to set priorities regarding biological invasions management, under a limited budget constraint and accounting for species interrelations.** This ranking formula is applied to a set of invasive species, which are already identified as strongly problematic.

The sketch of the chapter proceeds as follow. In section 2, we consider a simple stylized model of prioritization with two native and two invasive species. We define the optimization framework assuming specific class of utility and diversity functions and analyse the budget allocation choice of a manager whose aim is to minimize the disruptions due to biological invasions. We proceed in section 3 with a generalization of this optimization framework by considering any number of species and any class of utility and diversity functions. Section 4 concludes on the use of the resulting prioritization criterion for applications.

4.3 A STYLIZED MODEL

Consider an hypothetical ecosystem composed of four interacting species $i = 1, 2, 3, 4$. Among these species, two are invasive species, which we denote with subscript $k, k = 1, 2$; and two are native species, which we denote with subscript $l, l = 3, 4$. We distinguish two types of invasive species impacts to the ecosystem : (1) ecological impacts to the native ecosystem notably through species interactions like competition for ressources, predation, etc.²; and (2) economic impact, like eutrophication or obstruction of canalizations.³ Although impacts are mostly reported as strictly negative, they can in some cases be reported as positive, for native species or some stakeholders who benefit from its introduction.

Imagine that a manager in charge of this ecosystem is to efficiently limit the negative

2. e.g. the brown tree snake (*Boiga irregularis*) introduced in the snake-free Guam forest after World War II because of military equipment being moved onto Guam (Fritts and Rodda, 1995, Pimentel et al., 2005) participated in the extinction of 10 native forest birds (Rodda et al., 1997)

3. One of the many examples of disutility produced by an invasive species is the case of *Dreissena polymorpha*, also known as the European zebra mussels, invading and clogging water pipes, filtration systems, and electric generating plants; it is estimated that they cause 1 billion USD/year in damages and associated control costs per year (Vilà et al., 2011).

impacts due to invasive species. Given his limited resources, he has to efficiently allocate his budget in order to minimize net losses given the relative marginal costs of controlling species k . This translates into a maximization problem of an objective function under a monetary constraint.

Several expected diversity function can be considered, and choosing one functional form versus another is an important choice as it reflects a philosophy of conservation.⁴ In this chapter, we consider Weitzman (1998) expected diversity function. A generalization of our approach to any functional form being proposed in next section.

Weitzman considered that each species could be seen as a library containing a certain number of books. The value of a set of libraries is made of the collection of different books available, but also of the different libraries themselves because they can be considered as having an intrinsic value (for instance, the Trinity College Library in Dublin would be considered a wonder even if the book of Kells were not there). Biologically, libraries being species would mean that books would be genes, or phenotypic characteristics, or even something else. To keep it simple, we consider diversity in terms of different genes, like Weitzman did. Assume that species 3 contains E_3 genes and that species 4 contains E_4 genes. Furthermore, although the model could accommodate for gene sharing, we further assume in this stylized model that invasive species 1 and 2 do not have any gene in common.

Because impacts from invasive species are twofold, the objective function of this manager is made of two components.

(1) The first is an **ecological component**. The manager wants the expected diversity of the ecosystem to be as high as possible. In our two native species ecosystem, it means that given species dissimilarity and survival probabilities of these natives, the manager aims at controlling the negative impact of invasives on total expected diversity. We denote this function $W(\{P_l\}_{l=3}^4)$ with P_l the survival probability of the native species l . We assume that

4. Two expected diversity functions are particularly relevant for the current paper, Rao's quadratic entropy (Rao, 1986) and Weitzman's expected diversity function (Weitzman, 1992, 1998). Interested readers may refer to Mulier et al. (2015), and Baumgartner (2007)

$P_l \in [0, 1]$) is an index value, with $P_l = 0$ meaning extinction and $P_l = 1$ meaning profusion of native species l . We consider purposefully that invasive species do not participate to the diversity of this ecosystem, since we focus on the elimination of strictly "noxious" species for the ecosystem in which they arrived. Invasive species contribute to diversity, but of their own native system. This is obviously a very brave assumption to make, especially regarding the conclusions of the first chapters of this thesis. It is however a way to provide an example of extreme case management, in which we are sure only to target extremely harmful species. This first component of the objective function of our manager is thus the expected diversity function, which reads as :

$$\begin{aligned} W(\{P_l\}_{l=3}^4) &= P_3P_4(E_3 + E_4) + P_3(1 - P_4)E_3 + (1 - P_3)P_4E_4 + (1 - P_3)(1 - P_4)0 \\ &= E_3P_3 + E_4P_4 = \sum_{l=3}^4 E_l * P_l \end{aligned} \quad (4.1)$$

(2) The second component of the objective function is the **utility** derived from each species i . The utility of both native and invasive species sets on a range from positive to potentially negative values. We assume that the marginal utility of each species is constant at rate u_i and write :

$$U(\{P_i\}_{i=1}^4) = \sum_{i=1}^4 u_i * P_i \quad (4.2)$$

The overall objective function of the manager reads therefore as the sum of expected diversity function and the utility component :

$$W(\{P_i\}_{i=k+1}^n) + U(\{P_i\}_{i=1}^n)$$

Let us now focus on the constraints faced by the manager.

First, the manager must comply with his budget which is assumed to be limited. Let c_k be the marginal cost of the effort to control invasive species k . Denote by B the overall budget he can exhaust, an additional constraint is the budget constraint :

$$\sum_k c_k * x_k \leq B \quad (4.3)$$

Second, the manager has to account for species interrelations. We consider as in Courtois et al. (2014) that each species i has an autonomous surviving probability q_i which is the survival probability of species i in an ecosystem absent of species interactions and of manager. Because of species interaction, each species i surviving probability depends also on all the other species surviving probabilities, through interrelation parameters $r_{i,l \neq i}$.

Finally, the manager can decide to impact the surviving probabilities of the invasive species present in the ecosystem. His managing effort on species k is noted x_k . The resulting survival probabilities of species i in our stylized two-natives two-invasive species ecosystem read as :

$$\begin{cases} P_l = q_l + \sum_{i \neq l} r_{li} P_i & , q_l \in [0, 1] \\ P_k = q_k - x_k + \sum_{i \neq k} r_{ki} P_i & , q_k \in [0, 1], x_k \in [0, \bar{x}_k] \end{cases} \quad (4.4)$$

Formally, as in Courtois et al (2014), admissible ranges of efforts are $\times_{i=1}^k [0, \bar{x}_i]$. We can now establish the manager's optimization problem in terms of managing efforts x_k :

$$\begin{aligned} & \max_{\{x_k\}_{k=1}^2 \in \times_{k=1}^2 [0, \bar{x}_k]} \sum_{i=1}^4 u_i * P_i \\ & \text{subject to (4.4) and (4.3)} \end{aligned} \quad (4.5)$$

Solving the system of survival probabilities described by (4.4), we obtain a system of equations that links survival probability P_i to control effort values x_k :

$$\begin{cases} P_1 = \frac{\alpha_1}{\delta} + \frac{\theta_1}{\delta} + \frac{\gamma_1}{\delta} \\ P_2 = \frac{\alpha_2}{\delta} + \frac{\theta_2}{\delta} + \frac{\gamma_2}{\delta} \\ P_3 = \frac{\alpha_3}{\delta} + \frac{\theta_3}{\delta} + \frac{\gamma_3}{\delta} \\ P_4 = \frac{\alpha_4}{\delta} + \frac{\theta_4}{\delta} + \frac{\gamma_4}{\delta} \end{cases} \quad (4.6)$$

with $\delta' = \delta(1 - r_{12}r_{21})$ and $\delta, \alpha_i, \theta_i$ coefficients that only depend on the matrix of species interdependencies r_{ih} , and γ_i a coefficient that depends on both species interdependencies and autonomous surviving probabilities q_i . Plugging the equations of the system (4.6) in the objective function (4.5), the maximization shrinks to the trivial problem of the follo-

wing form :

$$\begin{aligned} \max \quad & ax_1 + bx_2 + cste \\ \text{s.t.} \quad & c_1x_1 + c_2x_2 \leq B \end{aligned} \tag{4.7}$$

where a and b are coefficients that only depend on the matrix of species interdependence r_{ih} , the vector q_i , the distinctiveness parameters E_l and the marginal utility u_i .

As the objective function is linear in efforts, the solution of the maximization program (4.7) is extreme, i.e. in the usual case where $a > 0$ and $b > 0$, effort is devoted in priority to the control of a single invasive species and if resources are more than sufficient to fulfill the control of this species, to the other. For simplicity and without loss of generality we consider budget B is limited enough to be completely exhausted with the control of a single species. We have then three extreme solutions, $(0, 0)$, $(\bar{x}_1, 0)$ and $(0, \bar{x}_2)$, with \bar{x}_1 and \bar{x}_2 standing for the maximal admissible ranges of efforts determined by economical and biological constraints.

Proposition 4.1 *In our stylized model, optimal management plan is the following :*

- if $a \leq 0$ and $b \leq 0$, no effort should be made to control the invasions because effort is not desirable. The solution to the maximization program is $(0, 0)$;
- if $a \leq 0$ and $b > 0$, effort is granted to species 2. The solution to the maximization program is $(0, \bar{x}_2)$;
- if $a > 0$ and $b \leq 0$, effort is granted to species 1. The solution to the maximization program is $(\bar{x}_1, 0)$;
- if $a > 0$ and $b > 0$, effort is granted to species 2 when $\frac{c_1}{c_2} > \frac{a}{b}$ and to species 1 else. The solution to the maximization programme is either $(\bar{x}_1, 0)$ or $(0, \bar{x}_2)$. In the very specific case where $\frac{c_1}{c_2} = \frac{a}{b}$, any combination of efforts is applicable.

Coefficients a and b depend on species interactions parameters $r_{i,h \neq i}$, the vector q_i , the distinctiveness parameters E_l and the marginal utility u_i . Key message of the proposition is that when both invasive species disrupts the ecosystem, effort is made toward the most cost-efficient plan. The idea is thus to limit ecosystem disruption at the lowest cost.

This stylized model provides a formal framework to think about the optimal management of biological invasions. However, it is not sufficient as such to make any clear-cut generalization about budget allocation and priorities in a more complex world. First, a

model with more species would translate in more interrelations that could make the problem particularly difficult to solve. Second, simple linear expected diversity and utility functions are restrictive assumptions. Other diversity functions among which the Rao general entropy concept (Rao, 1986), the Allan diversity function (Allan 1993) or even Weitzman's expected diversity with species sharing common genes, exhibit local convexities. Utility functions also often admit concavities or convexities, and our prioritization model must deal with any of these types of situations. Third, an easy-to-use tool should be developed from this optimization framework, in order to be used by a manager in any socio-ecosystem configuration. In the following section we address these three points, and develop a criterion in order for a manager to set priorities in any socio-ecosystem configuration.

4.4 A PRIORITIZATION CRITERION

Consider now an ecosystem made of $N = \llbracket 1; n \rrbracket$ distinct species, k of them being invasive and $n - k$ being native. Invasive species are indexed $\forall i \in \llbracket 1; k \rrbracket$, and native species are indexed $\forall i \in \llbracket k + 1; n \rrbracket$. Again, we ask how a manager should allocate his budget in order to limit the negative impacts associated with invasions.

The problem is more general as we consider many species and therefore many more interactions. We also wish the model to apply with several formulations of expected diversity functions. Weitzman (1998) diversity concept is indeed one among many others and although the concept is appropriate for various management projects, it can be limited for certain management scenarios types. In order to keep our results as general as possible, we consider the expected diversity function W and the utility function U to pertain to the class of C^2 functions, i.e whose first and second order derivative both exist and are continuous.

As in the stylized model, we consider that a manager must choose a vector of effort

X that maximizes an objective function, given species interdependence, and under the constraint of resources. We assume :

$$P_i = q_i - x_i + \sum_{i=1} r_{ih} * P_h, \quad q_i \in [0, 1[, \quad x_i \in [0, \bar{x}_i] \quad (4.8)$$

with $P_i \in \Pi_i = [\underline{\Pi}_i, \overline{\Pi}_i]$, $\forall i, \forall x_i \in [0, \bar{x}_i]$, with \bar{x}_i the admissible range of control, and q_i the probability of survival of species i in the absence of control and without species interactions. Note that for native species, we consider $x_i = 0$, meaning that effort of control is only toward invasive species. As previously considered, the budget constraint is linear in efforts and we have :

$$\sum_{i=1}^k c_i * x_i \leq B \quad (4.9)$$

where B is the total budget to be allocated to invasive species control and c_i is the cost per unit of effort to control species i . The maximization programme of the manager is :

$$\begin{aligned} \max_{\{x_k\}_{k=1}^2 \times \{x_k\}_{k=1}^2 \in [0, \bar{x}_k]} & W(\{P_i\}_{i=k+1}^n) + U(\{P_i\}_{i=1}^n) \\ & \text{subject to (4.8) and (4.9)} \end{aligned} \quad (4.10)$$

Remark that we follow the exact same assumptions than in the stylized model, in which we considered that only native species contribute to the diversity of their ecosystem, while utility of all species are considered in the objective. It goes without saying that the utility of a species might be negative.

It will be more convenient to work with matrix expressions, subsequently written in bold characters. For any matrix \mathbf{M} , let \mathbf{M}^T denote its transpose. Further, \mathbf{I}^n is the $(n \times n)$ identity matrix, and $\mathbf{1}^n$ is the n dimensional column vector whose elements are all 1.

We define :

$$\mathbf{Q} \equiv \begin{bmatrix} q_1 \\ q_2 \\ \vdots \\ q_k \end{bmatrix}, \mathbf{R} \equiv \begin{bmatrix} 0 & r_{12} & \dots & r_{1k} \\ r_{21} & 0 & \dots & r_{2k} \\ \dots & \dots & \ddots & \vdots \\ r_{k1} & r_{k2} & \dots & 0 \end{bmatrix}, \mathbf{P} \equiv \begin{bmatrix} P_1 \\ P_2 \\ \vdots \\ P_k \end{bmatrix}, \mathbf{c} \equiv \begin{bmatrix} c_1 \\ c_2 \\ \vdots \\ c_k \\ 0 \\ \vdots \\ 0 \end{bmatrix}$$

$$\bar{\mathbf{P}} \equiv \begin{bmatrix} \bar{P}_1 \\ \bar{P}_2 \\ \vdots \\ \bar{P}_k \end{bmatrix}, \underline{\mathbf{P}} \equiv \begin{bmatrix} \underline{P}_1 \\ \underline{P}_2 \\ \vdots \\ \underline{P}_k \end{bmatrix}, \mathbf{X} \equiv \begin{bmatrix} x_1 \\ x_2 \\ \vdots \\ x_k \\ 0 \\ \vdots \\ 0 \end{bmatrix}, \bar{\mathbf{X}} \equiv \begin{bmatrix} \bar{x}_1 \\ \bar{x}_2 \\ \vdots \\ \bar{x}_k \\ 0 \\ \vdots \\ 0 \end{bmatrix}.$$

In matrix form, the system (4.8) reads as :

$$\mathbf{P} = \mathbf{Q} - \mathbf{X} + \mathbf{R} * \mathbf{P} \quad (4.11)$$

Under the *weak* assumption that matrix $\mathbf{I}^n - \mathbf{R}$ is invertible , the system (4.11) is solvable and the solution of this system reads as :

$$\mathbf{P} = \Lambda * (\mathbf{Q} - \mathbf{X}), \quad (4.12)$$

where $\Lambda \equiv [\mathbf{I}^n - \mathbf{R}]$.

Let $\mathcal{P}(\mathbf{X}) \equiv \Lambda * (\mathbf{Q} - \mathbf{X})$ refer to the affine mapping from efforts to probabilities.

We plug (4.12) into (4.10) to get rid of probabilities, and express our management of invasive species only in terms of efforts. Define the two composite functions, which here

are mappings from the values taken by function $P(X)$ to the set of real numbers :

$$Wo\mathcal{P}(\mathbf{X}) \equiv W(\mathcal{P}(\mathbf{X})),$$

$$Uo\mathcal{P}(\mathbf{X}) \equiv U(\mathcal{P}(\mathbf{X}))$$

To each vector \mathbf{X} corresponds a unique vector $P = \mathcal{P}(\mathbf{X})$. Therefore the invasive species management problem becomes the constrained maximization of a function of management efforts \mathbf{X} :

$$\max_x Wo\mathcal{P}(\mathbf{X}) + Uo\mathcal{P}(\mathbf{X}), \quad (4.13)$$

subject to

$$\mathbf{c}^T * \mathbf{X} \leq B \quad (4.14)$$

$$0 * \mathbf{1}^n \leq \mathbf{X} \leq \bar{\mathbf{X}} \quad (4.15)$$

Finding the vector \mathbf{X} solution to the optimization problem above is strictly equivalent to finding the optimal set of management efforts $x_j, \forall j \in \llbracket 1; k \rrbracket$. **Should the budget be dispersed to deal with many different invasive species or should it be concentrated on a subset of few invasive species?** This second option could be seen as an extreme policy as in our stylized model where budget was allocated prioritarily to one species. Given the budget constraint is assumed linear, answering this question translates in **discussing the gradient of the objective function, that is the gradient of functions W and U .**

4.4.1 Case 1. Objective is not concave

It is a well know result that the maximization under a linear constraint of a function that is non-negative semi definitive, i.e. which is not concave, admits an extreme solution. Considering the case where $W(P) + U(P)$ is non-negative semi definite, we can easily see that because $\mathcal{P}(\mathbf{X})$ is an affine mapping, $Wo\mathcal{P}(\mathbf{X}) + Uo\mathcal{P}(\mathbf{X})$ is also non-negative semi definite.

When $\sum_{i=1}^n P_i \neq 1$, most diversity function $W(P)$ pertains to the class of non-negative semi-definite functions. We can thus easily prove that $W(P) + U(P)$ is non-negative semi-definite when $U(P)$ is positive semi-definite, i.e. linear and convex functional form. Else,

there exists **conditions on the gradient of $U(\mathbf{P})$ for $W(\mathbf{P}) + U(\mathbf{P})$ to be non-negative semi-definite.**

We deduce that in a large majority of cases, the objective of the manager pertains to this class of function and the solution to the maximization problem **lies on the boundary of the efforts set.** The boundary involves corners, e.g. $x_i = 0$ or $x_i = \bar{x}_i$, and possibly a segment between two corners, therefore with $x_i \in [0, \bar{x}_i]$ for at most one species.

As the objective function of the manager is usually not an affine mapping as it is the case in our stylized model, finding the solution to this problem is not trivial. Following Weitzman (1998) and Courtois et al. (2014), we resort to a linear approximation of the objective function in order to find this solution.⁵

Let us denote :

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

and define the two matrices :

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

The linearized problem in matrix form turns out to be :

$$\max_{\mathbf{X}} \mathbf{Y} * \mathbf{X} + \text{constant terms}, \quad (4.16)$$

subject to (4.14) and (4.15).

The matrix $\mathbf{\Lambda} = [\mathbf{I}^n - \mathbf{R}]^{-1}$ allows the transformation of the information about ecological interactions conveyed by matrix \mathbf{R} into operational data. The computation of the matrix $\mathbf{\Lambda}$ is easily made and if Λ_{ij} denotes a typical element of $\mathbf{\Lambda}$, then \mathbf{Y} is a n -dimensional line vector of the type :

$$\mathbf{Y} = [\alpha_1, \alpha_2, \dots, \alpha_n]$$

5. We suggest the interested reader to refer to (Courtois et al., 2014) for a discussion over the legitimacy of this approximation in this class of problems.

where

$$\alpha_i \equiv \sum_{h=1}^n (D_h + U_h) \Lambda_{hi}.$$

We can now define the "benefit-cost" ratios $\bar{R}^i \equiv \frac{\alpha_i}{c_i}$, or with explicit reference to relevant information :

$$\bar{R}^i \equiv \frac{\Delta P_i}{C_i} \sum_{h=1}^k (D_h + U_h) \Lambda_{hi}, \quad i = 1, \dots, k. \quad (4.17)$$

Assume invasive species $i, i \in \llbracket 1; k \rrbracket$ is assigned with the highest value of \bar{R}^i . Then, if this value is superior to zero, species i should be targeted first and control efforts should focus on this species until efforts reach a maximum, i.e until $x_i = \bar{x}_i$. Then, if $c_i \bar{x}_i < B$, the invasive species with the second highest $R_i > 0$ should be the next target and this iterative process would go on until budget B is fully exhausted.

As we can appreciate, the R_i score of invasive species i does not depend merely on its own impacts but actually on the overall impacts generated by this species on other species, $\sum_{h=1}^n (D_h + U_h) \Lambda_{hi}$, via ecological interactions. Therefore, a species with a strong disutility can be overridden by another, endowed with a lower disutility, but whose importance is enhanced because of its ecological role on other species.

Following (Courtois et al., 2014), we are able to make a ranking criterion operational to decide whether or not to spend money on the management of an invasive species :

Proposition 4.2 *In our optimization problem with ecological interactions, defined by (4.14), (4.15), (4.16), there exists a cutoff value R^* such that :*

- if $R_i > R^* \Rightarrow x_i = \bar{x}_i$, (species i is granted full management),
- if $R_i < R^* \Rightarrow x_i = 0$, (species i is granted zero management),

This myopic ranking criterion is a transparent measure to set management priorities and decide whether or not to allocate part of a budget toward the management of an invasive species. Note that the criterion being the result of an approximation of the objective, there exists an induced error that can be estimated on the basis of the gradient of the objective. The biggest the curvature of the function, the higher the error.⁶

6. We suggest interested readers to refer to (Courtois et al., 2014) for an evaluation of this error.

4.4.2 Case 2. Objective is concave

If a manager conveys informations on species interdependencies, species utilities, species contribution to expected diversity and cost of control of invasive species, the criterion proposed in proposition (4.2) is a simple rule for allocating budget. However, this rule can only be used as such if the objective of the manager is non-negative semi definite, that is if the objective is not concave. Unfortunately, although many classes of biological invasion management problems are not concave, some are. In particular, the utility function from controlling harmful invasive species may be negative semi definite and there exists conditions for the objective function $WoP(\mathbf{X}) + UoP(\mathbf{X})$ to be negative semi definite. In such a case, this is a well known result that the maximisation under a linear constraint of a negative semi definite function admits an interior solution, that is an optimal effort allocation vector.

Gradient method is useful in estimating this optimal effort vector. Linearizing the objective function and minimizing the distance between the gradient of the objective and of the constraint allows for gradually approximate the value of this optimal policy. However, we aim here at defining a simple rule of thumb that can be used by a manager and this approach is inappropriate in that it is rather complex to handle. Albeit not fully satisfying, another solution is for the manager to use an iterative algorithm in order to allocate his budget using myopic criterion presented in (4.2).

Let divide budget B in s shares, such that $b = B/s$. If s is sufficiently big then b is small, which allows to consider that allocation of budget b to the maximization problem lies on the boundary of the efforts set. This boundary involves corners, e.g. $x_i = 0$ or $x_i = \bar{x}_i$, and possibly a segment between two corners, therefore with $x_i \in [0, \bar{x}_i]$ for at most one species. The following iterative procedure gives an approximation of the interior solution of our maximisation problem with ecological interactions, using the simple myopic rule previously defined :

This algorithm is technically demanding as many computations are made necessary

Algorithme 1 :

- 1. Compute the **increased proportion ΔP_h** for any invasive species h given b is spent on the control of h only
 - 2. Compute R^h score for all invasive species h using ranking criterion formula (??)
 - 3. Allocate the share of budget b to the control of the invasive species with the highest score
 - 4. Update the proportion P_i given this allocation
 - 5. Allocate the next share, until all shares are allocated.
-

in order to approximate the solution of our maximization problem. It constitutes however an easy-to-use tool in order to set priorities in invasive species management.

4.5 CONCLUSION

Echoing the work of Witting and Loeschcke (1995) who stated that the optimization of biodiversity conservation should be a minimization of the future loss of biodiversity, we demonstrated in this paper that an optimization framework is relevant to tackle the issue of prioritizing invasive species management projects. **Such a framework is able to take into account pragmatic limitations, such as a budget constraint, as well as more unusual constraints such as ecological ones.** This model is to our knowledge the first prioritization tool that effectively takes into account relative management costs and impact cascades in choosing which invasions to control in priority.

A key output of the paper is the design of a **myopic rule, which may be used by a non expert manager in order to efficiently allocate his budget to limit ecosystem disruptions.** Recall that similar rules were used in order to set conservation priorities in New Zealand (Joseph et al., 2008). An straightforward continuation of the present work is to provide with an application of our decision criterion.

Several additional assumptions are required in order to perform this application. First, an **appropriate diversity function concept** is to be picked. Among the several available concepts in the literature, Weitzman expected diversity and Rao quadratic entropy are a priori good candidates but correspond to two distinct philosophy of diversity that needs

to be further discussed. Second, **measurement of species distinctiveness** is to be elicited, since genetic dissimilarity might not be the best information to measure diversity. Third, our model can either work with P_i standing for the **survival probability of species i** or for the **relative abundance of species i** within the ecosystem. According to the species selected in the application, one variable or the other is to be used but if the second option is selected the model needs to be **modified at the margin in order to incorporate the additional constraint $\sum_{i=1}^n P_i = 1$** . Finally, the crux of the framework is to account for species **interdependences**. The robustness of the ranking rule is fully dependent on the quality of the interdependence informations (i.e. R_{ih} matrix). Generally, a specific focus is to be put on availability of the data required for making use of this ranking criterion.

V

CONCLUSION

CONCLUSION

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The rising challenges regarding biodiversity preservation are coupled with a constant decrease in the amount of international funding dedicated to biodiversity. We are faced with the urgent, yet extremely difficult question : how to prioritize action for biodiversity given a limited financial support? And therefore how to use efficiently this limited amount of funding to maximize the amount of biodiversity that can still be spared. This question looks like a typical economic question of maximizing an objective function under a budget constraint. Defining a biodiversity objective function is however not straightforward. Indeed, the set of constraints on biodiversity management does not just boil down to a budget limit, and ecological interactions constitute another key constraint impacting conservation policy and the management of IS in particular. This thesis is a step towards accounting for those additional constraints. We define a class of biodiversity indices that incorporate information about ecological interactions, which may be important for example in the management of non-native species. The example of biological invasions in Chapter 1 reveals the complexity of biodiversity measurement and interactions. It demonstrates the intricacy and extremely context-dependant character of biological invasions impacts, at the crossroad of ecological, economic and social impacts. This highlights three crucial questions for the rest of the thesis : (1) If adding another species to a set is not systematically an "advantage", would it make sense to define a diversity index that may decrease with the addition of (some) species? (2) more generally, beyond the case of invasive species that may impact so badly the ecosystem, how can species interactions be taken into account for the overall level of measured diversity? (3) Given those complexi-

ties, is it feasible for policy-making to prioritize action for biodiversity? The introduction of potential interactions among species as a component of the diversity objective function is the object of Chapter 2, using a modified version of Noah's Ark metaphor. It shows how interactions may interfere with the outcome in terms of prioritization. Staying in this *in situ* framework in which species interact, Chapter 3 compares the outcomes of using two biodiversity indices, Weitzman's and Rao's, stemming respectively from economic and ecological literature. It shows that the retained objective function have important implications on the measurement of diversity and thus for prioritization. Based on the previously defined frameworks, Chapter 4 is an illustration of a prioritization case in which biodiversity is composed of native and invasive species. It proposes a myopic rule for a manager to determine which invasion should be controlled in priority, taking into account relative management costs and trophic cascades impacts. This enables a discussion on the shape of diversity objective function.

5.1 RESULTS

The first chapter on biological invasions impacts poses as a revealer of the complexities of biodiversity management through the example of biological invasions. Biological invasion impacts are defined as "ambivalent", i.e. rather "good", "bad", or "neutral" for the socio-ecosystem in which it arrives. In this chapter, we proposed an adaptive definition of the multidimensional biological invasions impacts, using a typology of the variability of impacts. This typology decomposes the impacts of biological invasions into three categories (ecological, social, and economic) and examine whether each category of impact is likely to exhibit ambivalence within a given socio-ecosystem, defined by a spatial scale, a timeframe, and a set of involved stakeholders. The principal results of this chapter lead to (1) understand the complexity of invasion impacts at the crossroads of several, non-quantitative and consequently non-additive dimensions, but also (2) to propose a methodology to evaluate the degree of ambivalence of each dimension of the impact assessment, which may influence policies prioritization. Indeed, a modification of

the context in which biological invasion impacts are measured can lead to modify management priorities. Overall, it highlights the difficulty of considering biodiversity as a homogeneous and monolithic reality, disconnected from species interactions and from the context in which it thrives.

Those conclusions lead us to evaluate the role of species interactions in the definition of preservation priorities in chapter 2. Starting from Noah's ark problem defined by Weitzman (1998), we modify his diversity objective function by introducing species interactions at the level of survival probabilities, set dependant on the protection efforts. We provide a cost-effectiveness methodology for the selection of best preserving diversity projects, under a limited budget constraint. The first result is that similarly to Weitzman's result, the optimal protection is an extreme solution. This comes from the property that the Hessian matrix of the *in-situ* objective function is not negative semi-definite. The second result uses the linear approximation of the objective function used by Weitzman (1998), leading to a classical linear programming problem, in order to assign grades to species and rank them in decreasing order of importance until the budget is exhausted. Here, the introduction of interactions only modifies the "slope" of the objective function. On this basis, we elaborate a rule giving a first order approximation of the optimal solution to Noah's ark problem with ecological interactions. The number assigned to each species through the evaluated cost/benefit ratio depend therefore not only on each species inherent "value", but also on the overall value generated by this peculiar species on all other species via ecological interactions. We discuss the limits of this approach for building an operational hierarchy between species to help policy making, by determining the approximation error resulting from the linearization of the objective function using the gradient method. This error is related to the inherent non-linearity of the objective function, which we further discuss in chapter 4.

The choice of a specific form of biodiversity index can be extremely important, for it may influence policy recommendations. Chapter 3 compares simple biodiversity protec-

tion policies using two different biodiversity indices stemming from different discipline : the previously defined Weitzman's criterion, and Rao's criterion for diversity. Again, we describe an *in situ* version of both criteria as a function of protection efforts, and focus on a three species ecosystem with ecological interactions. Both indices combine information about *i*) survival probabilities, *ii*) distinctiveness and *iii*) species interactions in slightly different ways, in accordance with their original purpose. The first result of this chapter is to clarify the role of each of those dimensions taken separately in both indices ; we compare the end-value of simple protection plans for both indices, when only one of the dimensions is allowed to vary. This leads to three major propositions, one for each dimension. The first proposition on the role of survival probabilities states that Weitzman's criterion would preserve the "strongest" species, whereas Rao's preserves the "weakest" species ; the second proposition on the influence of distinctiveness shows that both indices are indifferent between preserving the two least dissimilar species, and recommend to preserve the most dissimilar species ; the third proposition on the influence of interactions yields the same results for both indices, as both would protect the species with the largest beneficial influence on other species. Those conclusions are confirmed in a three species ecosystem. A second set of results of this chapter is based on the simultaneous variation of two dimensions within the indices. In this case, these dimensions appear as trade-off within the indices : when equivalent interactions across species are coupled to a measure of distinctiveness among species in each index, both dimensions appear as a solution of the final choice. Dissimilarity would prevail in this choice if and only if the strength of ecological interactions is limited ; otherwise conservation choices depend on the interactions rather than the number of common genes. Therefore, the role of ecological interactions in each of those two measurement frameworks seem to be an important additional information in order to determine conservation objectives, and the nature of the retained index for measuring biodiversity. The two indices under study thus tend to

help different species profile, and it is important to know this before use for informing policies in different contexts of biodiversity degradation.

Biological invasions are listed as the second cause of biodiversity degradation by the IUCN. As seen in the first chapter, the impacts from invasive species are complex and multidimensional. Chapter 4 focuses on the range of invasive species identified as having the strongest impact, with an objective of mitigating or eradicating those species. Based on the outputs from the second and third chapter, we developed a myopic ranking rule for a hypothetical manager of a four species ecosystem – two native species and two invasive species – wishing to deal with invasion. As in the previous chapters, we consider interactions between those species. Invasive species show ecological impacts on the ecosystem, as well as economic impacts, which may be positive or negative. The first result of this chapter is to adapt the framework of chapter 3 to the management of biological invasion, in which efforts are allocated to controlling invasion rather than preserving species. The objective for the manager is thus to limit their negative impacts given the limited resources available. The objective function of the manager is described as the sum of a diversity function and a utility function, subjected to a budget constraint and ecological constraint on species interactions. This objective function is supposed to be linear in efforts, leading to an extreme solution of the maximization program, *i.e.* efforts are allocated in priority to one single species. Each species is thus assigned a coefficient, which is a combination of the different vectors of matrices – species interdependence, survival probabilities, distinctiveness parameters and marginal utility. A comparison of those coefficients helps to determine which of the extreme solutions will be retained : (1) no effort on each of the invasive species ; (2) effort made on the eradication of species 1 ; (3) effort made on the eradication of species 2. Each species is assigned a coefficient. If resources are more than sufficient to fulfil the control of the species retained in priority, it will be directed towards the second species. The second result of this chapter is a generalization of this four species model, on the basis of the results obtained in chapter 3. We express in general terms

the constrained maximization of the function of management efforts, which helps to determine the optimal set of management control efforts. The third result of chapter 4 is a discussion on the allocation of the budget to either one or several species, based on two cases relatively to the gradient of the objective function, which is set as concave or not concave. In the non-concave case, a linear approximation of the objective function is used, and the solution to the constrained maximization program is extreme providing a restriction to the class \mathcal{C}_2 of functions, and boils down to a simple rule for allocating budget. In the concave case, the solution for species control is necessarily an interior solution. We propose an iterative procedure in order to approximate this interior solution by sharing the budget equally between each species and allocating iteratively those budget shares to invasive species in the order of priorities determined by the ranking criterion.

5.2 DISCUSSION

This thesis raised several important points in biodiversity management, but could certainly not answered completely all of them. It raises however several interesting research avenues which may be further investigated. For each of chapters, interesting applications could be developed and further scrutinized.

Facing the complexity of biological diversity, Chapter 1 highlighted the importance of gathering all reliable information to help the assessment of ambivalence cases, and the relative impacts of NIS. However, the tables developed in this chapter can neither produce a systematic and straight classification of the socio-ecosystems more vulnerable to invasions, nor can it identify with certainty the more problematic species. This general methodology which helps to look at NIS impact from three major angles – space, time, and stakeholders – goes along with a careful examination of the socio-ecosystem, among which the economic sectors at stake, the available mitigation technologies and potential political or legislative constraints. This approach is however an interesting grid to start identifying the important characteristics to consider for management.

The theoretical results developed in Chapter 2 and 3 could be usefully enhanced with an application using data from several species, first in a controlled ecosystem with constrained conditions such as an aquarium, and later using data of a real ecosystem. An interesting extension would be to compare the selected species with and without interactions, or with the use of one diversity index or another.

Chapter 4, which is specifically oriented towards species selection for management (eradication), is more directly applicable in order to test its usefulness in real invasion situations. The methodology developed in Chapter 2 could be a very useful complement in this setting, in order to describe the invasion problem considered and therefore discuss the shape of the objective function and its gradient.

This thesis focused principally on measurement for a better management of biodiversity, especially regarding the topic of invasive species. As a consequence of this reflection, interactions appears as a crucial, yet extremely difficult issue to deal with. Several research avenues could be opened, especially regarding the measurement of long term consequences from certain management policies. Beyond their obvious scientific value, the identification of keystone, patrimonial or even emblematic species could gain interest as representants of a larger network of interactions. This identification is interesting both from an efficiency point of view in order to justify fund-raising for other co-existing species but also to increase general public awareness about the intricacy of species interactions. Even if indices are only meant to inform policy making about the overall amount of biodiversity, an interesting way to go is to better understand how those living resources develop and thrive, in order to guide more accurately decision-making.

APPENDIX

IDENTIFICATION OF THE ADMISSIBLE RANGES OF EFFORTS

Probabilities, as functions of efforts, are given by $\mathcal{P}(\mathbf{X})$, a k -dimensional vector with typical element $\mathcal{P}_h(\mathbf{X})$, $h = 1, \dots, k$. The issue is to find bounds $[\bar{x}_1, \bar{x}_2, \dots, \bar{x}_k]^\top$ on efforts $\mathbf{X} = [x_1, x_2, \dots, x_k]^\top$ so that decisions $x_i \in [0, \bar{x}_i]$ are consistent with the system of inequalities :

$$0 \leq \mathcal{P}_h([x_1, x_2, \dots, x_k]^\top) \leq 1, \quad h = 1, \dots, k. \quad (\text{A.1})$$

Those inequalities hold by construction when $\mathbf{X} = [0, 0, \dots, 0]^\top$. This suggests that for limited departures from this zero vector, the system of inequalities still holds. Observe that $\mathcal{P}_h(\mathbf{X})$ is a linear function, therefore when some x_i increases from 0, each pair of inequalities (A.1) provides an upper bound for this effort because function $\mathcal{P}_h(\mathbf{X})$ approaches either 0 or 1, depending on the sign of the slope $\partial \mathcal{P}_h / \partial x_i$. An algorithm can be used to put admissible limits on those deviations. It has k steps.

- Step 1 : the first step of this algorithm is to set to zero all the efforts, except for species 1. The resulting system of inequalities is :

$$0 \leq \mathcal{P}_h([x_1, 0, \dots, 0]^\top) \leq 1, \quad h = 1, \dots, k.$$

This is a system of k pairs of inequalities where only x_1 can vary. Each pair h of inequalities defines an upper bound \bar{x}_1^h for x_1 . Let

$$\bar{x}_1 = \frac{\min \{ \bar{x}_1^h \}}{k}.$$

be the lowest of these upper bounds divided by k . By construction, as long as x_1 evolves between 0 and \bar{x}_1 , and all the other efforts are zero, all the inequalities are satisfied. Actually, because $\bar{x}_1 < \min \{ \bar{x}_1^h \}$, the possibility exists to increase the other efforts x_2, \dots, x_k to some extent without violation of (A.1).

— Step 2 : consider now the system of k pairs of inequalities where $x_1 = \bar{x}_1$, x_2 can vary and all the remaining efforts are zero :

$$0 \leq \mathcal{P}_h \left([\bar{x}_1, x_2, 0, \dots, 0]^\top \right) \leq 1, \quad h = 1, \dots, k.$$

To this first system, let us add k other pairs of inequalities where $x_1 = 0$, x_2 can vary and all the remaining efforts are zero :

$$0 \leq \mathcal{P}_s \left([0, x_2, 0, \dots, 0]^\top \right) \leq 1, \quad s = 1, \dots, k.$$

Considered together, those $2 * k$ pairs of inequalities defines upper bounds \bar{x}_2^j , $j = 1, \dots, 2 * k$ for x_2 . Let

$$\bar{x}_2 = \frac{\min \{ \bar{x}_2^j \}}{k}$$

be the lowest of these upper bounds divided by k . When x_2 lies between 0 and \bar{x}_2 , all the $2 * k$ above inequalities are satisfied. We claim now that, as long as $x_2 \in [0, \bar{x}_2]$, x_1 could take any value between 0 and \bar{x}_1 without violating (A.1). Indeed, take any $x_2 \in [0, \bar{x}_2]$ and consider any two pairs of inequalities

$$0 \leq \mathcal{P}_h \left([\bar{x}_1, x_2, 0, \dots, 0]^\top \right) \leq 1,$$

$$0 \leq \mathcal{P}_h \left([0, x_2, 0, \dots, 0]^\top \right) \leq 1.$$

Multiplying the first pair by any number $\alpha \in [0, 1]$, multiplying the second pair by $(1 - \alpha)$ and adding-up the two products :

$$0 \leq \alpha * \mathcal{P}_h \left([\bar{x}_1, x_2, 0, \dots, 0]^\top \right) + (1 - \alpha) * \mathcal{P}_h \left([0, x_2, 0, \dots, 0]^\top \right) \leq 1,$$

or given the linearity of \mathcal{P}_h :

$$0 \leq \mathcal{P}_h \left([\alpha * \bar{x}_1, x_2, 0, \dots, 0]^\top \right) \leq 1, \quad \forall \alpha \in [0, 1],$$

which means that for any $x_1 \in [0, \bar{x}_1]$ and any $x_2 \in [0, \bar{x}_2]$, when all the other efforts are zero the system (A.1) is satisfied. And the other efforts x_3, \dots, x_k could also vary to some degree.

— ...

- Step $h < k$: consider sub-vectors $\tilde{\mathbf{X}}_{h-1}$ made of the first $h-1$ efforts and where each of them takes only extreme values, *i.e.* $x_i = 0$ or $x_i = \bar{x}_i, i < h$; there are 2^{h-1} possible sub-vectors of this kind. Therefore, we can contemplate 2^{h-1} systems of pairs of k inequalities where $\tilde{\mathbf{X}}_{h-1}$ is fixed, x_h is allowed to vary and all the other efforts x_{h+1}, \dots, x_k are zero :

$$0 \leq \mathcal{P}_h \left(\left[\tilde{\mathbf{X}}_{h-1}, x_h, 0, \dots, 0 \right]^\top \right) \leq 1, \quad h = 1, \dots, k.$$

The overall system of $(2^{h-1}) * k$ pairs of inequalities defines candidate upper bounds $\bar{x}_h^j, j = 1, \dots, (2^{h-1}) * k$ for x_h . Let

$$\bar{x}_h = \frac{\min \left\{ \bar{x}_h^j \right\}}{k}$$

defines the upper bound for x_h . It is easy to check, as we did in step 2, that, as long as $x_h \in [0, \bar{x}_h]$, for any convex combination of any collection of sub-vectors $\tilde{\mathbf{X}}_{h-1}$, the system (A.1) is satisfied. This means that, when the efforts x_{h+1}, \dots, x_k are zero, the first h efforts can vary between zero and their upper bounds without violating the system (A.1). This provides margins of variation for the $k-h$ last efforts.

— ...

- Step k : consider the 2^{k-1} systems of pairs of inequalities where only x_k is allowed to vary :

$$0 \leq \mathcal{P}_h \left(\left[\tilde{\mathbf{X}}_{k-1}, x_k \right]^\top \right) \leq 1, \quad h = 1, \dots, k.$$

Those systems provide possible upper bounds $\bar{x}_k^j, j = 1, \dots, (2^{k-1}) * k$ for x_k . The only upper bound consistent with all the $(2^{k-1}) * k$ pairs of inequalities is :

$$\bar{x}_k = \min \left\{ \bar{x}_k^j \right\} .$$

And again it is easy to check that, as long as $x_k \in [0, \bar{x}_h]$, for any convex combination of any collection of sub-vectors $\tilde{\mathbf{X}}_{k-1}$, the system (A.1) is satisfied. After this k^{th} step we are obviously left with a feasible set of values for the efforts assigned to each species.

THE SYSTEM OF INTERDEPENDENT PROBABILITIES

Solving the system (3.2) of ecological interactions for P_1, P_2 and P_3 as functions of $\mathbf{X} = (x_1, x_2, x_3)^T$ gives :

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

$$P_2(\mathbf{X}) = \frac{(q_2 + x_2)(1 - r_{13}r_{31}) + (q_1 + x_1)(r_{21} + r_{31}r_{23}) + (q_3 + x_3)(r_{21}r_{13} + r_{23})}{1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}} \quad (\text{B.2})$$

$$P_3(\mathbf{X}) = \frac{(q_1 + x_1)(r_{31} + r_{32}r_{21}) + (q_2 + x_2)(r_{12}r_{31} + r_{32}) + (q_3 + x_3)(1 - r_{12}r_{21})}{1 - r_{23}r_{32} - r_{12}r_{21} - r_{13}r_{31} - r_{12}r_{31}r_{23} - r_{21}r_{13}r_{32}} \quad (\text{B.3})$$

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

In vector notations, probabilities as functions of efforts are :

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

WEITZMAN'S CRITERION FOR IN-SITU PROTECTION



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

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

Since G is close to zero, this expression simplifies to

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

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

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

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

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

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

Therefore :

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

More precisely, using (B.1), (B.2) and (B.3) :

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

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

We can rewrite this general form as follows :

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

where

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

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

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

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

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

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

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

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

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

Finally, a matrix form expression would be more compact than (C.2). Let us define :

$$\mathbf{A}_e^W = \begin{bmatrix} a_{11}^W & \frac{1}{2}a_{12}^W & \frac{1}{2}a_{13}^W \\ \frac{1}{2}a_{21}^W & a_{22}^W & \frac{1}{2}a_{23}^W \\ \frac{1}{2}a_{31}^W & \frac{1}{2}a_{32}^W & a_{33}^W \end{bmatrix}, \quad \mathbf{B}_e^W = \begin{bmatrix} b_1^W \\ b_2^W \\ b_3^W \end{bmatrix}.$$

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

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

RAO'S CRITERION FOR IN SITU PROTECTION

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

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

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

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

Using the survival probability system (B.1), (B.2), and (B.3), we obtain the following form for Rao's index :

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

This form can be rewritten as :

$$\mathcal{R}(x_1; x_2; x_3) = \begin{cases} a_{11}^R x_1^2 + a_{22}^R x_2^2 + a_{33}^R x_3^2 + a_{12}^R x_1 x_2 + a_{13}^R x_1 x_3 + a_{23}^R x_2 x_3 \\ + b_1^R x_1 + b_2^R x_2 + b_3^R x_3 + c^R. \end{cases} \quad (\text{D.1})$$

where

$$\begin{aligned} \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 \\ a_{11}^R &= \begin{bmatrix} E_1 (1 - r_{23}r_{32}) (r_{21} + r_{31}r_{23} + r_{31} + r_{21}r_{32}) + E_2 (r_{21} + r_{31}r_{23}) (1 - r_{23}r_{32} + r_{31} + r_{21}r_{32}) \\ + (E_3 + J) (r_{31} + r_{21}r_{32}) (1 - r_{23}r_{32} + r_{21} + r_{31}r_{23}) \end{bmatrix} \\ a_{22}^R &= \begin{bmatrix} E_1 (r_{12} + r_{13}r_{32}) (1 - r_{13}r_{31} + r_{32} + r_{31}r_{12}) + E_2 (1 - r_{13}r_{31}) (r_{12} + r_{13}r_{32} + r_{32} + r_{31}r_{12}) \\ + (E_3 + J) (r_{32} + r_{31}r_{12}) (r_{12} + r_{13}r_{32} + 1 - r_{13}r_{31}) \end{bmatrix} \\ a_{33}^R &= \begin{bmatrix} E_1 (r_{12}r_{23} + r_{13}) (r_{23} + r_{21}r_{13} + 1 - r_{21}r_{12}) + E_2 (r_{23} + r_{21}r_{13}) (r_{23} + r_{21}r_{13}) \\ + (E_3 + J) (1 - r_{21}r_{12}) (r_{12}r_{23} + r_{13} + r_{23} + r_{21}r_{13}) \end{bmatrix} \\ a_{12}^R &= \begin{bmatrix} E_1 [(1 - r_{23}r_{32}) (1 - r_{13}r_{31} + r_{32} + r_{31}r_{12}) + (r_{12} + r_{13}r_{32}) (r_{21} + r_{31}r_{23} + r_{31} + r_{21}r_{32})] \\ + E_2 [(r_{21} + r_{31}r_{23}) (r_{12} + r_{13}r_{32} + r_{32} + r_{31}r_{12}) + (1 - r_{13}r_{31}) (1 - r_{23}r_{32} + r_{31} + r_{21}r_{32})] \\ + (E_3 + J) [(r_{31} + r_{21}r_{32}) (r_{12} + r_{13}r_{32} + 1 - r_{13}r_{31}) + (r_{32} + r_{31}r_{12}) (1 - r_{23}r_{32} + r_{21} + r_{31}r_{23})] \end{bmatrix} \\ a_{13}^R &= \begin{bmatrix} E_1 [(1 - r_{23}r_{32}) (r_{23} + r_{21}r_{13} + 1 - r_{21}r_{12}) + (r_{12}r_{23} + r_{13}) (r_{21} + r_{31}r_{23} + r_{31} + r_{21}r_{32})] \\ + E_2 [(r_{21} + r_{31}r_{23}) (r_{23} + r_{21}r_{13}) + (r_{23} + r_{21}r_{13}) (1 - r_{23}r_{32} + r_{31} + r_{21}r_{32})] \\ + (E_3 + J) [(r_{31} + r_{21}r_{32}) (r_{12}r_{23} + r_{13} + r_{23} + r_{21}r_{13}) + (1 - r_{21}r_{12}) (1 - r_{23}r_{32} + r_{21} + r_{31}r_{23})] \end{bmatrix} \\ a_{23}^R &= \begin{bmatrix} E_1 [(r_{12} + r_{13}r_{32}) (r_{23} + r_{21}r_{13} + 1 - r_{21}r_{12}) + (r_{12}r_{23} + r_{13}) (1 - r_{13}r_{31} + r_{32} + r_{31}r_{12})] \\ + E_2 [(1 - r_{13}r_{31}) (r_{23} + r_{21}r_{13}) + (r_{23} + r_{21}r_{13}) (r_{12} + r_{13}r_{32} + r_{32} + r_{31}r_{12})] \\ + (E_3 + J) [(r_{32} + r_{31}r_{12}) (r_{12}r_{23} + r_{13} + r_{23} + r_{21}r_{13}) + (1 - r_{21}r_{12}) (r_{12} + r_{13}r_{32} + 1 - r_{13}r_{31})] \end{bmatrix} \\ b_1^R &= 2a_{11}^R q_1 + a_{12}^R q_2 + a_{13}^R q_3 \\ b_2^R &= a_{12}^R q_1 + 2a_{22}^R q_2 + a_{23}^R q_3 \\ b_3^R &= a_{13}^R q_1 + a_{23}^R q_2 + 2a_{33}^R q_3 \\ c^R &= a_{11}^R q_1^2 + a_{12}^R q_1 q_2 + a_{22}^R q_2^2 + a_{23}^R q_2 q_3 + a_{33}^R q_3^2 + a_{13}^R q_1 q_3 \end{aligned}$$

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

$$\mathbf{A}_e^R = \begin{bmatrix} a_{11}^R & \frac{1}{2}a_{12}^R & \frac{1}{2}a_{13}^R \\ \frac{1}{2}a_{21}^R & a_{22}^R & \frac{1}{2}a_{23}^R \\ \frac{1}{2}a_{31}^R & \frac{1}{2}a_{32}^R & a_{33}^R \end{bmatrix}, \quad \mathbf{B}_e^R = \begin{bmatrix} b_1^R \\ b_2^R \\ b_3^R \end{bmatrix}.$$

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

$$\mathcal{R}_e(\mathbf{X}) = \mathbf{X}^T * \mathbf{A}_e^R * \mathbf{X} + \mathbf{X}^T * \mathbf{B}_e^R + c^R. \quad (\text{D.2})$$

SPREADSHEET UNDER XCAS, EXAMPLE OF SECTION 4.1 **E**

Xcas Nouvelle Interface

File Edit Cfg Aide Outils Expression Cmds Prq Graphe Geo Tableau Phys Scolaire Tortue

/cygdrive/d/Users/figuiere/Documents/Charles/TravauxCours/Chloe/July_2015/Calculs_Tales_Two_Diversities_28_07_2015.wxw

Config Calculs Tales Two Diversities 28 07 2015.wxw : exact real RAD 12 xcas

restart //variables initialization

Dis. I. P1. P2. P3. Q. R. RTC. Ro1. Ro2. Ro3. WTC. Wo1. Wo2. Wo3. XI. X2. X3. r12. r13. r21. r23. r31. r32

Matrices and vectors

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

$$R = \begin{pmatrix} 0 & r_{12} & r_{13} \\ r_{21} & 0 & r_{23} \\ r_{31} & r_{32} & 0 \end{pmatrix}$$

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

$$I = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}$$

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

$$Q = \begin{pmatrix} q_1 \\ q_2 \\ q_3 \end{pmatrix}$$

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

$$X_1 = \begin{pmatrix} x \\ 0 \\ 0 \end{pmatrix}$$

X2 := matrix([0],[x],[0]) // vecteur of policy 2

$$X_2 = \begin{pmatrix} 0 \\ x \\ 0 \end{pmatrix}$$

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

$$X_3 = \begin{pmatrix} 0 \\ 0 \\ x \end{pmatrix}$$

Calculator interface with various mathematical functions and a toolbar.

Xcas Nouvelle Interface

File Edit Cfg Aide Outils Expression Cmds Prq Graphe Geo Tableau Phys Scolaire Tortue

/cygdrive/d/Users/figuiere/Documents/Charles/TravauxCours/Chloe/July_2015/Calculs_Tales_Two_Diversities_28_07_2015.wxw

Config Calculs Tales Two Diversities 28 07 2015.wxw : exact real RAD 12 xcas

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

$$X_3 = \begin{pmatrix} 0 \\ 0 \\ x \end{pmatrix}$$

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

$$P_1 = (I - R)^{-1} \cdot (Q \cdot X_1)$$

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

$$P_2 = (I - R)^{-1} \cdot (Q \cdot X_2)$$

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

$$P_3 = (I - R)^{-1} \cdot (Q \cdot X_3)$$

Diversity indices

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

$$WTC = \begin{pmatrix} 0 & 1 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

Calculator interface with various mathematical functions and a toolbar.

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