A cost-benefit approach for prioritizing invasive species

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Abstract

Biological invasions entail massive biodiversity losses and tremendous economic impacts that justify significant management efforts. Because the funds available to control biological invasions are limited, there is a need to identify priority species. This paper first reviews current invasive species prioritization methods and explicitly highlights their pitfalls. We then construct a cost-benefit optimization framework that incorporates species utility, ecological value, distinctiveness, and species interactions. This framework offers the theoretical foundations of a simple method for the management of multiple invasive species under a limited budget. We provide an algorithm to operationalize this framework and render explicit the assumptions required to satisfy the management objective.

Keywords: Prioritization, biological invasions, cost/benefit, optimization, diversity

JEL: Q28, Q57, Q58

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1 Introduction

Biological invasions are causing tremendous damages to ecosystems and economic activities (Pimentel et al., 2005; Vilà et al., 2011; Blackburn et al., 2014; Jeschke et al., 2014). In Europe alone, it is estimated that more than ten thousand non-native species have become invasive, with a total estimated monetary damage of 12 billion euros per year (EEA, 2012).[1] The impacts of invasive species on economic activities, as well as their impacts on ecosystems and native biodiversity, justify meaningful management efforts. However, budgets allocated to biological invasions management are limited and both the implementation costs and the benefits of management programs vary greatly (Scalera, 2010; Oreska and Aldridge, 2011; Hoffmann and Broadhurst, 2016). We are faced with an uncomfortable choice: which management strategies should we employ? How do we best spend a limited budget when addressing multiple endangered species, multiple invasive species, or multiple invasion pathways?

Solving this prioritization problem is a major concern for policy makers, conservationists, and land managers. To achieve effective management, progress indicators and decision-support tools must be developed in order to best allocate budgets (McGeoch et al., 2016).[2] As highlighted by Aichi Target 9 of the Convention on Biological Diversity, the ultimate goal for invasive species management is that "by 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated and measures are in place to manage pathways to prevent their introduction and establishment".

However, while invasive species prioritization is acknowledged to be an essential task, selecting the appropriate course of action remains controversial (Simberloff et al., 2013). In some instances, invasions are unmanaged even when immediate actions are urgently required in order to avoid substantial damages. In France for example, a reiterated but unattended call for management funds was made at the early stage of the invasion of the Asiatic hornet, *Vespa velutina* (MNHN, 2009). From two nests formally identified in 2004, 1613 nests were localized in 2007, the colonization covering up to 150000km2 in 2008. Despite reported impacts on apiculture and expected collateral impacts on pollination services due to its massive predation of the European honey bee, *Apis mellifera*, as of 2009, no coordinated control policy was implemented and no funds were allocated.[3] In other instances, significant amounts of money are spent managing invasive species that do not appear to be particularly harmful. In the European Union, for example,

[1] Report available online at *https://www.eea.europa.eu/publications/impacts-of-invasive-alien-species*.

[2] Interested readers may refer to McGeoch et al. (2016) for an extensive discussion about the concept of prioritization.

[3] Report available online at *spn.mnhn.fr*.

a considerable amount of effort and money has been devoted to the eradication of the North American ruddy duck, *Oxyura jamaicensis*. As a result of interbreeding, the ruddy duck has become a threat to the survival of the white-headed duck, *Oxyura leucocephala*, the only stiff-tailed duck indigenous to Europe. The European Union co-funded an eradication program in the United Kingdom, which cost 3.7 million euros for the 2005-2011 period alone, that is, approximately 0.5 million euros per year.[4] While one cannot dispute the fact that the extinction of the white-headed duck would be a tremendous loss, one could also argue that with a EU management budget of only 132 million euros per year (Scalera, 2010), we should take into account costs and benefits while setting management priorities. Another example is the effort to control the spread of *Impatiens glandulifera Royle* in several European countries. Impatiens is ranked as one of the top twenty "high impact" invasive plants in the United Kingdom (UKTAG, 2008). It also occurs on Swiss and Norwegian black lists of harmful invasive species and is considered to be an invasion threat in Germany, against which specific control measures are directed (Kowarik, 2003). However, Hejda and Pyzek (2006) and Hulme and Bremner (2006) show that this species does not represent a major problem for the preservation of native biodiversity in Europe. Given the limited economic impacts reported and its relatively large control costs, management in affected riparian areas may appear questionable.[5] Looking at management costs in the UK, for instance, 1 million pounds per year is spent on control, with management cost estimates ranging from 150 to 300 million pounds for eradicating the species from the territory (Hemming, 2011). In this context, which prioritization framework seems best-suited to help policy makers and park managers more efficiently allocate funding for the management of invasive species?

This paper contributes to the invasive species prioritization literature in three important ways. First, we review current invasive species prioritization methods and explicitly highlight their pitfalls. We argue that a cost-benefit approach rooted in optimization theory can overcome these pitfalls. Second, we develop a cost-benefit optimization model which allows us to approach accurately and exhaustively the cascade of benefits resulting from invasive species control. Two key theoretical contributions are made: i) we explicitly model species interdependences allowing *per se* to apprehend the complexity of impacts resulting from invasive species, and ii) we assume a multi-component objective function combining ecological and economic considerations. Consequently, as in Weitzman's Noah's Ark approach (Weitzman, 1998) and related literature (Baumgärtner, 2004; van der Heide

[4]It is currently being hailed for its success and adapted to other European countries, and may likely lead to the first continental-scale eradication of an invasive species (Robertson et al., 2014).

[5]Control costs range from £$0.50/m^2$ for a single chemical application, or manual control by strimming up to £$10/m^2$ when habitat restoration is included (Tanner et al., 2008).

et al., 2005; Simianer, 2008; Courtois et al., 2014), a multi-component objective as well as species interrelations are accounted for in our optimization procedure. Finally, a last contribution and key motivation of this paper is to develop the theoretical foundations of a cost-benefit decision criterion enabling decision-makers to efficiently allocate their budget toward the management of multiple invasive species. Echoing the increasing demand for simple tools that guide managers and politicians to optimize their investments based on objective and measurable criteria (Tilman, 2000; Roura-Pascual et al., 2009; Dana et al., 2014; Koch et al., 2016), we define the theoretical groundwork of a general ranking formula that could be used as a rule of thumb in order to design a reliable, easy to apply, and economically sound tool to derive management decisions.

The paper proceeds as follows. In section 2, we discuss the main invasive species prioritization tools and their limits. In section 3, we consider a simple stylized prioritization model with two native and two invasive species. We define the optimization framework assuming specific functions and analyze the budget allocation decision faced by a manager aiming to minimize disruptions due to multiple biological invasions. In section 4, we generalize this optimization framework by considering any number of species as well as a broad class of objective functions. We develop an optimization algorithm that could be used in order to design an easy to apply decision criterion for management decisions. Section 5 concludes and discusses relevant extensions of this work.

2 Related literature on species prioritization

While well-developed and globally-applicable indicators and decision-support tools are still lacking (Dana et al., 2014), species prioritization is often grounded on the basis of invasive species watch lists, the best known being the IUCN GISD blacklist of the 100 worst invasive species worldwide, developed in the early 2000s.[6] Because the impacts of invasions are often site-specific, national and regional lists were simultaneously developed and are key indicators used to support management for pre-border assessments (Faulkner et al., 2014).[7] Three key criticisms of these lists are: i) they are miss-perceived as comprehensive (Daehler et al., 2004) while they clearly underestimate the number of invasions (McGeoch et al., 2012), ii) they reflect expert judgments and may under or over estimate economic and/or ecological impacts (Pheloung et al., 1999), and iii) they fail to account for range

[6]Similarly, red lists of threatened species were also provided to ground conservation prioritization.

[7]For example, regional lists were developed in the US, in Brazil or in the UK. France is currently building national and regional lists within the definition of the French national strategy against biological invasions.

and risk measures of the invasiveness of ecosystems, e.g. (Pheloung et al., 1999; Roura-Pascual et al., 2009).

Closely related to invasive species lists and partly developed to overcome their flaws, most other methods are based on risk assessment and scoring approaches that involve ranking invasive species on the basis of a set of criteria (Heikkilä, 2008; McGeoch et al., 2016; Kerr et al., 2016). In scoring approaches, the species with the highest overall score (or lowest, depending on the convention used) is considered the top management priority. It requires environmental managers or stakeholders to choose from pre-defined ordered categories that are then translated to a set of ordered scores; e.g. high-risk invaders are those with a high resulting score. Non exhaustively, Batianoff and Butler (2002, 2003) compiled a list of expert ranked scores on the degree of invasiveness of a variety of species and compared the ranking they obtained to impact scores. Thorp and Lynch (2000) implemented additional criteria such as the potential for spread and sociological values to rank weeds. Thiele et al. (2010) and Leung et al. (2012) added other specific parameters for the classification of an invader. Liu et al. (2011a,b) proposed a framework that specifically accounts for uncertainty while prioritizing risks. Randall et al. (2008), Nentwig et al. (2010), Vaes-Petignat and Nentwig (2014) and Blackburn et al. (2014) developed impact-scoring systems based on a set of ecological and economic impacts. Finally, Kumschick and Nentwig (2010) and Kumschick et al. (2012, 2015) developed frameworks to prioritize actions against alien species according to their impacts, incorporating expert opinions as well as the diverging interests of various stakeholders, thereby capturing, to some degree, a political issue that often underlies prioritization.

Although the scoring approach has proven useful for guiding management prioritization (Roura-Pascual et al., 2009), the method has been developed outside of any formal optimization framework. In particular, this approach exhibits four major flaws: i) the assessment inevitably reflects expert judgments and scores can be controversial, ii) scores' aggregation is problematic, iii) management constraints and, in particular, costs associated with management activities are rarely explicitly taken into account, iv) interactions among species are, at best, superficially accounted for. While the first two flaws could be qualified by the fact that scoring procedures are documented and usually validated by peer review processes, the last two are troublesome and can induce the scoring approach to lead to inefficient allocations.

As argued by Dana et al. (2014), despite the advancements achieved, the practical use of existing decision tools has often been limited and may be misleading as they typically ignore economic, social, technical, institutional or political factors related to conservation and management practices. In particular, as noted by Koch et al. (2016), managing and monitoring is quite costly and decisions thus

need to be made on a sound basis to avoid wasting resources. Limited financial resources as well as management costs are key components of invasive species prioritization that ought to be taken into account. As implementation costs and benefits vary widely from one species to another, a minimum decision rule should be that management efforts be directed towards species whose control admits the higher benefit/cost ratio. However, many control and prevention programs including the North American ruddy duck eradication campaign in Europe and the Impatiens management campaign in the UK seem to break this rule. Failing to consider species interactions can also lead to serious mismanagement. This shortsightedness ignores the cascade of economic and ecological impacts associated with changes in the ecosystem. It implies a mistaken assessment of benefits. Zavaleta et al. (2001), Courchamp et al. (2011) and Ballari et al. (2016), for instance, show that ignoring species interactions when eradicating an invasive species could lead to major unexpected changes to other ecosystem elements, potentially creating unwanted secondary impacts. Griffith (2011) argues that targeting multiple species simultaneously may increase the efficiency of eradication programs as a result of interactions between species. This hypothesis is reinforced by experimental results obtained by Flory and Bauer (2014) in an artificial ecosystem, as well as by the analysis of Orchan et al. (2012) regarding interactions among invasive birds.

Cost-benefit optimization modeling is an appropriate tool to overcome these flaws. By design, this approach aims at optimizing invested resources while accounting for relative costs and benefits, making costs and benefits an integral part of allocation choices. Optimization is a formal approach that allows one to explicitly consider many different management objectives and constraints. Management objectives can be to maximize ecosystem services, ecosystem diversity or any combination of economic and ecological benefits related to invasive species management.[8] These benefits need to be measurable, they need not be monetary values nor even cardinal values. Several constraints can be considered simultaneously. On top of financial resource constraints, this approach makes it possible to account for additional and more complex constraints, such as species interactions, ecosystem carrying capacity, etc. This makes this approach particularly appropriate in order to account for species interactions and the wide range of collateral benefits resulting from invasive species management.

Although cost-benefit and optimization approaches have been increasingly used to study invasive species management, few studies have applied optimization modeling to study budget allocation toward multiple invasive species. In an exhaustive review on the economics of biological invasion management, Epanchin-Niell (2017) examines key research questions raised by the literature. Most papers reviewed are

[8]Note that when discussing management of biological invasions, "benefits" are usually "avoided negative impacts from invasive species".

dedicated to the study of where, when and how to prevent and control a single invasion[9]. In particular, much of the literature focuses on spatial prioritization, with several papers formally studying effort allocation over space in order to efficiently respond to a single biological invasion, e.g. Chades et al. (2011); Epanchin-Niell and Wilen (2012); Chalak et al. (2016) and Costello et al. (2017). Many papers also focus on optimal surveillance and detection strategies to limit the spread of a single invasive species with papers including Hauser and McCarthy (2009); McCarthy et al. (2008); Epanchin-Niell et al. (2014) and Holden et al. (2016). In accordance with Dana et al. (2014), the review by Epanchin-Niell (2017) shows that only one cost-benefit optimization paper addresses the question of species prioritization by assessing allocation choices among multiple invasions.[10,11]

In their seminal paper, Carrasco et al. (2010) analyze optimal budget allocation to address multiple invasions using an optimal control framework. Assuming simple cost and benefit functions, the key of this approach is to combine analytical methods with generic algorithm simulation in order to examine the role of Allee effects and propagule pressure on species prioritization. The principal result is that resource allocation toward a given species relies on its relative species invasiveness and marginal cost of control. Funding should be allocated based on cost-effective strategies targeting species with Allee effects, low rate of satellite colony generation, and low propagule pressure, with a focus on control rather than exclusion. Complementarily, we propose to address a related research question by explicitly focusing on how invasive species impact ecological and economic variables. Carrasco et al. (2010) consider a generic damage function related to invasive species but fail to explicitly account for the impact each invasive species has on other species within the ecosystem. As argued by Glen et al. (2013), this is a major issue because disruptions caused by biological invasions result mainly from these interactions. In the following section, we present an optimization framework that accounts explicitly for species interactions as well as for the collateral economic

[9] For other reviews on the economics of managing bio-invasions, see Olson (2006), Gren (2008) and Finnoff et al. (2010).

[10] In a review based on ISI web of science, Dana et al. (2014) report that among 43 relevant research papers on invasive species prioritization, only two are based on a cost-benefit optimization modeling, most of the remaining being risk analysis ranking species on the basis of impacts and/or invasiveness. Among the two cost-benefit optimization papers discussed, only Carrasco et al. (2010) studies species prioritization by assessing allocation choices among multiple invasions.

[11] More precisely, Epanchin-Niell (2017) quotes two papers studying multi-species prioritization on the basis of relative costs and benefits. The first is a return on investment paper by Donlan et al. (2015). Although it considers strategies involving multiple invasive species, this paper is more concerned with site prioritization than species prioritization. Furthermore, it is not an optimization paper and does not address the question of budget allocation under a budget constraint. The second paper is Carrasco et al. (2010) which we discuss in the core of the article.

and ecological impacts of biological invasions. On the basis of this optimization model, we present a species prioritization criterion algorithm that could be used to design a decision-support tool to help allocate limited funding toward multiple biological invasions.

3 A stylized model

In order to present our cost-benefit optimization framework and introduce our decision criterion, it is useful to start with a simplified stylized model with a few species and a specific management objective function. We consider a hypothetical ecosystem composed of four interacting species indexed $i \in \{1, 2, 3, 4\}$. Among these species, two are invasive species that we denote with subscript k, $k \in \{1, 2\}$, and two are native species that we denote with subscript l, $l \in \{3, 4\}$.

We consider that a decision-maker, a manager in charge of this 4-species ecosystem, must efficiently allocate her budget in order to limit the negative impacts resulting from the invasive species. Given a limited amount of financial resources, we assume she must allocate her budget so as 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 budget constraint.

To examine this allocation problem, we first need a clearly stated management objective, defined so that it can be measured quantitatively. For example, the objective of the decision-maker can be to conserve the maximum number of native species, the most diverse set of species, the value of ecosystem services, the minimization of economic impacts caused by invasive species, or a combination of these objectives. Without loss of generality we assume that the two invasive species have ecological impacts, including impacts on the native ecosystem through species interactions, competition for resources, etc., as well as economic impacts, such as those associated with the loss of ecosystem services. Although often negative, these impacts may be positive as invasive species may positively affect other native species in the ecosystem through predation or mutualism (Evans et al., 2016). They can also positively impact economic activities or be favorably received by segments of the population (see Box 1).

Box 1: Illustrations of economic and ecological impacts

Although ecological impacts of biological invasions are still imperfectly documented (Evans et al., 2016), invasive species are known to be the second most important reason for biodiversity loss worldwide (after direct habitat loss or destruction) (EEA, 2012). A notable example is the impact of the invasion of the brown tree snake, *Boiga irregularis*, into the snake-free forests of Guam after World War II. The introduction of this invasive species which occurred through the transportation of military equipment (Fritts and Rodda, 1995; Pimentel et al., 2005), precipitated the extinction of 10 native forest birds (Rodda et al., 1997). Biological invasions can however precipitate both positive and negative ecological impacts. This is for instance the case of the so-called red swamp crayfish, *Procambarus clarkii*, included in several invasive species black lists. The rapid propagation of the crayfish in the French Camargue 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*. It also positively impacted several populations of birds including the glossy ibis, *Plegadis falcinellus*, Eurasian spoonbill, *Patalea leucorodia*, and Western cattle egret, *Bubulcus ibis* (Kayser et al., 2008).
Economic impacts of biological invasions remain only partially assessed. One documented example is the impact of the invasion of *Dreissena polymorpha*, also known as the European zebra mussel, in the US. The damages caused by the mussel, which invaded and clogged water pipes, filtration systems, and power plants, are valued at around one billion USD per year (Vilà et al., 2011). Although poorly reported, biological invasions may also benefit stakeholders who exploit or appreciate it. In fact, the above mentioned red swamp crayfish was voluntarily introduced in Spain for economic exploitation (Gutiérrez-Yurrita and Montes, 1999). Additionally, there is now a Society for the protection of the African sacred ibis, *Threskiornis aethiopicus*, in France, and Simberloff et al. (2013) reported that plans to eradicate feral domestic mammals (e.g. camels in Australia, deer in New Caledonia, gray squirrels in Europe) encountered opposition from a large segment of the public.

As noted by Courchamp et al. (2017), even if economic impacts can be relatively straightforward to estimate, recent studies show that little is known on the topic (Bradshaw et al. 2016). Defining an ecological impact is even more difficult

because the metric of the impact, its amplitude and the means of observation need to be defined, assessed, and distinguished from the background noise of normal ecological variations (Blackburn et al., 2014; Jeschke et al., 2014).

For the sake of generality, we consider a multiple management objective and we assume that the manager gives value to both native species conservation, *i.e.* "ecological benefit', and ecosystem services, *i.e.* economic benefits.[12]

Measuring ecological benefits is a complex task. A natural assumption is to consider that the manager wishes for the ecosystem to be as healthy as possible. One possible way of measuring ecological health is to define the state of the ecosystem in terms of diversity, which implies that the ecological component of our objective function is a diversity function.[13] In our two native species ecosystem, this means that, given species dissimilarity and survival probabilities, the decision-maker aims to control the negative impact of invasive species on *expected diversity*. We denote this function $D(\{P_i\}_{i=1}^4)$, with P_i as the survival probability of species i, with $P_i \in [0, 1]$.[14] Several competing diversity functions can be considered, and the selection of a function is an important choice as it reflects a philosophy of conservation (Baumgärtner, 2007; Courtois et al., 2015). Three diversity functions are particularly relevant here: Rao's quadratic entropy (Rao, 1982), Alam's diversity measure (Alam and Williams, 1993) and Weitzman's expected diversity (Weitzman, 1992, 1998). These three functions define diversity as a combination of species robustness (e.g. survival probabilities, relative species populations) and species distinctiveness.

For the purpose of tractability, we consider an expected diversity function derived from Weitzman's (1992), and in the next section, we propose a generalization of our approach to any diversity function. Weitzman assumes that each species could be considered analogous to a library containing a certain number of books. The value of a set of libraries is determined by the collection of different books available, but also by the different libraries themselves, since they can be considered as having an intrinsic value (the Trinity College Library in Dublin, for instance, would be considered a wonder even if the Book of Kells were not there).

[12]It is important to note that our analysis can be undertaken with any clearly specified objective and is not restricted to this specific twofold objective. In the next section, this assumption is relaxed in order to account for more (or less) than two components. Formally, the manager's objective function can contain as many components as needed.

[13]Weitzman (1998) first studied conservation choices using this methodology and extensions of his work were proposed by Baumgärtner (2004), van der Heide et al. (2005), Simianer (2008) and Courtois et al. (2014). Other ecological objectives could be considered such as preserving the ecological functions of the ecosystem. In the following section, we present an analysis of this optimization problem considering a general objective function.

[14]Note that we assume biological invasions participate in the diversity of the invaded ecosystem. An alternative is to assume these species only contribute to the diversity of their own native system. Our model applies considering one assumption or the other.

Biologically speaking, this analogy suggests that books are akin to genes, phenotypic characteristics, functional traits, or any other characteristic that may differ between species. In order to maintain generality, we consider diversity in terms of different attributes, species i containing A_i specific attributes.

Formally, this diversity index is the expected number of attributes present in the ecosystem with respect to species' extinction probabilities. Assuming a set of N species, and considering any subset S of species, the expected diversity function for this N-species ecosystem reads as:

$$D(\mathbf{P}) = \sum_{S \subseteq N} \left(\prod_{m \in S} P_m \right) \left(\prod_{n \in N \setminus S} (1 - P_n) \right) V(S)$$

where $V(S)$ is the number of different attributes in subset S. When applied in our 4-species ecosystem,

- If no species disappears, an event that occurs with probability $P_1 P_2 P_3 P_4$, the total number of different attributes that exist if the four species survive is $A_1 + A_2 + A_3 + A_4$,
- if only species 1 survives, an event occurring with probability $P_1 (1 - P_2)$ $(1 - P_3)(1 - P_4)$, the number of attributes is A_1,
- if only species 1 and 2 survive, an event occurring with probability $P_1 P_2$ $(1 - P_3)(1 - P_4)$, the number of attributes is $A_1 + A_2$,
- and so on...

Processing this expected value, we end up with a simple linear function[15] which reads as:

$$D(\{P_i\}_{i=1}^{4}) = \sum_{i=1}^{4} A_i * P_i \tag{1}$$

This means that diversity is measured here as the expected number of attributes we get from the four species composing the ecosystem.

The second component of the objective function is the utility derived from each species i. By utility, we mean the anthropocentric value attached to a certain species. We consider that for both native and invasive species, this utility may range from positive to negative values. An invasive species seen as undesirable

[15]Note that linearity here is due to the fact that species are assumed to not share any common attributes.

because of its economic impacts, for instance, would have a negative utility. For tractability reasons, we assume that the marginal utility of species is constant, with $u_i \in \mathbb{R}$. The utility function of the decision-maker writes:

$$U(\{P_i\}_{i=1}^4) = \sum_{i=1}^{4} u_i * P_i \tag{2}$$

This equation means that the species utility is substitutable and that no complementarities between species come into play. In other words, the utility we get from one species is substitutable from the utility we get from another species and we discard the possibility of a utility derived from species synergies. In the next section, we propose a generalization of our approach to any utility function, including functions with strategic complements.

Overall, the multi-objective of our decision-maker is to allocate her budget so that diversity and utility are maximized. Following Weitzman (1998), in this stylized model, we assume a perfect substitutability between diversity and utility such that:

$$\text{objective} = \max D(\{P_i\}_{i=1}^4) + U(\{P_i\}_{i=1}^4) \tag{3}$$

Perfect substitutability is a strong assumption because it implies that ecological losses may be perfectly compensated by economics gains and *vice versa*. Note that adding weights to each component would not theoretically impact our results. However, considering complementaries between the two components would impact our results, as it will change the gradient of the composed function. Again, this substitutability hypothesis is relaxed in the next section where we assume a general objective allowing us to analyze this optimization problem considering any functional composition.

Now that the management objective has been defined, let us focus on the constraints. First, we must account for species interactions, as disruptions caused by biological invasions result mainly from these species interdependences (Glen et al., 2013). An invasive species competing for resource with a native species, or running a native species to extinction due to predation, also impacts other species interacting with the native species, involving a potentially large cascade of economic and ecological impacts. Similarly, an invasive species can hybridize with a native one, bring foreign diseases and parasites with which native species have not evolved to cope, and deeply modify the composition of the ecosystem.[16]

[16]For example, less than 10% of fish species composing the Camargue lagoon in southern France are native and we observed a complete change in the composition of this ecosystem within the last century due to imported fishes and hybridization (Berrebi et al., 2005).

To model species interactions, we follow Courtois et al. (2014). We model each species i as having an autonomous survival probability q_i which is the survival probability of species i in an ecosystem free of species interactions and without any management activity. Autonomous survival probability is a measure of the robustness of a species. A low survival probability characterizes species on the brink of extinction while a high survival probability characterizes healthy species such as spreading ones. As a result of the interactions that occur between species, the survival probability of each species i also depends on the survival probabilities of all other species through interaction parameters $r_{i,j\neq i}$, with $r_{i,j\neq i} \in \mathbb{R}$. Finally, the decision-maker can choose to target the survival probabilities of the invasive species present in the ecosystem. The amount of effort she invests in controlling invasive species k is denoted x_k, and we denote by $\overline{x}_k$ the maximum control effort constrained by $P_i \in [0,1], \forall i$.[17] The resulting survival probabilities in our stylized two-native two-invasive species ecosystem reads as:

$$\left\{ \begin{array}{l} P_k = q_k - x_k + \sum_{k\neq j} r_{kj} \ P_j \ , \\ P_l = q_l + \sum_{l\neq j} r_{lj} \ P_j \ , \end{array} \right. \tag{4}$$

with the additional constraint:

$$x_k \in [0, \overline{x}_k] \ \ \forall k \ . \tag{5}$$

System of equations (4) describes the stationary law of evolution of survival probabilities of native and invasive species composing the ecosystem.[18]

[17] An algorithm that computes $\overline{x}_k$ is available upon request.

[18] "Stationary" here refers to the fact that it can be interpreted as the steady state of an explicit dynamic system. Each species i contains a total number of individual beings at date t indicated by $n_{i,t}$. The dynamic system is:

$$\left\{ \begin{array}{l} n_{k,t+1} = \widehat{q}_k - \widehat{x}_k + \sum_{k\neq j} r_{kj} \ n_{j,t} \ , \\ n_{l,t+1} = \widehat{q}_l + \sum_{l\neq j} r_{lj} \ n_{j,t} \ , \end{array} \right. \tag{6}$$

Let N_t be the total number of individual beings at date $t : N_t = n_t^1 + n_t^2 + n_t^3 + n_t^4$. Now define the frequencies:

$$P_{i,t} = \frac{n_t^i}{N_t} \ .$$

With obvious changes of variables, the above dynamic system is equivalent to:

$$\left\{ \begin{array}{l} P_{k,t+1} * N_{t+1} = \widehat{q}_k - \widehat{x}_k + \sum_{k\neq j} r_{kj} \ \ (P_{j,t} * N_t) \ , \\ P_{l,t+1} * N_{t+1} = \widehat{q}_l + \sum_{l\neq j} r_{lj} \ \ (P_{j,t} * N_t) \ , \end{array} \right.$$

At the steady state, time subscripts can be deleted to give:

$$\left\{ \begin{array}{l} P_k * N = \widehat{q}_k - \widehat{x}_k + \sum_{k\neq j} r_{kj} \ \ (P_j * N) \ , \\ P_l * N = \widehat{q}_l + \sum_{l\neq j} r_{lj} \ \ (P_j * N) \ , \end{array} \right.$$

The survival probability of invasive species k is the aggregated sum of species' autonomous survival probability q_k, control effort x_k and interactions with other species composing the ecosystem, $\sum_{k \neq j} r_{kj} \; P_j$. A similar myopic law of evolution describes the survival probability of native species, except that by definition no control effort is exerted. Additional constraint (5) is a technical requirement as for $P_i \in [0,1] \; \forall i$ we need $x_k \in [0, \overline{x}_k] \; \forall k$. For all k, $\overline{x}_k$ is defined such that survival probabilities remain between 0 and 1. Thereafter we consider this technical requirement to be fulfilled and consider that $x_1 \in [0, \overline{x}_1]$ and $x_2 \in [0, \overline{x}_2]$. Therefore, as far as probabilities are concerned, one has:

$$P_i \in \Pi_i = \left[\underline{\Pi}_i, \overline{\Pi}_i\right] \sqsubseteq [0,1] \, , \quad i = 1, ..., 4 \; ,$$

meaning that probabilities evolve in the range:

$$\Delta P_i = \overline{\Pi}_i - \underline{\Pi}_i \; , \quad i = 1, ..., 4 \, .$$

Second, we need to account for financial constraints as well as for the management cost to control each biological invasion.[19] Measures of the cost of control are closely linked to the type of investment being considered. It may include investment in manual, mechanical, chemical or biological treatments and involve expenses in machines, herbicides or manpower. Information on management costs is still sparse but there is a growing effort to collect this information.[20] This is important because, in an allocation choice, relative management costs are as important as benefits. Let C_k denote the cost to be incurred when the survival probability of species k is raised from $\underline{\Pi}_i$ to $\overline{\Pi}_i$. Then $c_k = C_k / \Delta P_i$ approximates the marginal cost of x_k, the control of this invasive species k. Let B stand for the overall budget available to the manager. The budget constraint reads as:

Dividing both sides of those equations by N, one obtains:

$$\begin{cases} P_k = q_k - x_k + \sum_{k \neq j} r_{kj} \;\; (P_j) \; , \\ P_l = q_l + \sum_{l \neq j} r_{lj} \;\; (P_j) \; , \end{cases}$$

where:

$$q_k \equiv \frac{\widehat{q}_k}{N} \; , \quad x_k \equiv \frac{\widehat{x}_k}{N} \; , \; q_l \equiv \frac{\widehat{q}_l}{N} \; .$$

Formally, this is the system of interdependent probabilities used in our framework.

[19]Note that in practice there may be many other constraints, such as available manpower, acceptability of actions, access to land, cooperation from relevant stakeholders, etc. These constraints are implicitly incorporated in our model framework as we only compare a feasible set of control strategies.

[20]see Scalera (2010), Oreska and Aldridge (2011) and Hoffmann and Broadhurst (2016) for reviews on management costs of biological invasions in Europe, in the UK and in Australia.

$$\sum_k c_k * x_k \leq B. \tag{7}$$

Combining the objective and the constraints, the maximization program writes:

$$\max_{(x_1,x_2)\in[0,\bar{x}]^2} (D(\{P_i\}_{i=1}^4) + U(\{P_i\}_{i=1}^4)) = \max_{x_1,x_2} \sum_{i=1}^4 (A_i + u_i) * P_i \tag{8}$$

subject to (4) and (7).

Solving the system of survival probabilities described by (4), we obtain the following system of equations expressing survival probability P_i as functions of control effort values x_k:

$$\begin{cases} P_1 &= \frac{\alpha_1}{\delta} x_1 + \frac{\theta_1}{\delta} x_2 + \frac{\gamma_1}{\delta} \ , \\ P_2 &= \frac{\alpha_2}{\delta} x_1 + \frac{\theta_2}{\delta} x_2 + \frac{\gamma_2}{\delta} \ , \\ P_3 &= \frac{\alpha_3}{\delta} x_1 + \frac{\theta_3}{\delta} x_2 + \frac{\gamma_3}{\delta} \ , \\ P_4 &= \frac{\alpha_4}{\delta} x_1 + \frac{\theta_4}{\delta} x_2 + \frac{\gamma_4}{\delta} \ , \end{cases} \tag{9}$$

where δ, α_i and θ_i are coefficients that only depend on the combinations of species interaction coefficients r_{ij}, and γ_i are coefficients that depend on both species interaction coefficients and on autonomous survival probabilities q_i (see Appendix 1.). This means that the survival probability of any species i is impacted by the control of invasive species 1 (resp. 2) unless interaction parameters are such that $\alpha_i = 0$ (resp. $\theta_i = 0$), independently from the distribution of autonomous survival probabilities.

Plugging the solution of the system of equations (9) into the multi-objective function (8), the maximization shrinks to the following linear programming problem:

$$\max_{(x_1,x_2)\in[0,\bar{x}]^2} \beta_1 x_1 + \beta_2 x_2 + \text{ constant terms} \tag{10}$$

subject to $c_1 x_1 + c_2 x_2 \leq B$.

with $\beta_1 = \sum_{i=1}^4 (A_i + u_i) * \frac{\alpha_i}{\delta}$, $\beta_2 = \sum_{i=1}^4 (A_i + u_i) * \frac{\theta_i}{\delta}$ and the constant terms is $\sum_{i=1}^4 (A_i + u_i) * \frac{\gamma_i}{\delta}$.

Formally, β_1 and β_2 are gradient coefficients that depend only on species interaction parameters r_{ij}, species attributes A_i, and species marginal utility u_i (see Appendix 1.). Interestingly, β_1 and β_2 do not rely on probability q_i, which means that species' autonomous survival probabilities are not of direct interest to the

decision-maker. This is somehow counter-intuitive as it tells us that allocation of effort toward the control of invasive species is made independently from the autonomous survival probabilities of native species. This result is a consequence of using Weitzman's diversity function as the ecological component of the manager's objective function. Indeed, Weitzman's diversity function aims at maximizing expected diversity. In our stylized model, species do not share any common attributes, and since all attributes are similarly valuable, the index is indifferent to preserving one attribute or the other.

The following proposition proceeds:

Proposition 1 *The optimization problem with ecological interactions, defined by (3), (4) and (7), leads to an extreme solution. Efforts are allocated towards species with the highest benefit/cost ratios. These ratios are:*

$$\begin{cases} R_1 \equiv \frac{\Delta P_1}{C_1}\beta_1 \equiv \frac{\Delta P_1}{C_1}\sum_{i=1}^{4}(A_i + u_i) * \frac{\alpha_i}{\delta} \ , \\ \\ R_2 \equiv \frac{\Delta P_2}{C_2}\beta_2 \equiv \frac{\Delta P_2}{C_2}\sum_{i=1}^{4}(A_i + u_i) * \frac{\theta_i}{\delta} \ . \end{cases}$$

Proof. Remark that the maximization problem shrinks to the maximization of (10) subject to (5) and (7). Because in this program both the objective function and the budget constraint are linear in efforts, we know from *the maximum principle* that the solution is extreme. It means that an optimal solution is to allocate financial resources towards the control of the invasive species with the highest benefit/cost ratio first, and then allocate any remaining financial resources to the invasive species with the second highest benefit/cost ratio, and so on and so forth until the budget is exhausted. As the objective function is linear in efforts, marginal benefit to control invasive species k is β_k. Similarly, as the budget constraint is linear in efforts, marginal cost to control invasive species k is $c_k = C_k/\Delta P_k$. We deduce that optimally, efforts are allocated in priority toward the species with the highest ratio $\frac{\beta_k}{c_k}$, which ends the proof. ■

Note that in the absence of species interactions, parameters $r_{i,j\neq i} = 0$, $\forall i, j$. System of equations (4) writes:

$$\begin{cases} P_k = q_k - x_k \ , \\ P_l = q_l, \end{cases}$$

meaning that survival probabilities of species are independent. Then, the only harm caused by biological invasions is their possible negative impact on economic variables through the direct disutility these species can forward. The cascade of

impacts through species interactions vanishes and as we have $\alpha_1 = -1$, $\theta_2 = -1$ and $\delta = 1$ (see Appendix), benefit/cost ratios become:

$$\begin{cases} R_1 \equiv \frac{\Delta P_1}{C_1} * (A_1 + u_1) * (-1)\,, \\ \\ R_2 \equiv \frac{\Delta P_2}{C_2} * (A_2 + u_2) * (-1)\,. \end{cases}$$

From proposition 1, we know that resources are allocated toward the invasion whose control forwards the highest benefit/cost ratio. Independent survival probabilities insure that benefits are only related to the direct avoided impact the invasion causes to the ecosystem. In other words, if we have two invasive species that are equally expensive to control ($C_1 = C_2$) and that do not contribute to the diversity of the ecosystem ($A_1 \approx A_2 \approx 0$), effort will be allocated toward the invasive species which produces the biggest nuisance (i.e negative utility). It is straightforward to deduce that ignoring indirect impacts resulting from species interconnections is likely to invert allocation priorities and will likely lead to incorrect budget allocation prescriptions.

In order to make use of proposition 1 for targeting management priorities, an additional requirement is that budget should be allocated to the control of invasive species if and only if these species are bads.[21] Formally, if β_k is negative, the benefit/cost ratio is negative also and no investment should be made on invasive species k. To illustrate our proposition, let us assume that budget B is completely exhausted by efforts to control a single species. We then obtain three corner solutions, $(0, 0)$, $(\overline{x}_1, 0)$ and $(0, \overline{x}_2)$, where $\overline{x}_1$ and $\overline{x}_2$ stand for the maximal admissible ranges of efforts determined by economic and biological constraints.

The optimal management plan then proceeds as follows:

- if $R_1 \leq 0$ and $R_2 \leq 0$, no effort should be made to control invasions. The solution to the maximization program is $(0, 0)$;
- if $R_1 \leq 0$ and $R_2 > 0$, control effort targets species 2. The solution to the maximization program is $(0, \overline{x}_2)$;
- if $R_1 > 0$ and $R_2 \leq 0$, control effort targets species 1. The solution to the maximization program is $(\overline{x}_1, 0)$;

[21] Note that we employ the terminology of consumer theory, a bad being the opposite of a good. Here, an invasive species is a bad if it has net negative impacts, it is a good if it has net positive impacts.

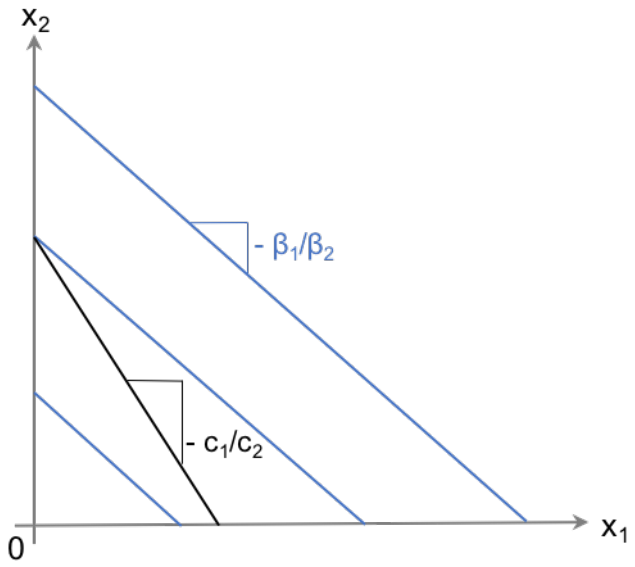
- if $R_1 > 0$ and $R_2 > 0$, control effort targets species 2 when $R_2 > R_1$ and species 1 otherwise. The solution to the maximization program is either $(0, \overline{x}_2)$ or $(\overline{x}_1, 0)$. In the very specific case where $R_2 = R_1$, any combination of efforts is applicable.

Item 1 characterizes the situation in which the objective function and the budget constraint do not intersect: the control is not desirable as the invasive species can be assimilated to goods. $R_1 \leq 0$ and $R_2 \leq 0$ means that controlling the two invasive species is of no net benefit as the decision maker benefit is decreasing in the level of efforts. As R_i depends on species interaction parameters r_{ij}, species attributes A_i, and species marginal utility u_i, it can be a negative number for several reasons. First, an invasive species may have positive impacts on economic and/or ecological values (see Box 1). It can for instance be exploited and generate profit. Second, and this is the crux of this model, an invasive species may positively impact other species through species interrelations. It can for instance be the prey of a native predator and forward positive collateral benefits to this native species. One possible candidate example is the American crayfish in the Camargue lagoons for which it is difficult to value whether negative impacts overcome positive impacts. Items 2 and 3 characterize situations in which one invasive species is a bad, and the other is a good. Budget is then allocated toward the control of the bad, whatever the distribution of costs is. A hypothetical example could be the allocation trade off between controlling the American crayfish and the Asian hornet in the Camargue lagoons. The last item and most interesting case is when the two invasive species are bads. In that case, benefit/cost ratios of the two control strategies should be compared. Again, benefits are to be understood as the direct benefit we get from control but also the indirect benefit we get from species interrelations. Graphically this last case is illustrated in Figure 1, when $\Delta P_1 = \Delta P_2 = 1$ and $\frac{\beta_2}{c_2} > \frac{\beta_1}{c_1}$. The budget constraint is represented by the black line (with slope $-\frac{c_1}{c_2}$) and the isoquants of the objective function of the decision maker are represented by the blue lines (with slope $-\frac{\beta_1}{\beta_2}$).

Given the budget constraint and the relative costs, the greatest benefit that can be obtain leads us to choose point $(0, \overline{x}_2)$, meaning targeting species 2 first. Considering an allocation trade off such as controlling invasion of the Asian hornet or of the ruddy duck in Europe, one could expect that unless the management of the hornet is amazingly expensive, ruddy duck should be species 1.

The result we derive from this stylized model is that when both invasive species are bads, it becomes necessary to examine aggregated benefit-cost ratios in order to set management priorities. The management strategy can thus be characterized as one of limiting the economic and ecological disruption of ecosystem at the lowest possible cost. A key insight from our model is that benefit/cost ratios depend on

Figure 1: Optimal control efforts in the stylized model



species' interactions, distinctiveness, marginal utilities, as well as the relative control costs of invasive species. Contrary to most species prioritization approaches, an important insight of this model is that the principal coefficient affecting the benefit of invasive species control is species' interactions. This makes the laws of evolution of survival probabilities of native and invasive species composing the ecosystem an essential ingredient of species prioritization.

Although this model is useful in that it provides us with a formal framework with which to analyze the optimal management of biological invasions, it is not sufficient as such to define the theoretical foundations of a general indicator for allocating budgets and setting priorities in a more complex world. First, a model that incorporates more species entails more interactions between species, which could render the maximization problem intractable. Second, simple linear expected diversity and utility functions are restrictive assumptions. Other diversity functions or indicators of the ecological state, such as the Rao general entropy concept (Rao, 1982) or even Weitzman's expected diversity with common species attributes, exhibit local convexities. Utility functions also often admit concavities or convexities. Third, preferences over utility and diversity do not need to be substitutable and may well exhibit complementarity. In the following section we address these three points and propose a prioritization criterion that would allow one to set priorities in a more complex socio-ecological system.

4 Species prioritization: general description

Our overall goal is to define the theoretical foundations of species prioritization criteria that could be used to allocate a limited budget for the control of multiple invasive species.

To reach this goal, we need our optimization setting to accommodate for: *i*) any number of species, and *ii*) any objective functions. With this purpose, we now consider an ecosystem composed of $N = [\![1; n]\!]$ distinct species, where k of them are invasive and $n - k$ are native.

As previously, we assume that given species interactions and a limited budget constraint, a manager chooses a vector of effort X that maximizes a multi-objective function that is comprised of an ecological and an economic component.

In order for our results to remain as general as possible and to facilitate an application to a wide range of manager's objectives, we assume that the ecological component function D and the economic component function U pertain to the class of $\mathcal{C}^2$ functions, *i.e* those whose first and second order derivatives both exist and are continuous.

From this point on, it is convenient to work with matrices, which we write in bold characters. For any matrix $\mathbf{M}$, let $\mathbf{M}^\top$ denote its transpose. Further, $\mathbf{I}^n$ is the $(n \times n)$ identity matrix, ι^n is the n-dimension column vector whose elements are all equal to 1.

We define $\mathbf{Q}, \mathbf{P}, \underline{\mathbf{P}}$ as the n-dimension column vectors whose i-th elements respectively are q_i, P_i, and $\underline{P}_i$, where $\underline{P}_i$ denotes the survival probability of species i in an ecosystem absent of any control policy. We define $\mathbf{c}, \mathbf{X}, \overline{\mathbf{X}}$ as the n-elements column vectors whose i-th elements respectively are c_i, x_i, and $\overline{x}_i$ for $i \in [\![1; k]\!]$ and 0 for $i \in [\![k; n]\!]$

Generalizing our stylized model, we now assume that the objective function of the manager is

$$\mathcal{F}(D(\mathbf{P}), U(\mathbf{P}))\,. \tag{11}$$

The manager's preferences over the ecological state of the system and the economic benefits derived from it are therefore reflected in the general functional form of $\mathcal{F}$. It follows that from this point on D and U could either be substitutable, as in the stylized model, or admit complementarity reflecting the fact that economic and ecological benefits are interdependent. Furthermore, while we previously assumed specific ecological and economic components, we now consider a generic objective function such that any ecological functional forms, e.g. any diversity functions, and any utility functions, *e.g.* concave utility functions, be under consideration.

We generalized the system of survival probabilities described in (4). With N species in matrix form, this system reads as

$$\mathbf{P} = \mathbf{Q} - \mathbf{X} + \mathbf{R} * \mathbf{P}. \tag{12}$$

To ensure $0 * \iota^{\mathbf{n}} \leq \mathbf{P} \leq \iota^{\mathbf{n}}$ we impose $0 * \iota^{\mathbf{n}} \leq \mathbf{X} \leq \overline{\mathbf{X}}$. Under the *weak* assumption that matrix $\mathbf{I}^n - \mathbf{R}$ is invertible , system (12) has a solution that reads as:

$$\mathbf{P} = \mathbf{\Lambda} * (\mathbf{Q} - \mathbf{X}), \tag{13}$$

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

Note that the solution (13) is a generalization of (9) to a N-species ecosystem. As in the stylized model, species' survival probabilities are linear functions of efforts. Let $\mathcal{P}(\mathbf{X}) \equiv \mathbf{\Lambda} * (\mathbf{Q} - \mathbf{X})$ refer to the affine mapping from management efforts to probabilities. Plugging (13) into (11) we obtain two *composite* functions, which are mappings from the values taken by the vector of efforts $\mathbf{X}$ to the set of real numbers:

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

Therefore the manager's objective function can be expressed as a function:

$$F(\mathbf{X}) = \mathcal{F}(D(\mathbf{P}(\mathbf{X})), U(\mathbf{P}(\mathbf{X}))), \tag{14}$$

and the invasive species management problem becomes the constrained maximization of a function of management efforts $\mathbf{X}$:

$$\max_{\mathbf{X}} F(\mathbf{X}) \tag{15}$$

subject to

$$\mathbf{c}^\top * \mathbf{X} \leq B, \tag{16}$$

$$0 * \iota^{\mathbf{n}} \leq \mathbf{X} \leq \overline{\mathbf{X}}, \tag{17}$$

where the two remaining constraints are the budget constraint and the admissible range of efforts.

The whole problem boils down to finding the optimal set of management efforts $x_i, \forall i \in [\![1; k]\!]$ for problem (15), (16) and (17). The N-species optimization program is a direct generalization of the 4-species optimization program (10) presented in the previous section. Considering more species raises no new conceptual difficulties. Furthermore, it is a well-behaved problem: the constraints form a compact (and convex) set, the objective is C^2, and thus there trivially exists a solution. Let us denote $\mathbf{X}^*$ this optimal solution, for future reference.

Finding this exact solution $\mathbf{X}^*$ is no trivial task. This question has been extensively studied in the Applied Mathematics literature and well-known iterative methods exist to approach - and eventually attain - the solution (for instance the famous Frank-Wolfe algorithm and its numerous variants). Those algorithms have different convergence properties and even the most straight-forward or simplistic algorithms are time-consuming. Often, a stopping rule needs to be introduced, leaving the user with a "nearly" optimal solution. In other words, from a practical point of view, there is a trade-off between the accuracy of the "nearly" optimal solution delivered by a method and its ability to single out an answer in a quick and tractable manner.

Inspired by this literature on algorithms we propose below heuristic approaches in order to quickly provide answers that are not necessarily optimal but offer an improvement compared to the *laisser-faire* and are amenable to intuitive interpretations, *i.e.* they are rational in a sense that is made explicit. As with the gradient-based algorithms, the general idea is to search for an admissible ascent direction by solving for a derived optimization problem where the objective function is replaced by its linear approximation.[22]

A first step is therefore to approximate the objective function $F(\mathbf{X})$ by its first order Taylor approximation evaluated at a given point $\hat{\boldsymbol{X}}$:

$$F(\mathbf{X}) \simeq F\left(\hat{\boldsymbol{X}}\right) + \nabla F\left(\hat{\boldsymbol{X}}\right) * \left(\mathbf{X} - \overline{\boldsymbol{X}}\right) . \tag{18}$$

To begin with, let us set $\hat{\boldsymbol{X}} = 0 * \iota^n$, *i.e.* the starting point is the one without control policy. Let us now see how to compute the gradient $\nabla F\left(0 * \iota^{\mathbf{n}}\right)$ in the above expression. Recalling the chain rule, and that in the absence of control policy probabilities are $\underline{\mathbf{P}}$, one has:

$$\nabla F\left(0 * \iota^{\mathbf{n}}\right) = \nabla \mathcal{F}\left(D\left(\underline{\mathbf{P}}\right), U\left(\underline{\mathbf{P}}\right)\right) * \nabla \mathcal{P}\left(0 * \iota^{\mathbf{n}}\right) .$$

Let us denote:

$$\mathcal{F}_i\left(\underline{\mathbf{P}}\right) \equiv \left.\frac{\partial \mathcal{F}(D(\mathbf{P}), U(\mathbf{P}))}{\partial P_i}\right|_{\mathbf{P}=\underline{\mathbf{P}}}, \quad \forall i \in [1; n] .$$

By definition, the gradient $\nabla \mathcal{F}$ is the vector:

$$\nabla \mathcal{F}\left(D\left(\underline{\mathbf{P}}\right), U\left(\underline{\mathbf{P}}\right)\right) \equiv \begin{bmatrix} \mathcal{F}_1\left(\underline{\mathbf{P}}\right) \\ \mathcal{F}_2\left(\underline{\mathbf{P}}\right) \\ \vdots \\ \mathcal{F}_n\left(\underline{\mathbf{P}}\right) \end{bmatrix} .$$

[22] We refer the interested reader to Courtois et al. (2014) for a discussion of the legitimacy of this approximation in this class of problems and an estimation of the error that is introduced when following this approach.

Finally, observing that:

$$\nabla \mathcal{P}(\mathbf{X}) = -\mathbf{\Lambda} \ ,$$

the gradient $\nabla F(0 * \iota^{\mathbf{n}})$ in (18) is simply the matrix $\mathbf{\Upsilon}(0 * \iota^{\mathbf{n}})$, or using the simpler notation $\mathbf{\Upsilon}^0$:

$$\mathbf{\Upsilon}^0 \equiv -\nabla \mathcal{F}^{\top}(D(\underline{\mathbf{P}}), U(\underline{\mathbf{P}})) * \ \mathbf{\Lambda} \, .$$

Matrix $\mathbf{\Lambda}$ is easily computed and if Λ_{ji} denotes a typical element of $\mathbf{\Lambda}$, then $\mathbf{\Upsilon}^0$ is a n-dimensional line vector of the type:

$$\mathbf{\Upsilon}^0 = \left[\beta_1^0 \ , \ \beta_2^0 \ , \ \ ..., \ \beta_n^0\right] \ ,$$

where

$$\beta_i^0 \equiv -\sum_{j=1}^{n} \left(\frac{\partial F(D((\underline{\mathbf{P}}), U(\underline{\mathbf{P}}))}{\partial P_j} \right) \Lambda_{ji} \ .$$

This expression of the gradient of the objective function shows the product of two terms that capture two marginal effects of the control of a biological invasion. First, control effort has a direct impact on the ecological state and utility, which is brought about by lowering the survival probability of the controlled invasive species. Second, there is a cascade of additional impacts resulting from this control effort, conveyed by the matrix $\mathbf{\Lambda} \equiv [\mathbf{I}^n - \mathbf{R}]^{-1}$. When the survival probability of an invasive species decreases, this modifies the survival probabilities of the other species present in the interconnected ecosystem, which causes collateral positive or negative impacts.

We are now equipped to express the linearized problem in matrix form:

$$\begin{aligned} &\max_{\mathbf{X}} \ \mathbf{\Upsilon}^0 * \mathbf{X} + \text{ constant terms}, \\ &\text{subject to (16) and (17)} \end{aligned} \tag{19}$$

It is interesting to note the similarity between this general problem and the one we addressed in the previous section discussing gradient parameters β_1 and β_2. A key difference between the stylized model and this generalized model lies in the gradient of the objective function and therefore on the solution of the program. While previously considered linear, F may be non linear. How does this affect the recommendations of our model? More accurately, one can ask whether it is feasible to propose a simple functional methodology for assessing species priorities whatever the objective considered. Answering these questions entails a discussion about the resolution of this maximization program considering two classes of interest: *i*) the class of problems that admits extreme solutions, and *ii*) the class of problems that admits all the other possibilities. While in the stylized model the objective falls in the first class, a manager aiming for example at maximizing a utility function that happens to be concave would fall in the second.

4.1 Prioritizations policies

4.1.1 Approximation of extreme solutions

Sometimes it is possible to know, before any computations, qualitative properties of the optimal control. For instance, it is well know that the maximum of a convex function on a compact convex set S is attained on the boundary of S (see for instance Section 32 in Rockafellar (1970)). It follows that when $F(\mathbf{X})$ is convex, the maximization program (15) admits an extreme solution. An extreme policy fully controls a subset of species, partially controls at most one species, and does not control any remaining invasive species. This is a qualitative result that does not identify which invasive species should be targeted.

In order to approximate this optimal solution and prioritize the control of invasive species given the available budget, a possibility derived from Weitzman (1998) and Courtois et al. (2014) is to rank all benefit-cost ratios:

$$R_i^0 \equiv \frac{\Delta P_i}{C_i} \beta_i^0 \ ,$$

computed at the no-policy initial point. Assume invasive species $i, i \in [\![1;k]\!]$ is assigned with the highest ratio value. If $R_i^0 \geq 0$, species i should be targeted first. If budget is sufficient, control efforts should focus on this species until efforts reach a maximum, *i.e* until $x_i = \overline{x_i}$. Then, if $c_i\overline{x_i} < B$, the invasive species j with the second highest score $R_j^0 \geq 0$ should be the next species targeted and this iterative process continues until budget B is fully exhausted.

This algorithm is highlighted in Box 2 below:

Box 2

Algorithm 1 *Prioritization algorithm for extreme solutions*

1. *Assess for each invasive species i the ratio R_i^0.*
2. *Rank the benefit-cost ratios of those invasive species.*
3. *Allocate maximum control effort to species with the highest positive ratio. In case of tie, one species is randomly chosen.*
4. *Proceed with next highest positive ratio species until the budget is exhausted. The last selected species is given maximum or partial attention, depending on what the budget allows.*

When the objective is convex, we can establish the following properties for this

algorithm:

Proposition 2 *When $F(.)$ is convex:*

i) the approximation $\mathbf{X}^{**}$ achieved by Algorithm 1 produces an improvement compared to inaction,

ii) the approximation error, $F(\mathbf{X}^{*}) - F(\mathbf{X}^{**})$, is no larger than $K * \left(\overline{\mathbf{X}}^{\intercal}\iota^{k}\right)^{2}$, where $K = \max\left\{\partial^{2}F/\left(\partial x_{i}\partial x_{i}\right)\right\}$.

Proof. *i)* By definition $\mathbf{X}^{**}$ solves the linear programing problem (19). Therefore one has:

$$\boldsymbol{\Upsilon}^{0} * \left(\mathbf{X}^{**} - 0 * \iota^{\mathbf{n}}\right) \geq 0. \tag{20}$$

This means that, starting from $F\left(0 * \iota^{\mathbf{n}}\right)$, vector $\mathbf{X}^{**} - 0 * \iota^{\mathbf{n}}$ is an ascent direction. This, however, is only a local information around the initial situation $0 * \iota^{\mathbf{n}}$. Since $F(.)$ is non linear, we cannot yet conclude that $F(\mathbf{X}^{**}) \geq F\left(0 * \iota^{\mathbf{n}}\right)$. But recall that convexity of $F(.)$ means:

$$F(\mathbf{X}^{**}) - F\left(0 * \iota^{\mathbf{n}}\right) \geq \boldsymbol{\Upsilon}^{0} * \left(\mathbf{X}^{**} - 0 * \iota^{\mathbf{n}}\right) \geq 0 \ ,$$

where the second inequality stems from (20). We end up with $F(\mathbf{X}^{**}) - F\left(0 * \iota^{\mathbf{n}}\right) \geq 0$, which proves the first statement.

ii) A second order Taylor expansion of $F(\mathbf{X}^{*})$ is:

$$F(\mathbf{X}^{*}) = F\left(0 * \iota^{\mathbf{n}}\right) + \boldsymbol{\Upsilon}^{0} * \left(\mathbf{X}^{*} - 0 * \iota^{\mathbf{n}}\right) + \frac{1}{2}\left(\mathbf{X}^{*}\right)^{\intercal} * \nabla^{2}F\left(\mathbf{Z}^{*}\right) * \mathbf{X}^{*} \ ,$$

for some admissible vector $\mathbf{Z}^{*}$, where $\nabla^{2}F(.)$ is the Hessian matrix of $F(.)$. Similarly, we can write:

$$F(\mathbf{X}^{**}) = F\left(0 * \iota^{\mathbf{n}}\right) + \boldsymbol{\Upsilon}^{0} * \left(\mathbf{X}^{**} - 0 * \iota^{\mathbf{n}}\right) + \frac{1}{2}\left(\mathbf{X}^{**}\right)^{\intercal} * \nabla^{2}F\left(\mathbf{Z}^{**}\right) * \mathbf{X}^{**} \ ,$$

for some adequate vector $\mathbf{Z}^{**}$. Subtracting those two expansions:

$$\begin{aligned} F(\mathbf{X}^{*}) - F(\mathbf{X}^{**}) \quad = \quad & \boldsymbol{\Upsilon}^{0} * \left(\mathbf{X}^{*} - \mathbf{X}^{**}\right) \\ & + \frac{1}{2}\left(\mathbf{X}^{*}\right)^{\intercal} * \nabla^{2}F\left(\mathbf{Z}^{*}\right) * \mathbf{X}^{*} \\ & - \frac{1}{2}\left(\mathbf{X}^{**}\right)^{\intercal} * \nabla^{2}F\left(\mathbf{Z}^{**}\right) * \mathbf{X}^{**} \ . \end{aligned}$$

By definition of $\mathbf{X}^{**}$:

$$\boldsymbol{\Upsilon}^{0} * \left(\mathbf{X}^{*} - \mathbf{X}^{**}\right) \leq 0 \ ,$$

therefore:

$$\begin{aligned} F(\mathbf{X}^*) - F(\mathbf{X}^{**}) &\leq \frac{1}{2}(\mathbf{X}^*)^\intercal * \nabla^2 F(\mathbf{Z}^*) * \mathbf{X}^* \\ &\quad -\frac{1}{2}(\mathbf{X}^{**})^\intercal * \nabla^2 F(\mathbf{Z}^{**}) * \mathbf{X}^{**} \\ &\leq \frac{K}{2}\left[(\mathbf{X}^*)^\intercal \iota^{\mathbf{n}}\right]^2 - \frac{K}{2}\left[(\mathbf{X}^{**})^\intercal \iota^{\mathbf{n}}\right]^2 \\ &\leq K\left(\overline{\mathbf{X}}^\intercal \iota^k\right)^2 , \end{aligned}$$

where $K = \max\left\{\partial^2 F/\left(\partial x_i \partial x_i\right)\right\}$. ■

Importantly, the R_i^0 score of invasive species i does not only depend on the direct impacts of the species on the ecosystem, but also on its indirect impacts, *i.e.*, impacts generated through its effects on other species, $\sum_{i=1}^{n}\left(-\frac{\partial F(W(\mathbf{P}),U(\mathbf{P}))}{\partial P_i}\right)\Lambda_{ij}$ via ecological interactions. Therefore, a species with a high dis-utility can be ranked below another species with a lower dis-utility, but whose indirect impacts resulting from interactions with other species are overwhelming.

This prioritization criterion accounts for management constraints as well as for direct and indirect benefits from invasive species control. It constitutes therefore a transparent measure that can be used as a theoretical foundation to build a simple decision-support tool enabling managers to set control priorities and to decide whether or not to allocate part of their budget toward the management of an invasive species. Of course there is a price to be paid for simplicity: this tool gives an approximation of the optimal solution. The upper bound K for the approximation error mentioned in the above proposition is linked to the non-linearity of $F(.)$, *i.e.* the second order derivatives $\partial^2 F/\left(\partial x_i \partial x_j\right)$. To relate this matter to usual concepts in decision theory under risk and uncertainty, one may say that the stronger the curvature of F (the stronger the preference for diversity if F is convex) the larger this upper bound.

To conclude this sub-section, recall the algorithm only applies to management situations in which the objective of the manager is convex. In the following sub-section, we propose a method for the criterion to apply to any objective function. This leads us to consider the non convex case.

4.1.2 An approximated solution for a wider class of problems

If the manager's objective function $F(.)$ is arbitrary, its maximization under linear constraints may lead in particular to an interior solution. It is clear in this case that the first algorithm is inadequate since, by construction, it leads to choosing an extreme solution. It would be helpful to have an algorithm that allows any kind

of solution and which does not force one to choose systematically among boundary outcomes. Our proposal extends iterative algorithm 1 so that it also handles interior solution allocations.

To derive this extended iterative algorithm, we follow Simianer et al. (2003) and we divide budget B into s shares, such that $b = B/s$. If s is sufficiently big then b is small enough and the set of achievable allocations via the algorithm tends to the whole set of constraints. They include both interior and extreme solutions (those that are on the envelope of constraints). If b is allocated to species i, then the control effort dedicated to this particular species is $x_i = b/c_i$. Let $\mathbf{B}^i$ stand for the n-dimensional vector where each element is zero, except element i which is equal to b/c_i. Instead of computing derivatives evaluated at the initial situation (as we did in the first algorithm), it will prove useful to consider the following differences:

$$\widehat{\beta}_i^t(q) \equiv \frac{F(\mathbf{X}_t + q\mathbf{B}^i) - F(\mathbf{X}_t)}{q}, \quad q \in]0,1].$$

Notice that when $q = 1$:

$$\widehat{\beta}_i^t(1) \equiv F\left(\mathbf{X}_t + \mathbf{B}^i\right) - F(\mathbf{X}_t)$$

is simply the change of $F(.)$ due to the change $\Delta x_i = b/c_i$.

Notice also that when q tends to zero, $\widehat{\beta}_i^t(q)$ tends to the directional derivative of $F(.)$, in the direction given by vector $\mathbf{B}^i$. And it is also the partial derivative of $F(.)$ with respect to x_i:

$$\lim_{q>0\longrightarrow 0} \widehat{\beta}_i^t = D_{\mathbf{B}^i} F(\mathbf{X}_t) = \frac{\partial}{\partial x_i} F(\mathbf{X}_t).$$

Consider now the following extended iterative procedure for prioritization:

Box 3

Algorithm 2 *Extended prioritization algorithm*

1. *Divide budget B into s shares, such that $b = B/s$.*
2. *Assess for each invasive species i the ratio*
$$R_i^t \equiv \widehat{\beta}_i^t(1) \ .$$
3. *Allocate the share of budget b to the control of the invasive species with the highest positive score. When scores are equal, a species is selected randomly among them.*
4. *Update $\mathbf{P}$ given this allocation of b.*
5. *Return to step 2, recalculate the ratios R_i^t and allocate the next budget share, until either all R_i^t are equal or all shares are allocated.*

In the following it will be useful to denote $\mathbf{X}_0, \mathbf{X}_1, ..., \mathbf{X}_t, ...$ the sequence of decisions produced by Algorithm 2.

By inspection of steps 2 and 3 of Algorithm 2 an immediate - yet important - observation is that a sequence of decisions produces no detoriation of the objective $F(.)$, and may even brings about gradual improvements. Let us emphasize this general property:

Proposition 3 *In our optimization problem with ecological interactions, along a sequence of decisions produced by Algorithm 2 the objective $F(.)$ is non decreasing, whatever the properties of $F(.)$.*

This nice general property comes at a cost: one has to compute $\widehat{\beta}_i^t(1)$ at each stage. Sometimes function $F(.)$ may take a functional form with well-know or easy to compute partial derivatives, and in this case it is possible to save computing time. This is obviously the case when $F(.)$ is linear as in our motivating example of Section 3. On the other hand, the information about the best ascent direction provided by partial derivatives is valid only locally, and may be seriously misleading when the changes in $\mathbf{X}_t$ are incremental and not infinitesimal. The question, then, is what would be the consequence of replacing $\widehat{\beta}_i^t(1)$ by $\partial F(\mathbf{X}_t)/\partial x_i$? Are there cases where such a replacement would not deteriorate the value of the objective $F(.)$? The proposition below provides some answers:

Proposition 4 *Consider our optimization problem with ecological interactions, and Algorithm 2 where $\widehat{\beta}_i^t(1)$ is replaced by $\partial F(\mathbf{X}_t)/\partial x_i$. The following conditions are sufficient to produce an improvement compared to the initial situation:*

i) $F(.)$ behaves monotonically in every variable,

ii) $F(.)$ is convex,

iii) b is infinitesimal.

Proof. *i*) When $F(.)$ behaves monotonically in every variable, each and every step 3 of the algorithm results in a positive increase of $F(.)$, whatever the size of b.

ii) Consider a sequence of decisions produced by the algorithm, and $\boldsymbol{\Upsilon}^0, \boldsymbol{\Upsilon}^1, ..., \boldsymbol{\Upsilon}^t, ...$ the corresponding sequence of gradients (*i.e.* $\boldsymbol{\Upsilon}^t \equiv \nabla F(\mathbf{X}_t)$). Without loss of generality, call i the species that is selected by the algorithm at stage t. And recall that, by convexity of $F(.)$:

$$F(\mathbf{X}_{t+1}) - F(\mathbf{X}_t) \geq \boldsymbol{\Upsilon}^t * (\mathbf{X}_{t+1} - \mathbf{X}_t) = \frac{b}{c_i}\frac{\partial}{\partial x_i}F(\mathbf{X}_t) \geq 0 \ ,$$

where the last inequality makes use of step 3 of the algorithm, by which only species with positive ratios ($\partial F(\mathbf{X}_t)/\partial x_i \geq 0$) are allocated b, and the result follows.

iii) if b is infinitesimal, the local information given by the ratios R_i applies to the whole proposed increment: the positive sign of the partial derivative of the variable to which b is allocated means a positive marginal increase in $F(.)$. ■

So, when $F(.)$ is convex, this second algorithm also improves upon the initial no-policy situation, as does the first algorithm under the assumption of convexity. Another independent and sufficient condition for this property is that $F(.)$ behaves monotonically in every variable. A convex function may or may not respect this condition. The same can be said for a concave function. And There are functions that possess this property, yet they are neither convex nor concave. So this second algorithm can be applied on a wider class of situations in order to increase the value of $F(.)$. And finally, the manager can dispense from Condition *i*) and/or Condition *ii*) if she sets arbitrarily small shares b.

Now let us turn to other important properties of Algorithm 2, which hold regardless of whether $\widehat{\beta}_i^t(1)$ or $\partial F(\mathbf{X}_t)/\partial x_i$ is used in step 2.

Proposition 5 *In our optimization problem with ecological interactions and with any objective functions, Algorithm 2 is feasible and an interior optimal solution, if there exists any, is a steady state of this algorithm.*

Proof. At an interior solution, all R_i are equal. Such an allocation is invariant for the dynamics defined by Algorithm 2 (see step 5). ■

According to the above proposition, if the algorithm is initiated at $\mathbf{X}^*$, no further change is implemented. This property does not depend on any restriction on function $F(.)$. It should not be misconstrued as a statement about convergence towards $\mathbf{X}^*$. To elaborate on that question, let us first recall the following definitions of stability:

Definition 1 $\mathbf{X}^*$ *is a* stable *steady state of 2 if for any* $\epsilon > 0$ *there exists some* $\delta \in (0, \epsilon)$ *such that:*

$$\|\mathbf{X}_t - \mathbf{X}^*\| < \delta \implies \|\mathbf{X}_s - \mathbf{X}^*\| < \epsilon, \quad \forall s \geq t.$$

In other words, if at some stage t the sequence of decisions enters a ball of radius δ around $\mathbf{X}^*$, it then remains forever within a ball of radius ϵ (possibly larger than δ) around $\mathbf{X}^*$.

Definition 2 $\mathbf{X}^*$ *is an* asymptotically stable *steady state of 2 if it is stable and if the constant* δ *can be chosen so that* $\|\mathbf{X}_t - \mathbf{X}^*\| < \delta$, $\forall t$ *implies:*

$$\|\mathbf{X}_s - \mathbf{X}^*\| \longrightarrow 0 \text{ as } s \longrightarrow \infty.$$

So, when $\mathbf{X}^*$ is asymptotically stable, sequences of decisions that reach a neighborhood of it not only stay close, but approach it as time passes by.

Proposition 6 *Assume* $F(.)$ *has a unique maximum* $\mathbf{X}^*$. *Along the sequence of decisions* $\mathbf{X}_0, \mathbf{X}_1, ..., \mathbf{X}_t, ...$ *produced by Algorithm 2, define* $L(\mathbf{X}_t) = F(\mathbf{X}^*) - F(\mathbf{X}_t)$.

i) If $L(\mathbf{X}_t)$ *is increasing for all admissible* $\mathbf{X}_t \neq \mathbf{X}^*$, *then* $\mathbf{X}^*$ *is stable.*

ii) If $L(\mathbf{X}_t)$ *is strictly increasing for all admissible* $\mathbf{X}_t \neq \mathbf{X}^*$, *then* $\mathbf{X}^*$ *is asymptotically stable.*

Proof. To prove this Proposition, one simply has to check that $L(\mathbf{X}_t)$ qualifies as a Lyapunov function. Those conditions are:

a) $L(\mathbf{X}_t)$ is a continuous function. Obviously, this property is simply inherited from function F.

b) $L(\mathbf{X}^*) = 0$. True by construction.

c) $L(\mathbf{X}_t) \geq 0$. Also true by construction.

d) Finally, Conditions *i*) or *ii*) of the Proposition are the last requirements for $L(\mathbf{X}_t)$ to qualify as a Lyapunov function. ■

This extended prioritization criterion algorithm is consistent for any objective function and any number of species. It works with convex and non-convex objective functions. This algorithm is recursive and is thus computationally demanding.

Many iterations are necessary in order to approximate the solution to our maximization problem. It does, however, constitute a simple theoretical method that can be used in the design of an easy to use decision-support tool for managers to set priorities in invasive species management. The next step and obvious continuation of this work is to build an easy to use computer interface enabling managers to allocate their budget efficiently.

5 Conclusion

Considering a cost-benefit optimization model, we analyze how to allocate limited resources toward the control of multiple invasive species. Our principal achievements can be summarized in two major points.

From a theoretical perspective, this paper is, to our knowledge, the first cost-benefit optimization approach that deals with multi-invasive species prioritization while accounting explicitly for species interactions. The novelty of our optimization approach lies in its assessment of the benefits of control efforts by explicitly considering species interactions and therefore by accounting explicitly for indirect impacts resulting from invasive species' control. Carrasco et al. (2010) developed a multi-invasive species cost-benefit optimization approach. However, they failed to account for species interdependences and instead focused on the invasiveness of species. They show that funding should be preferentially allocated towards cost-efficient control strategies of invasive species with Allee effects, i.e. whose survival probability increases with the density of the population, and low propagule pressure. Complementing this work, our model provides two major theoretical insights. The first is that species interactions, for example through competition or predation, may well counterbalance an Allee effect or a low propagule pressure. Although the survival probability of an invasive species depends on intrinsic reproduction capabilities and propagule pressure, interaction with other species is also a key determinant of this probability. The survival probability of an invasive species potentially increases with the survival probability of its prey and potentially decreases with the survival probability of its predators or competitors. It follows that species interactions ought to be taken into account when prioritizing species. A second insight is that the relative survival probabilities of invasive species are not sufficient to assess the relative harmfulness of these species. Again, due to species interactions, the survival probability of an invasive species is likely to impact the survival probability of other species and so on and so forth. It follows that invasive species generate indirect impacts through interconnected species. Our model shows that a species that causes severe direct damages can in fact be a lower management priority than another that generates lower direct damages, but whose overall damages are higher due to extensive interactions with other species. As indirect

impacts may outweigh direct impacts, it is not the relative survival probabilities of invasive species that matter but rather how these relative survival probabilities affect the overall survival probabilities of all species in an ecosystem. In other words, relative harmfulness of invasive species should be assessed by accounting for indirect benefits and damages resulting from species interactions.

From a practical perspective, we show that optimal management consists of assessing the benefit-cost ratio of each invasion and identifying the invasive species with the highest ratios as priority management targets. Two relevant policy recommendations for the design of species prioritization protocols can be made. First, prioritization criteria should be driven by an exhaustive assessment of the relative benefit-cost ratios of all invasive species. Because management resources are limited, the relative costs of control are as important a consideration as the relative benefits when selecting management priorities. Although highlighted by other papers including Carrasco et al. (2010); Dana et al. (2014) and Epanchin-Niell (2017), this is an especially important message given that management costs are often neglected in current prioritization protocols. Second, prioritization criteria must account for indirect impacts of biological invasions. Interactions between species are crucially important variables in assessing the outcomes of control efforts and understanding species interdependences should be a top priority.
An important contribution of this work is to provide the theoretical foundation for a species prioritization criterion that could be used to design a reliable, easy to apply, and economically sound tool to derive management decisions. While the paper is first and foremost addressed to a scientific audience, a specific attention has been placed on defining a simple algorithm that could next be implemented in a progress indicator to help decision makers, conservationists and land managers to allocate limited funding toward efficient management strategies.

There are several promising research directions for future work on this topic. The first is an operational research perspective aimed at designing a progress indicator based on this work. For our prioritization criterion to be operational, an easy to use interactive interface is required. Although it would be an effective way to bridge theoretical research and management practices, to our knowledge, no such interface exists. The second avenue for future research concerns applications of our methodology to other management problems involving species interactions. An obvious application is conservation policy and budget allocation towards conservation plans. Site prioritization is another appealing potential application. Deciding where and when to implement invasive species controls or where to build national reserves requires considering budget constraints and species interdependences. Finally, optimizing the allocation of funds through multiple invasion pathways is a key research perspective that could be addressed by employing similar methods.

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Appendix

The system of survival probabilities described by (4) writes:

$$\begin{cases} P_1 &= q_1 - x_1 + r_{12}P_2 + r_{13}P_3 + r_{14}P_4 \\ P_2 &= q_2 - x_2 + r_{21}P_1 + r_{23}P_3 + r_{24}P_4 \\ P_3 &= q_3 + r_{31}P_1 + r_{32}P_2 + r_{34}P_4 \\ P_4 &= q_4 + r_{41}P_1 + r_{42}P_2 + r_{43}P_3 \end{cases}$$

Solving it, we obtain a system of equations that maps survival probability P_i to control effort values x_k:

$$\begin{cases} P_1 &= \frac{\alpha_1}{\delta}x_1 + \frac{\theta_1}{\delta}x_2 + \frac{\gamma_1}{\delta} \\ P_2 &= \frac{\alpha_2}{\delta}x_1 + \frac{\theta_2}{\delta}x_2 + \frac{\gamma_2}{\delta} \\ P_3 &= \frac{\alpha_3}{\delta}x_1 + \frac{\theta_3}{\delta}x_2 + \frac{\gamma_3}{\delta} \\ P_4 &= \frac{\alpha_4}{\delta}x_1 + \frac{\theta_4}{\delta}x_2 + \frac{\gamma_4}{\delta} \end{cases}$$

We can see that δ, α_i and θ_i are coefficients that only depend on the combinations of species interaction coefficients r_{ij}:

$$
\begin{aligned}
\delta \quad &= r_{12}r_{21}r_{34}r_{43} - r_{12}r_{23}r_{34}r_{41} - r_{12}r_{24}r_{31}r_{43} - r_{13}r_{21}r_{34}r_{42} + r_{13}r_{24}r_{31}r_{42} \\
&-r_{13}r_{24}r_{32}r_{41} - r_{14}r_{21}r_{32}r_{43} - r_{14}r_{23}r_{31}r_{42} + r_{14}r_{23}r_{32}r_{41} - r_{12}r_{23}r_{31} \\
&-r_{12}r_{24}r_{41} - r_{13}r_{21}r_{32} - r_{13}r_{34}r_{41} - r_{14}r_{21}r_{42} - r_{14}r_{31}r_{43} - r_{23}r_{34}r_{42} \\
&-r_{24}r_{32}r_{43} - r_{12}r_{21} - r_{13}r_{31} - r_{14}r_{41} - r_{23}r_{32} - r_{24}r_{42} - r_{34}r_{43} + 1
\end{aligned}
$$

$$
\begin{aligned}
\alpha_1 \quad &= r_{23}r_{34}r_{42} + r_{24}r_{32}r_{43} + r_{23}r_{32} + r_{24}r_{42} + r_{34}r_{43} - 1 \\
\alpha_2 \quad &= r_{21}r_{34}r_{43} - r_{23}r_{34}r_{41} - r_{24}r_{31}r_{43} - r_{23}r_{31} - r_{24}r_{41} - r_{21} \\
\alpha_3 \quad &= r_{24}r_{31}r_{42} - r_{21}r_{34}r_{42} - r_{24}r_{32}r_{41} - r_{21}r_{32} - r_{34}r_{41} - r_{31} \\
\alpha_4 \quad &= r_{23}r_{32}r_{41} - r_{21}r_{32}r_{43} - r_{23}r_{31}r_{42} - r_{21}r_{42} - r_{31}r_{43} - r_{41}
\end{aligned}
$$

$$
\begin{aligned}
\theta_1 \quad &= r_{12}r_{34}r_{43} - r_{13}r_{34}r_{42} - r_{14}r_{32}r_{43} - r_{13}r_{32} - r_{14}r_{42} - r_{12} \\
\theta_2 \quad &= r_{13}r_{34}r_{41} + r_{14}r_{31}r_{43} + r_{13}r_{31} + r_{14}r_{41} + r_{34}r_{43} - 1 \\
\theta_3 \quad &= r_{14}r_{32}r_{41} - r_{12}r_{34}r_{41} - r_{14}r_{31}r_{42} - r_{12}r_{31} - r_{34}r_{42} - r_{32} \\
\theta_4 \quad &= r_{13}r_{31}r_{42} - r_{12}r_{31}r_{43} - r_{13}r_{32}r_{41} - r_{12}r_{41} - r_{32}r_{43} - r_{42}
\end{aligned}
$$

and γ_i are coefficients that depend on both species interaction coefficients and on autonomous survival probabilities q_i:

$$
\begin{aligned}
\gamma_1 \quad &= -q_1r_{23}r_{34}r_{42} - q_1r_{24}r_{32}r_{43} - q_2r_{12}r_{34}r_{43} + q_2r_{13}r_{34}r_{42} + q_2r_{14}r_{32}r_{43} \\
&+q_3r_{12}r_{24}r_{43} - q_3r_{13}r_{24}r_{42} + q_3r_{14}r_{23}r_{42} + q_4r_{12}r_{23}r_{34} + q_4r_{13}r_{24}r_{32} \\
&-q_4r_{14}r_{23}r_{32} - q_1r_{23}r_{32} - q_1r_{24}r_{42} - q_1r_{34}r_{43} + q_2r_{13}r_{32} + q_2r_{14}r_{42} + q_3r_{12}r_{23} \\
&+q_3r_{14}r_{43} + q_4r_{12}r_{24} + q_4r_{13}r_{34} + q_2r_{12} + q_3r_{13} + q_4r_{14} + q_1 \\
\gamma_2 \quad &= -q_1r_{21}r_{34}r_{43} + q_1r_{23}r_{34}r_{41} + q_1r_{24}r_{31}r_{43} - q_2r_{13}r_{34}r_{41} - q_2r_{14}r_{31}r_{43} \\
&+q_3r_{13}r_{24}r_{41} + q_3r_{14}r_{21}r_{43} - q_3r_{14}r_{23}r_{41} + q_4r_{13}r_{21}r_{34} - q_4r_{13}r_{24}r_{31} \\
&+q_4r_{14}r_{23}r_{31} + q_1r_{23}r_{31} + q_1r_{24}r_{41} - q_2r_{13}r_{31} - q_2r_{14}r_{41} - q_2r_{34}r_{43} + q_3r_{13}r_{21} \\
&+q_3r_{24}r_{43} + q_4r_{14}r_{21} + q_4r_{23}r_{34} + q_1r_{21} + q_3r_{23} + q_4r_{24} + q_2 \\
\gamma_3 \quad &= q_1r_{21}r_{34}r_{42} - q_1r_{24}r_{31}r_{42} + q_1r_{24}r_{32}r_{41} + q_2r_{12}r_{34}r_{41} + q_2r_{14}r_{31}r_{42} \\
&-q_2r_{14}r_{32}r_{41} - q_3r_{12}r_{24}r_{41} - q_3r_{14}r_{21}r_{42} - q_4r_{12}r_{21}r_{34} + q_4r_{12}r_{24}r_{31} \\
&+q_4r_{14}r_{21}r_{32} + q_1r_{21}r_{32} + q_1r_{34}r_{41} + q_2r_{12}r_{31} + q_2r_{34}r_{42} - q_3r_{12}r_{21} - q_3r_{14}r_{41} \\
&-q_3r_{24}r_{42} + q_4r_{14}r_{31} + q_4r_{24}r_{32} + q_1r_{31} + q_2r_{32} + q_4r_{34} + q_3 \\
\gamma_4 \quad &= q_1r_{21}r_{32}r_{43} + q_1r_{23}r_{31}r_{42} - q_1r_{23}r_{32}r_{41} + q_2r_{12}r_{31}r_{43} - q_2r_{13}r_{31}r_{42} \\
&+q_2r_{13}r_{32}r_{41} - q_3r_{12}r_{21}r_{43} + q_3r_{12}r_{23}r_{41} + q_3r_{13}r_{21}r_{42} - q_4r_{12}r_{23}r_{31} \\
&-q_4r_{13}r_{21}r_{32} + q_1r_{21}r_{42} + q_1r_{31}r_{43} + q_2r_{12}r_{41} + q_2r_{32}r_{43} + q_3r_{13}r_{41} + q_3r_{23}r_{42} \\
&-q_4r_{12}r_{21} - q_4r_{13}r_{31} - q_4r_{23}r_{32} + q_1r_{41} + q_2r_{42} + q_3r_{43} + q_4
\end{aligned}
$$

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