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Optimal Investment in Multi-species Protection: Interacting Species and Ecosystem Health

Stefan Baumgärtner

Interdisciplinary Institute for Environmental Economics, University of Heidelberg, Bergheimer Strasse 20, D-69115, Heidelberg, Germany

Abstract: This article uses an ecological-economic approach to study optimal investment in multi-species protection when species interact in an ecosystem. The analysis is based on a model of stochastic species extinction in which survival probabilities are interdependent. Individual species protection plans can increase a species' survival probability within certain limits and contingent upon the existence or absence of other species. Protection plans are costly and the conservation budget is fixed. It is assumed that human well-being depends solely on the services provided by one particular species, but other species contribute to overall ecosystem functioning and thus influence the first species' survival probability. One result is that it may be optimal to invest in the protection of those species that do not directly contribute to human well-being, even if biological conservation decisions are exclusively derived from such a utilitarian framework. Another result is that the rank ordering of spending priorities among different species protection plans, as obtained under the assumption of independent species, may be completely reversed by taking species interaction into account. The conclusion is that effective species protection should go beyond targeting individual species, and consider species relations within whole ecosystems as well as overall ecosystem functioning. Ecosystem health is identified as a necessary prerequisite for successful species protection in situ.

Key words: conservation of endangered species, ecosystem health, ecosystem services, multi-species protection, species interaction, stochastic extinction

INTRODUCTION

The global loss of biodiversity currently proceeds at rates exceeding the natural rate of species extinction by a factor of 100 to 1000, mainly due to human disturbance of natural ecosystems (Watson et al., 1995). As a response, in the past decades there have been an increasing number of policies targeted at the protection of endangered species, such as the U.S. Endangered Species Act (Brown and Shogren, 1998). Only recently have these conservation policies come under scrutiny not only for their conservational effectiveness (Hoekstra et al., 2002; Shouse, 2002) but also for their economic efficiency (Metrick and Weitzman, 1996, 1998; Cullen et al., 2001; Dawson and Shogren, 2001).

Under the U.S. Endangered Species Act, the U.S. Fish and Wildlife Service, a division of the Department of the Interior, lists species as endangered in the United States after (1) they have been suggested for listing by some individual or organization, public or private, (2) scientific

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Correspondence to: Stefan Baumgärtner, e-mail: baumgaertner@uni-hd.de

studies support the proposed listing, and (3) no serious reasons against a listing emerge during a 60-day period for public comments. Listed species enjoy special protection from harm and must have official recovery plans created by the Fish and Wildlife Service. They are eligible for public spending on the federal and state levels. In 1995, there were 957 species listed as endangered in the United States, and expenditures by federal and state agencies for all species recovery plans totalled US$ 280 million (Dawson and Shogren, 2001).

As of the mid-1990s, almost all endangered species had official recovery plans, but the expenditures were distributed rather unevenly among the different plans. Nearly 95% of the total reported spending by federal agencies were spent on about 200 vertebrate species, and only 5% were spent on about 800 invertebrate and plant species (Dawson and Shogren, 2001). This has lead to the suggestion that the status of a species as "charismatic megafauna" is a major factor in explaining the amount of funding for a recovery plan (Metrick and Weitzman, 1996, 1998). While the number of species listed as endangered has almost doubled over the past decade—from 554 in 1989 up to 957 in 1995—and total expenditure on species recovery programs has increased by a factor of almost seven—from US$ 44 million in 1989 to US$ 280 million in 1995 (Dawson and Shogren, 2001)—only 13 species have actually recovered enough to warrant removal from the list (Shouse, 2002).

One reason for the obviously poor performance of species recovery plans may be our poor understanding of the functioning of the natural ecosystems in which the target species live. The design of species recovery plans requires extensive knowledge of the species' life history and ecology (Bowles and Whelan, 1994; MacMahon, 1997). Yet, recent ecological surveys stress the large extent of uncertainty about the functioning of ecosystems (Holling et al., 1995; Tilman, 1997; Brown et al., 2001; Loreau et al., 2001). Given this large uncertainty, it is understandable that species recovery plans under the Endangered Species Act traditionally target single species, with the respective expenditure being highly species-specific. Likewise, influential economic studies on optimal species protection plans for multi-species ecosystems assume that species are independent (Solow et al., 1993; Weitzman, 1993, 1998).

However, considering species interactions is potentially important for the design of multi-species protection plans and to ensure the efficient allocation of limited conservation budgets (Wu and Bogess, 1998). Taking species interaction into account makes a crucial difference for how to optimally allocate a given conservation budget. The conclusion is that effective species protection should go beyond targeting individual species, and consider species relations within whole ecosystems as well as overall ecosystem functioning. To make this conclusion operational, looking at indicators of ecosystem health is suggested, which is a necessary prerequisite for successful species protection in situ.

Ecosystems and Species Extinction Risk

The formal framework used here follows and expands the one of Solow et al. (1993) and (Weitzman, 1998). Consider an ecosystem of $n \in \mathbb{N}$ different species. Each of them may be subject to stochastic extinction. Let p_i (with $i = 1,\ldots,$n) denote species i's survival probability, i.e., the probability that species i still exists after a time-period of T years. The concepts of *extinction risk* of a population of species i, $1-p_i$, and its *survival probability*, p_i, are equivalent measures of population viability (Burgman et al., 1993). Here, survival probabilities are used for the ease of interpretation. Another equivalent measure of population viability is its *expected lifetime*, τ_i. It is related to the survival probability p_i over a time-period T via the equation $p_i = \exp(-T/\tau_i)$ (Wissel et al., 1994). T is typically taken to be 10, 50, or 100 years in population viability analysis. On a more fundamental level, the survival probabilities are determined by a number of factors such as the species' population size, geographic range, age structure, and spatial distribution (Lande, 1993).

Let E_i (with $i = 1,\ldots,n$) be the status variable indicating whether species i will still be in existence after T years or whether it will have gone extinct:

$$E_i = \begin{cases} 1 & \text{if species } i \text{ survives,} \\ 0 & \text{if species } i \text{ becomes extinct.} \end{cases} \tag{1}$$

Due to the stochastic nature of extinction, the variable E_i is a random variable. In general, the different E_i are not independent. The existence of certain species will influence the survival probabilities of others. This is most obvious for species that interact directly, for instance through a mutualistic relation (positive correlation between survival probabilities), competition for a common resource (negative correlation between survival probabilities), or a predator–prey relation. More generally, the relations among species in an ecosystem can be analyzed in terms of a trophic network.

Such a food-web depicts the flow of food (measured in biomass) between the different species. The normalized flow between two species may be taken as a measure of the interaction strength between the two (Paine, 1992). Food-web analysis permits identification of indirect interactions among species which are coupled through a food chain that comprises one or more intermediate nodes. Food-web analysis reveals the high degree of connectance and a complex pattern of species interactions even when looking at only a limited number of species in relatively few trophic groups (Elton, 1927).

Human Appreciation of Species and Ecosystem Services

Individual species as well as entire ecosystems are valuable for humans for a number of reasons. Many species have direct use value as food, fuel, construction material, industrial resource, or pharmaceutical substance (Farnsworth, 1988; Plotkin, 1988). More recently, it has been stressed that biodiversity, i.e., the set of all species, also has an important indirect use value in so far as entire ecosystems perform valuable services such as nutrient cycling, control of water runoff, purification of air and water, soil regeneration, pollination of crops and natural vegetation, or partial climate stabilization (Perrings et al., 1995; Daily, 1997; Mooney and Ehrlich, 1997). These ecosystem services are essential to support the human existence on Earth. They can only be provided by more or less intact ecosystems and result from the complex—and, up to now, not well understood—interplay of many different species in these ecosystems (Holling et al., 1995; Tilman, 1997).

Following Weitzman (1998) and Metrick and Weitzman (1998), the utility gained directly and indirectly from a multi-species ecosystem can be written as a sum of the direct utilities of all individual species, U_i ($i = 1,\ldots,n$), and the utility gained indirectly from the entire ecosystem through the ecosystem services provided collectively by all species, U_{ES}. In general, the utility of ecosystem services will be a function of the existence or nonexistence of all species, $U_{ES} = U_{ES}\ (E_1,\ldots,E_n)$. Hence:

$$U = U_{ES}(E_1, \ldots, E_n) + \sum_{i=1}^{n} U_i. \qquad (2)$$

For example, Weitzman (1998) specifies U_{ES} as the diversity of the set of all actually existing species. His diversity function provides an aggregate measure of the diversity of a set of species based on the pairwise dissimilarities among them (Weitzman, 1992). This is in line with the idea that biodiversity may be taken as a proxy for an ecosystem's capability of providing the valuable services described above (Holling et al., 1995; Perrings et al., 1995; Tilman, 1997; Loreau et al., 2001).

Because of the stochastic risk of species extinction, a decision maker will consider not the utility, U, but the expected utility, $E[U]$. With p_i as species i's survival probability, the expected direct utility of that species is given by $p_i U_i$. Hence,

$$E[U] = E[U_{ES}(E_1, \ldots, E_n)] + \sum_{i=1}^{n} p_i U_i. \qquad (3)$$

Specification of the function U_{ES} would require a detailed ecological model of how all the species in an ecosystem collectively provide certain ecosystem services. In order to keep matters simple, assume that the ecosystem provides all its services at full scale if, and only if, species 1 exists. The level of utility derived from ecosystem services then only depends on whether species 1 exists or not. Furthermore, in order to focus on species interaction in the ecosystem (instead of trade-offs on the utility side), assume that all species have vanishing direct utility: $U_1 = \ldots = U_n = 0$. The value of all the different species, thus, is an indirect one and consists of their contribution to ecosystem functioning and, in particular, in their support of species 1. Hence, the relevant objective function for making conservation decisions is

$$E[U] = p_1 U_{ES}, \qquad (4)$$

where U_{ES} is a positive constant. While species 1 thus plays a prime role, all the other species are potentially important, too, as their existence or absence may influence species 1's survival probability, p_1. This latter point will be addressed explicitly in the section headed Species Interaction.

Species Protection Plans and Optimal Allocation of a Conservation Budget

Consider now the economic decision problem of how to allocate a conservation budget among different species protection plans. The time structure of the problem is as follows. The decision about how to allocate the conservation budget is made today, and the corresponding species protection plans are enacted immediately. The result in terms of actual species survival or extinction is observed tomorrow (which means, more precisely, after the course of

T years). The actual ecosystem situation tomorrow yields a certain utility, the expectation of which is the basis for today's decision.

For the moment, species interaction will be neglected, as it is done in the existing economic literature (Solow et al., 1993; Weitzman, 1993, 1998). That is, in this section, the economic decision framework for the case that all n species are independent will be introduced. Species interaction will then be introduced in the section headed Species Interaction.

Following Weitzman (1998), assume that investment in some protection plan aimed at species i can enhance that species' survival probability p_i within certain limits:

$$\underline{p_i} \leq p_i \leq \overline{p_i} \quad \text{with} \quad \underline{p_i} \geq 0 \quad \text{and} \quad \overline{p_i} \leq 1. \tag{5}$$

The probability $\underline{p_i}$ gives the "down-risk" for species i's survival. This is the survival probability if no investment in protection is made. On the other hand, $\overline{p_i}$ indicates the "up-risk" species i. This is the maximum survival probability amenable for species i through the particular protection plan under consideration. In the extreme, $\underline{p_i} = 0$ and $\overline{p_i} = 1$. That is, without protection, species i will become extinct for sure, but undertaking the protection plan at full scale will save it for sure. Any protection plan can also be undertaken at any level in between not-at-all and full-scale, leading to survival probabilities p_i which are on a continuum $\underline{p_i} \leq p_i \leq \overline{p_i}$.

Species protection plans are also costly. Suppose that, out of an exogenously given and fixed budget $b > 0$, an amount $b_i \geq 0$ is spent on protecting species i. Then the following budget constraint holds:

$$\sum_{i=1}^{n} b_i \leq b. \tag{6}$$

Investment b_i in protecting species i will enhance the species' survival probability p_i according to a "survival probability enhancement function," or "enhancement function" for short:

$$p_i = P_i(b_i) \quad \text{with } P_i(0) = \underline{p_i},\ P_i(b_i) \leq \overline{p_i} \quad \text{for all } b_i,\ P_i' \geq 0. \tag{7}$$

The qualifying properties state that without any investment, species i's survival probability will stay at the lower bound, $\underline{p_i}$. On the other hand, species i's survival probability cannot exceed its upper bound, $\overline{p_i}$. On the other hand, species i's survival probability cannot exceed its upper bound, $\overline{p_i}$, no matter how much is invested in its protection. Generally, the more money that is spent to enhance species i's survival probability, the higher p_i will actually turn out to be. For example, Weitzman (1998) uses linear enhancement functions with

$$P_i(b_i) = \min\left\{\frac{b_i}{c_i}\left(\overline{p_i} - \underline{p_i}\right) + \underline{p_i},\ \overline{p_i}\right\}, \tag{8}$$

where the parameter $c_i > 0$ indicates the costs of enhancing the survival probability all the way from its lower bound, $\underline{p_i}$, to its upper bound, $\overline{p_i}$.

The economic decision problem can then be stated as follows: choose a budget allocation such as to maximize the expected utility function (Eq. 3) subject to the budget constraint (Eq. 6) and the feasible possibilities for survival probability enhancement as described by Eq. (7). Formally:

$$\text{maximize}_{\{b_i\}_{i=1,\ldots,n}}\ E[U] \text{ s.t. } \sum_{i=1}^{n} b_i \leq b \text{ and } p_i = P_i(b_i) \text{ for all } i = 1, \ldots, n. \tag{9}$$

This is a typical stochastic programming problem which is continuous in the b_i.

Weitzman (1998) has characterized the solution to the problem in Eq. (9) under the assumptions that (1) $E[U_{ES}(E_1, \ldots, E_n)]$ is specified as the expected diversity of the set of all species, (2) all species are independent, and (3) the enhancement functions are linear and given by Eq. (8). Obviously, with the simple objective function (Eq. 4), the optimal solution, $\{b_i^*\}_{i=1,\ldots,n}$, is that the entire conservation budget is spent on species 1. For $c_1 < b$, the budget will not be completely exhausted by funding a full-scale protection plan for species 1. Since spending money on protecting other species would not increase utility under the objective function (Eq. 3), the remaining budget, $b - b_1$, could either be left idle or allocated randomly among the other species.

$$b_1^* = b \text{ and } b_i^* = 0 \quad \text{for } i = 2, \ldots, n. \tag{10}$$

Species Interaction

The formalization of the problem in Eq. (9) above, as well as the properties of its solution (Eq. 10), rely heavily on the simplifying assumption of independent species. To illustrate how one could construct a more general framework for the case of interacting species, the effect of species interaction is introduced for a simple model ecosystem that consists of just two species ($n = 2$), and in which the existence of species 2 influences the survival probability of species 1 but not vice versa. For example, one could think of species 2 as a

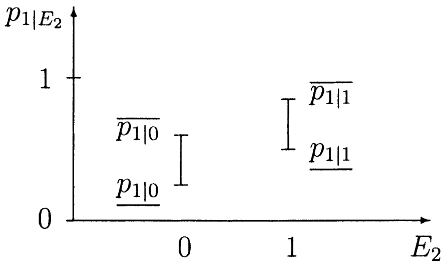

Figure 1. Feasible range of species 1's survival probability conditional on the the existence or absence of species 2, $p_{1|E_2}$ in the case of a positive influence.

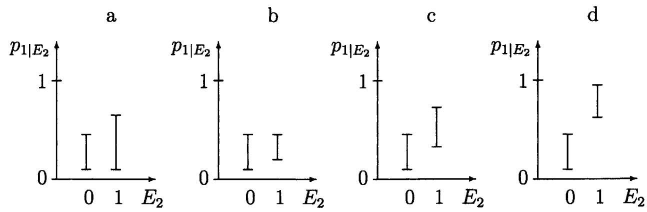

Figure 2. Different possibilities (**a–d**) of how the existence of species 2 may have a positive influence on species 1's feasible range of conditional survival probabilities.

potential prey for species 1 (positive interaction), or as a predator of it (negative interaction). Focusing on $n = 2$ is not as restrictive as it may appear at first sight. For species 2 may be interpreted as "all the rest of the ecosystem" besides species 1. In this interpretation, it then also appears plausible to assume that while species 2 influences species 1's survival probability, the reverse influence is negligible.

In this case, the survival probability of species 1 ("target species") depends on the existence of species 2 ("support species"). Let $p_{1|E_2}$ denote the conditional survival probability of species 1 given the existence or non-existence of species 2. In particular, $p_{1|1}$ is the survival probability of species 1 if species 2 exists ($E_2 = 1$) and $p_{1|0}$ is the survival probability of species 1 if species 2 does not exist ($E_2 = 0$). The (unconditional) survival probability of species 1, taking into account that species 2 exists with probability p_2 is then given by

$$p_1 = p_{1|1} p_2 + p_{1|0}\,(1 - p_2). \tag{11}$$

An investment in a protection plan for species 1 will increase the conditional survival probability $p_{1|E_2}$:

$$p_{1|E_2} = P_{1|E_2}(b_1), \text{ where } E_2 = \begin{cases} 1 \text{ if species 2 exists} \\ 0 \text{ if species 2 is exists.} \end{cases} \tag{12}$$

In particular, the existence of species 2 may be thought of as having an influence on the up- and down-risk for species 1, which also become conditional probabilities: $\underline{p_{1|E_2}}$ and $\overline{p_{1|E_2}}$. If the existence of species 2 has a positive influence on species 1, it seems natural to assume that

$$\underline{p_{1|1}} \geq \underline{p_{1|0}} \quad \text{and} \quad \overline{p_{1|1}} \geq \overline{p_{1|0}} \tag{13}$$

with at least one inequality holding as a strict inequality. This is illustrated in Figure 1 which shows the feasible range of species 1's survival probability, $p_{1|E_2}$, conditional on the the absence ($E_2 = 0$) or existence ($E_2 = 1$) of species 2. The effect of a positive species interaction essentially is that it shifts the up-risk and the down-risk for species 1, and therefore the entire feasible range of survival probabilities, upward.

Note that there is actually a number of ways, all consistent with the condition in Eq. (13), in which the existence of species 2 may have a positive influence on species 1's range of survival probabilities (Fig. 2). One possibility (Fig. 2a) is that under the positive influence of species 2 ($E_2 = 1$) the upper bound for species 1's conditional survival probability increases while the lower bound is not altered compared with a situation in which species 2 is absent ($E_2 = 0$). Or, the lower bound for the conditional survival probabilities may increase while the upper bound is not altered (Fig. 2b). Another possibility is that both the lower and upper bound increase such that the entire range of feasible conditional survival probabilities shifts upward (Fig. 2c, d). This may happen in such a way that the range with and without existence of species 2 overlap (Fig. 2c), or such that they do not overlap (Fig. 2d). The latter case may be particularly relevant for evolutionary old ecosystems in which target species have coevolved with, and are well adapted in a special way to, their support species and ecosystem. For well-adapted and specialized target species, the existence of supporting species and ecosystems may have a larger effect on the species' survival probability than any protection plan aimed directly at that species.

If the existence of species 2 has a negative influence on species 1, one has:

$$\underline{p_{1|1}} \leq \underline{p_{1|0}} \quad \text{and} \quad \overline{p_{1|1}} \leq \overline{p_{1|0}}, \tag{14}$$

where at least one inequality holds as a strict inequality. Like in the case of positive interaction, the condition in Eq. (14) can be fulfilled in a variety of ways. And if the existence of species 2 does not have any influence on species 1, one has

$$\underline{p_{1|1}} = \underline{p_{1|0}} \quad \text{and} \quad \overline{p_{1|1}} = \overline{p_{1|0}}. \tag{15}$$

In this formal framework, the economic decision problem of how to allocate a conservation budget among interacting species now reads as follows:

$$\text{maximize}_{\{b_1,b_2\}}\ E[U] \text{ s.t. } b_1 + b_2 \leq b, \quad p_{1|E_2} = P_{1|E_2}(b_1) \text{ and } p_2 = P_2(b_2). \tag{16}$$

Species Interaction and Optimal Allocation of the Conservation Budget

Species interaction can make a big difference for how to optimally allocate a conservation budget among different species protection plans. This is illustrated in this section by the example of a concrete parameterization of species interaction based on the formal framework developed in the previous section.

According to the objective function (Eq. 4), if species 1 exists, the utility is U_{ES}, and it is zero otherwise. Assume that the feasible range of survival probabilities for species 2 comprises the entire interval [0, 1], i.e., $\underline{p_{2}}\ 0$ and $\overline{p_{2}\ 1}$. The feasible range of survival probabilities for species 1 is contingent upon the existence of species 2 and, furthermore, depends on the type and strength of influence of species 2 on species 1:

$$\begin{array}{ll} \text{with species 2 } (E_2 = 1)\text{:} & \frac{1}{5}(2+2\kappa) \leq p_{1|1} \leq \frac{1}{5}(3+2\kappa), \\ \text{without species 2 } (E_2 = 0)\text{:} & \quad \frac{2}{5} \quad\quad \leq p_{1|0} \leq \frac{3}{5}, \end{array} \tag{17}$$

where $\kappa \in [-1, +1]$ parameterizes the influence of species 2 on species 1's survival probability conditional on the existence of species 2. With $\kappa = 0$, the two are independent and the existence of species 2 does not make any difference for the range of survival probabilities of species 1. With $\kappa > 0$ (<0), species 2 has a positive (negative) influence on species 1's survival probability. The entire range of feasible survival probabilities is shifted upwards (downwards). Figure 3 shows the feasible range of survival probabilities for species 1, with and without existence of species 2, depending on the interaction parameter κ.

Assume that the total conservation budget is $b = 1$ and the enhancement functions for both species are as follows:

$$P_{1|E_2}(b_1) = \begin{cases} \frac{1}{5}\sqrt{b_1} + \frac{2}{5} & \text{without species } 2 (E_2 = 0), \\ \frac{1}{5}\sqrt{b_1} + \frac{2}{5}(1+\kappa) & \text{with species } 2 (E_2 = 1) \end{cases} \tag{18}$$

$$P_2(b_2) = \sqrt{b_2}. \tag{19}$$

Note that the enhancement functions for both species exhibit strictly decreasing returns. With a budget of $b = 1$ and en-

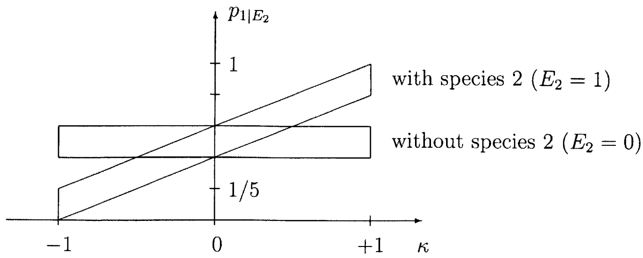

Figure 3. Feasible range of species 1's survival probability conditional on the existence or nonexistence of species 2, $p_{1|E_2}$, depending on the interaction parameter κ.

hancement possibilities as specified here, the economically viable survival probabilities for both species are within the feasible range described by Eq. (17). The budget of $b = 1$ allows either a full-scale conservation project for species 1, or a full-scale project for species 2, or projects for both of them at less than full scale. Spending the entire budget on species 1 increases its survival probability, given interaction strength κ and contingent on the existence or nonexistence of species 2, from its lower bound to its upper bound. Similarly, spending the entire budget on species 2 increases its survival probability from its lower bound to its upper bound. As these bounds for species 2 are given by 0 and 1, the size of the budget ($b = 1$) and the particular form of enhancement function (Eq. 19) allows full control over species 2. With $b_2 = 0$, species 2 will be extinct for sure; with $b_2 = 1$, it will exist for sure; and for all levels $0 < b_2 < 1$, it will exist with probability $p_2 = \sqrt{b_2}$. This simple setting focuses on the influence of the interaction between the two species and how to split up the total budget between the two in order to maximize species 1's expected survival probability.

With $b = 1$ and b_2 as the expenditure on species 2, the remaining budget of $b_1 = 1 - b_2$ can be spent on species 1. The expected utility is given as the survival probability of species 1 times the utility derived from it. With Eqs. (4) and (11):

$$E[U] = p_1 U_{ES} = [p_{1|1}p_2 + p_{1|0}(1-p_2)]U_{ES}, \tag{20}$$

where $p_{1|1}$, $p_{1|0}$, and p_2 depend on the expenditures b_1 and b_2 according to the enhancement functions (Eqs. 18 and 19). With $b_1 = 1 - b_2$, one has

$$\begin{aligned} E[U] &= \left[\left(\frac{1}{5}\sqrt{1-b_2} + \frac{2}{5}(1+\kappa)\right)\sqrt{b_2} \right. \\ &\quad \left. + \left(\frac{1}{5}\sqrt{1-b_2} + \frac{2}{5}\right)(1-\sqrt{b_2})\right] U_{ES} \\ &= \left[\frac{2}{5} + \frac{2}{5}\kappa\sqrt{b_2} + \frac{1}{5}\sqrt{1-b_2}\right] U_{ES}. \end{aligned} \tag{21}$$

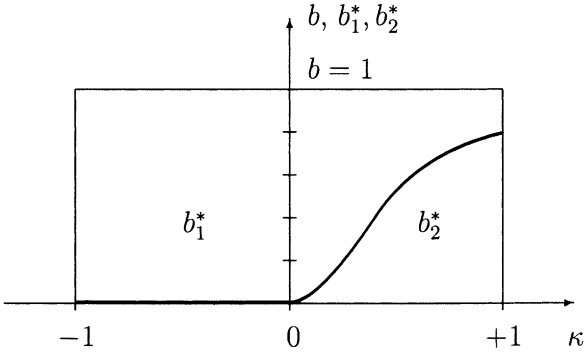

Figure 4. Optimal allocation of the conservation budget ($b = 1$) among the target species (b_1^*) and the support species (b_2^*), depending on the interaction strength κ. The curve shows b_2^* as a function of the interaction parameter κ, with the distance between the curve and $b = 1$ corresponding to b_1^*.

The term in brackets is the survival probability for species 1 in terms of b_2. Maximizing this expression over $0 \leq b_2 \leq 1$ yields the following optimal conservation expenditures b_2^* and $b_1^* = 1 - b_2^*$:

$$b_1^* = \begin{cases} 1; & \kappa < 0 \\ \frac{1}{1+4\kappa^2}; & \kappa \geq 0 \end{cases} \quad \text{and} \quad b_2^* = \begin{cases} 0; & \kappa < 0 \\ \frac{4\kappa^2}{1+4\kappa^2}; & \kappa \geq 0. \end{cases} \tag{22}$$

Figure 4 illustrates the result. It shows how the optimal allocation of the conservation budget depends on the interaction strength κ. As long as species 2 has a negative ($\kappa < 0$) or neutral ($\kappa = 0$) influence on the target species 1, the optimal allocation of the conservation budget is to entirely devote it to protection of species 1. If species 2 has a negative influence on the desired target species and no direct utility in itself, it may even be optimal to not only *not* invest in its protection, but to invest in its reduction. For example, species 2 may be a pest or parasite for species 1 and, for the sake of protecting species 1, it may seem desirable to eliminate this pest or parasite. However, in the formal framework employed here, the only consideration is species *protection* plans, i.e., one can only invest into *enhancing* a species' survival probability. Note that for vanishing interaction strength, $\kappa = 0$, the solution (Eq. 22) reduces to the solution (Eq.10) obtained in the section headed Species Protection Plans and Optimal Allocation of a Conservation Budget for the case of independent species. Obviously, spending money on conserving species 2 which then negatively impacts species 1 will not be optimal if, in the end, all utility derives from species 1. But if the support species 2 has a positive ($\kappa > 0$) influence on the target species 1, it is optimal to allocate a certain fraction of the allocation budget to the protection of the support species as well. This fraction grows as the positive interspecific influence (κ) grows in strength.

For $\kappa = +1$, the optimal allocation of the conservation budget is $b_1^* = 0.2$, $b_2^* = 0.8$. In this case, the positive influence from species 2 on species 1 is so strong that by spending the largest part of the budget on protecting species 2, one obtains a higher survival probability of species 1 than any direct investment into that species would produce. The reason for this result is in the assumption, illustrated in Figure 3, that for $\kappa = +1$ the entire feasible range of conditional survival probabilities for species 1 with species 2 in existence, [4/5, 1], is higher than in the absence of species 2, [2/5, 3/5]. As argued above (Fig. 2d), this corresponds to an evolutionary old ecosystem with a high degree of mutual adaptation among species. Existence of the support species can then provide a better service to the survival of the target species than any direct investment into protecting the target species could possibly achieve. Hence, spending money on increasing the support species' survival probability, thus indirectly also increasing the target species' survival probability, is more cost-effective than spending the entire budget directly on the target species.

The result, thus, is that species interaction can completely reverse the optimal allocation of a conservation budget. In the example studied here, while the entire conservation budget would be allocated to species 1 without any interaction, a strongly positive interaction will make it optimal to allocate almost the entire budget to conservation of species 2.

If one substitutes result (Eq. 22) back into expression (Eq. 21) for the unconditional survival probability of species 1, one obtains

$$p_1^* = \left[\frac{2}{5} + \frac{2}{5}\kappa\sqrt{b_2^*} + \frac{1}{5}\sqrt{1 - b_2^*}\right] = \frac{2\sqrt{1+4\kappa^2} + 4\kappa^2 + 1}{5\sqrt{1+4\kappa^2}}. \tag{23}$$

Figure 5 illustrates this result. It shows how the optimal survival probability of the target species, p_1^*, increases with the interaction strength for $\kappa \geq 0$.

Summary and Discussion of Results

This analysis has shown that taking into account species interactions in an ecosystem is crucial for the optimal allocation of a conservation budget. Compared with policy recommendations obtained under the assumption of

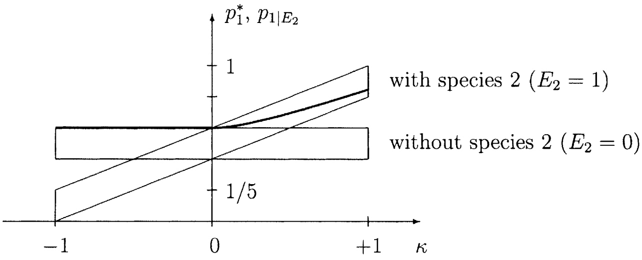

Figure 5. Optimal survival probability p_1^* of the target species (thick curve), depending on the interaction strength κ between support and target species.

independent species, interactions in an ecosystem can reverse the rank ordering of spending priorities among species conservation projects. Hence, an approach to species protection that is efficient in terms of both species conservation and budget resources should be based on a multi-species framework and should take into account the basic underlying ecological relations. Another interesting result is that even if biological conservation decisions are exclusively derived from a utilitarian framework, with species interaction it may be optimal to invest in the protection of species that do not directly contribute to human well-being. This is due to their role for overall ecosystem functioning and for safeguarding the existence of those species that are the ultimate target of environmental policy.

For practical purposes, however, one is confronted with a large extent of uncertainty about the functioning of ecosystems, including fundamental uncertainty about the exact nature of species interaction (Holling et al., 1995; Tilman, 1997; Brown et al., 2001; Loreau et al., 2001). In many cases, it is not even known whether two species have a positive or negative interaction. In terms of the model outlined above, this means that neither the exact value of κ nor its sign are known. It may be due to this large ecological uncertainty that the multi-species recovery plans, which have become more and more important in the U.S. Fish and Wildlife Service's approach to protecting endangered species, turned out to be even less successful in terms of species recovery than the more traditional single-species plans (Clark and Harvey, 2002).

The description of species interactions proposed here is very simple since it takes into account species and their interaction only on a discrete basis (species i exists/does not exist). A more realistic picture would involve population size and population dynamics for each species. Yet, this would not alter the qualitative results obtained here. The description of species protection plans is equally simple, as it is assumed that each plan affects only the very species at which it is directed. In practice, however, every species protection plan is likely to affect other species in the ecosystem as well.

The analysis here was mainly based on the illustrating example of a two-species ecosystem with one-way interaction. The absence of feedbacks excludes any kind of complex dynamics among the species. While this is a very simple and special setting, it can be generalized. With n different species, all of which are potentially interacting, there are $n\ (n-1)$ pairwise directed interactions, leading to indirect interactions among species as well as positive and negative feedback loops. This number rises very fast as n becomes large. Empirical evidence suggests, however, that the vast majority of pairwise interactions in real ecosystems are weak (Paine, 1992; Wootton, 1997; McCann et al., 1998). The hope may thus be that in applied studies of how to allocate a conservation budget, one can safely neglect many whole interactions, except for the few strong ones for each species, and that there are considerably less than $n(n-1)$ interactions to be taken into account.

However, empirical evidence also suggests that even the weak interactions are important: the complex interdependence of species survival probabilities, together with the existence of extinction thresholds (Lande, 1987; Muradian, 2001), is known to give rise to so-called extinction cascades (Borrvall et al., 2000; Lundberg et al., 2000). This means that extinction of one species could entail a cascade of further extinctions. Thus, the extinction of some species may threaten even the existence of other species that are only very weakly linked to the former.

Conclusions: Managing for Ecosystem Health

This discussion suggests that, for conservation purposes, not only are interactions among individual species important, but also the functioning of ecosystems at large is tantamount. Indeed, conservationists have been arguing for years that effective species protection should go beyond targeting individual species, and aim at whole ecosystems or landscapes. Individual species may nevertheless be of crucial importance for devising, assessing and marketing such a more holistic approach, for instance, as so-called keystone, flagship, or umbrella species (Simberloff, 1998). This analysis suggests how such a claim can be made more substantial and operational.

In the multi-species-interaction approach taken here, systemic properties of an ecosystem, e.g., their structural and functional organization, their productivity, their resilience under disturbances, and their ability to mitigate the impact of various stresses, underly and influence the survival probabilities of individual species. Thus, individual species' survival depends on, and is determined by, what has been called "ecosystem health." The concept of ecosystem health is a complex one, as it involves considerations from the natural, social, and health sciences (Rapport et al., 1998). Although difficult to measure and operationalize (Mageau et al., 1995), the notion of ecosystem health reminds one that species conservation in situ ultimately depends on certain properties of the entire system in which the target species lives.

As an encompassing and detailed analysis of the myriad of mutual interactions on the species level in an ecosystem may generally not be possible for a particular species protection plan, a useful alternative and complement can be to take a system approach and manage ecosystems for their functions and health. Mageau et al. [1995], among others, suggest an operational and quantifiable definition of "ecosystem health" in terms of ecosystem functions. Ecosystem functioning and health is a necessary prerequisite for species conservation in situ.

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