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RESEARCH ARTICLE

Accounting for non-independence of extinction probabilities in the derivation of conservation priorities based on Weitzman's diversity concept

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Abstract In the original formulation of Weitzman's diversity concept, extinction probabilities of different operational taxonomic units (OTUs) are implicitly defined to be independent. In this study, it is shown, that dependencies like concurrence or synergistic relations between OTUs can be accounted for by assuming that joint extinction probabilities differ from the product of the extinction probabilities of the interacting OTUs. A fully analytical treatment is provided for the case of two interacting OTUs, and all cases are illustrated with an example data set. For the case of concurring OTUs, the following general results are derived: (a) concurrence between OTUs always reduces the amount of diversity expected to be conserved in the future; (b) concurrence has a more adverse effect on the more endangered OTUs involved; (c) concurrence can change conservation priorities between OTUs; and (d) with high levels of concurrence, investments in the conservation of some of the concurring OTUs can have a negative effect on the overall diversity conserved. In addition to conservation activities targeted towards some of the OTUs, reduction of the causes of concurrence may be a valid and cost-efficient alternative. For the case of synergistic dependencies between OTUs it was found, that such dependencies always increase the conservation potential of the involved OTUs but may lead to a change of priority ranking in extreme cases. Finally possible extensions and generalisations of the suggested approach are discussed and it is argued, that by adopting these extensions Weitzman's diversity concept becomes an even more powerful and flexible tool to derive conservation priorities both in an ecological and in a farm animal context.

Keywords Weitzman diversity · Conservation priorities · Concurrence · Synergy

Introduction

In many cases it is necessary to make decisions as to which species or, more generally, operational taxonomic unit (OTU) should be conserved in a set of phylogenetically or ecologically interacting OTUs. Weitzman (1992, 1993) has proposed to base decisions on conservation priorities of OTUs on the effect of such activities on the expected overall diversity of the set of OTUs the considered OTU belongs to. Based on a formal definition of the necessary quantities, he defines criteria like marginal diversity and conservation potential, the latter being the amount of expected overall diversity of the set saved if a certain OTU was made completely safe from extinction. Under a limited budget constraint, the conservation potential was found to be a good guideline to identify OTUs with highest conservation priorities (Weitzman 1993; Simianer et al. 2003). Weitzman's diversity concept has a strong appeal due to its rigorous mathematical justification and the possibility to derive optimum conservation decisions with well-defined properties. While it is widely accepted as the fundamental framework for decision-making in livestock conservation (for a review see Simianer 2005), the concept needs to be introduced to a wider conservation audience to become relevant to core conservation areas.

A critical assumption in Weitzman's diversity concept is that extinction probabilities of the OTUs are known and are

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exogenous (van der Heide et al. 2005), i.e. they are not variables in the system to be optimised, but are given fixed parameters. In most cases the risk status of populations is assessed mainly by the number of live animals, in some cases the effective population size and the population trend (increasing or decreasing) are included. In wild species, population viability analyses (e.g. Ginzburg et al. 1982; Boyce 1992) allow an assessment of the future development of population size. Bennewitz and Meuwissen (2005) suggested to adopt this technique for farm animal populations. In a study on conservation programs of African cattle breeds Reist-Marti et al. (2003) suggested a semi-quantitative scoring system based on 10 different criteria, which were assessed for each breed included in the study. These criteria did not only reflect population size and demographic trend, but also geographic distribution, cultural importance or risk of indiscriminate crossbreeding.

Extinction probabilities are not only fixed parameters in Weitzman's diversity concept, but it is implicitly assumed that extinction probabilities of different OTUs are considered to be independent, since probabilistic multiplication rules for independent events are used to calculate probabilities of joint survival or extinction. If extinction probabilities of OTU A and B are denoted as z_A and z_B, the probability that both breeds go extinct is $z_A z_B$ and that both breeds survive is $(1 - z_A)(1 - z_B)$, respectively.

Witting et al. (2000) address this restriction and introduce the concept of network theory (Higashi and Burns 1991) to take dependencies of interacting OTUs in to account. In an illustrative example they suggest to account not only for extinction probabilities of single OTUs, but also for pairwise joint extinction probabilities of all interacting OTUs. With n interacting OTUs, n^2 extinction probabilities are required, which, as the authors suggest, can be obtained by population viability analysis. They focus decisions on a minimisation of the expected loss of diversity and show that non-trivial solutions exist.

van der Heide et al. (2005) argue, that Weitzman's diversity concept cannot account for ecological relationships and thus may lead to incorrect policy advise on biodiversity protection. They especially focus on the decision rule suggested by Weitzman (1998), which indeed is shown to be inadequate if extinction probabilities between OTUs are dependent.

Such dependencies of extinction probabilities between OTUs are not only due to ecological causes, like food web and ecosystem relations (Polis 1998) but in the farm animal context can also have an economic background, if e.g. different breeds compete for a small production niche, which can either be an environment, a production system, or a market for specific products.

In this paper, it will be shown how dependencies between extinction probabilities can be built into Weitzman's diversity concept. Using the conservation potential as the criterion to rank OTUs according to their priority for conservation, two cases of dependencies will be examined in detail:

- OTUs are in concurrence, which formally is the case if the probability that two OTUs survive is less than the product of the individual survival probabilities of the two OTUs. This may e.g. reflect the case that two or more OTUs concur for a common, but limited resource;
- OTUs are dependent on each other. Formally this is the case if the survival probability of one OTU is reduced if another OTU is extinct. Such a situation arises e.g. in predator-prey system or in complex ecological networks.

The paper is structured as follows: first, the basic model underlying Weitzman's diversity concept is defined and a useful reparameterisation is introduced. Then, formal definitions of concurrence and dependency between two OTUs are given, and the impact of these two forms of dependency on conservation priorities is derived in a fully analytical approach. Both cases will be illustrated with a somewhat artificial, but instructive example. Finally, generalisations of the approach and its relevance for practical applications will be discussed.

Methods

The basic model

We assume that a set S of OTUs, which includes N different OTUs has a given actual diversity $D(S)$. OTUs may represent species or subpopulations such as breeds within species. Note that the following considerations are not assuming that a specific diversity metric, e.g. Weitzman's (1992) diversity metric, is used. The only necessary assumption is that $D(S)$ is monotonous in OTUs, i.e. that $D(S) < D(S \cup X)$ where $X \notin S$.

For each OTU $i = 1, \ldots, N$ we can specify the extinction probability $0 \leq z_i \leq 1$, reflecting the probability that the OTU will be extinct at the end of the given planning horizon.

The expected diversity can be computed as

$$E[D(S)] = \sum_{\forall K} P(K)D(K) \tag{1}$$

where K are all the different possible subsets of breeds, $P(K)$ is the probability that subset K will exist at the end of the planning horizon, and $D(K)$ is the diversity of subset K. It was shown by Simianer et al. (2003) that with N different OTUs the number of different subsets is 2^N.

The marginal diversity for OTU i is defined as

$$m_i = \frac{\partial E[D(S)]}{\partial z_i} \tag{2}$$

and reflects the change of the expected diversity of the whole set if extinction probability of OTU i is increased by one unit. Note that m_i is always negative and differs in sign from the definition given by Weitzman (1992). Simianer et al. (2003) presented an efficient algorithm to calculate m_i for all OTUs simultaneously for large values of N.

The conservation potential of OTU i is defined as

$$CP_i = -m_i \times z_i \tag{3}$$

and reflects the amount of expected diversity that can be conserved if breed i was made completely safe. Weitzman (1993) suggested the conservation potential as the '... single most useful species alert indicator'. This was confirmed in an application of Weitzman's diversity concept to define conservation priorities for a set of African cattle breeds (Simianer et al. 2003) where the breeds with highest conservation potential also obtained the largest amount of conservation funds from a sophisticated optimum allocation analysis. Therefore the conservation potential is a suitable criterion to identify OTUs with highest priority for conservation and to rank OTUs with respect to conservation priority.

A reduced model to study dependent extinction probabilities

In the original concept suggested by Weitzman (1992, 1993), extinction probabilities of different OTUs are considered to be independent, i.e. for OTU i and j the probability that both OTUs go extinct is $z_i z_j$ and that both breeds survive is $(1 - z_i)(1 - z_j)$, respectively. However, Eq. 1–3 hold in general, also with dependent extinction probabilities.

This will be examined for the situation where in a set of $N > 2$ OTUs a subset of two OTUs has dependent extinction probabilities. For this case, the impact of the degree and type of connectedness on marginal diversity and conservation potential of these two OTUs can be derived. The restriction to consider only two OTUs is for simplicity and to allow a full analytic treatment, but is without loss of generality, since the general concept can be used with any number of OTUs.

Consider the set $S = A \cup B \cup X$, where A and B are the two OTUs chosen for analysis and X is the complementary, not empty set of OTUs. Let K_X be all possible subsets of X, and

$$E[D(X)] = \sum_{\forall K_X} P(K_X)D(K_X)$$

Making use of a result presented by Reist-Marti et al. (2006), the expected total diversity of the complete set S can be written as

$$\begin{aligned} E[D(S)] =& P(A,B)\sum_{\forall K_X} P(K_X)D(K_X \cup A \cup B) \\ &+ P(A,-)\sum_{\forall K_X} P(K_X)D(K_X \cup A) \\ &+ P(-,B)\sum_{\forall K_X} P(K_X)D(K_X \cup B) \\ &+ P(-,-)\sum_{\forall K_X} P(K_X)D(K_X) \end{aligned} \tag{4}$$

where $P(AB)$, $P(A,–)$, $P(–,B)$, $P(–,–)$ are the probabilities that both OTU A and B, only A, only B, or none of both are present. By using the symbols

$$D_{ABX} = \sum_{\forall K_X} P(K_X)D(K_X \cup A \cup B)$$

$$D_{AX} = \sum_{\forall K_X} P(K_X)D(K_X \cup A)$$

$$D_{BX} = \sum_{\forall K_X} P(K_X)D(K_X \cup B)$$

$$D_X = \sum_{\forall K_X} P(K_X)D(K_X)$$

Eq. 4 can be written as

$$\begin{aligned} E[D(S)] =& P(A,B)D_{ABX} + P(A,-)D_{AX} + P(-,B)D_{BX} \\ &+ P(-,-)D_X \end{aligned} \tag{5}$$

The advantage of this form is that the quantities D_{ABX}, D_{AX}, D_{BX}, and D_X are constant and only need to be calculated once for a given set S. The expected diversity then is only a function of the pattern of extinction probabilities in the subset $\{A, B\}$.

Results

Conservation priorities when OTUs are in concurrence

OTUs may be in concurrence if they compete for the same resources, as food, space, etc. The case of OTUs A and B being in concurrence can be modelled by defining the joint extinction probabilities conditional on a concurrence parameter λ as follows:

$$P(AB|\lambda) = (1 - z_A)(1 - z_B)(1 - \lambda)$$

$$P(A, -) = (1 - z_A)z_B$$

$$P(-, B) = z_A(1 - z_B)$$

$$\begin{aligned} P(-,-|\lambda) &= 1 - P(A,B|\lambda) - P(A,-) - P(-,B) \\ &= z_A z_B + \lambda(1 - z_A)(1 - z_B) \end{aligned}$$

The parameter $0 \leq \lambda \leq 1$ reflects the degree of concurrence. With $\lambda = 0$, extinction probabilities of both OTUs are independent, i.e. we have the situation considered in the usual application of Weitzman's (1992) diversity concept. With $\lambda = 1$, the probability that both OTUs jointly survive until the end of the planning horizon is zero, i.e. there is only room for one of the two. Intermediate values of λ reflect respective degrees of concurrence.

Using this set of conditional extinction probabilities in Eq. 5 and taking the first derivative with respect to z_A and z_B, respectively, yields the marginal diversities:

$$\begin{aligned} m_A^\lambda = \frac{\partial E[D(S)]}{\partial z_A} &= (\lambda - 1)(1 - z_B)D_{ABX} - z_B D_{AX} \\ &+ (1 - z_B)D_{BX} + (z_B - \lambda + \lambda z_B)D_X \end{aligned} \tag{6a}$$

$$\begin{aligned} m_B^\lambda = \frac{\partial E[D(S)]}{\partial z_B} &= (\lambda - 1)(1 - z_A)D_{ABX} \\ &+ (1 - z_A)D_{AX} - z_A D_{BX} + (z_A - \lambda + \lambda z_A)D_X \end{aligned} \tag{6b}$$

Using these results in Eq. 3, the conservation potential of the two OTUs can be assessed and priority can be given to the OTU with the highest conservation potential. However, with $\lambda > 0$ extinction probabilities of OTU A and B increase, since the probability that both survive is reduced. The effective extinction probabilities, denoted as z_A^λ and z_B^λ, then are

$$\begin{aligned} z_A^\lambda &= 1 - P(A,B|\lambda) - P(A,-) \\ &= 1 - (1 - z_A)(1 - z_B)(1 - \lambda) - (1 - z_A)z_B \\ &= z_A + \lambda(1 - z_A - z_B + z_A z_B) \end{aligned}$$

and

$$z_B^\lambda = z_B + \lambda(1 - z_A - z_B + z_A z_B)$$

Therefore it is suggested to use the effective extinction probability for the given value of λ in Eq. 3, so that the effective conservation potentials are

$$CP_A^\lambda = -m_A^\lambda \times z_A^\lambda \tag{7a}$$

and

$$CP_B^\lambda = -m_B^\lambda \times z_B^\lambda \tag{7b}$$

Illustration of the method

The method will be illustrated with a data set on four primate species, which were already used by Thaon d'Arnoldi et al. (1998) to illustrate the main features of the Weitzman approach. The set is a subset of data used by Weitzman (1992), from where the pairwise distances are taken. The distance matrix and the assumed extinction probabilities are given in Table 1. Note that this is just an example to illustrate the method, and that assumed extinction probabilities and their interaction do not reflect the real degree of endangerment and interaction of the species considered.

The total actual diversity is $D(S) = 1015$, and the diversities of the different subsets can be calculated by applying Weitzman's (1992) rules.

For illustration, dependencies of extinction probabilities of the two gibbon species A and B will be assumed, so that $X = \{C, D\}$. Using the suggested extinction probabilities for gorilla and orangutan, we get

$$\begin{aligned} D_{ABX} &= (1 - 0.1)^2 \times D(A,B,C,D) + (1 - 0.1) \times 0.1 \\ &\times [D(A,B,C) + D(A,B,D)] + 0.1^2 \times D(A,B) \\ &= 0.81 \times 1015 + 0.09 \times [658 + 614] + 0.01 \times 126 \\ &= 937.89 \end{aligned}$$

and similarly $D_{AX} = 810.90$, $D_{BX} = 781.29$, and $D_X = 289.17$.

Using these values, the marginal diversities of the two gibbon species can be calculated with Eq. 6a, b and are plotted as a function of the concurrence parameter λ in

Table 1 Primate species used to illustrate the method, pairwise distances (from Weitzman 1992), and assumed extinction probabilities

Name	Code	Distance to				Extinction probability
		A	B	C	D	
Common Gibbon (*Hylobates lar*)	A	–	126	532	477	0.4
Siamang Gibbon (*Hylobates syndactylus*)	B	126	–	498	488	0.2
Gorilla (*Gorilla gorilla*)	C	532	498	–	357	0.1
Orangutan (*Pongo pygmaeus*)	D	477	488	357	–	0.1

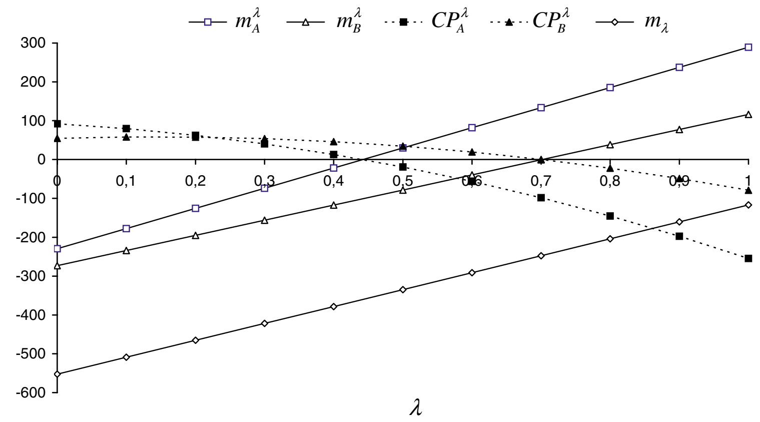

Fig. 1 Marginal diversities of OTUs A and B (m_A^λ and m_B^λ), conservation potentials of OTUs A and B (CP_A^λ and CP_B^λ), and marginal diversity with repect to λ (m_λ) as a function of the concurrence parameter λ for the example data set

Fig. 1. For $\lambda = 0$ both marginal diversities $m_A = -229,63$ and $m_B = -273,04$ are negative, with $m_A < m_B$ a change of extinction probability of species B by one unit has a larger effect than a change of extinction probability of species A.

With increasing values of λ there is a linear increase in both marginal diversities, which means that, due to the assumed concurrence, a reduction of extinction probability of one species has a reduced advantageous effect on the overall expected diversity. For $\lambda \approx 0,45$ ($\lambda \approx 0,7$), $m_A^\lambda (m_B^\lambda)$ even turn positive, meaning that a reduction of the extinction probability of one of the species alone will lead to a lower expected diversity of the whole set at the end of the planning horizon.

By rearranging terms in Eq. 6a we can write m_A^λ as a linear function of λ:

$$\begin{aligned} m_A^\lambda = & [(1 - z_B)(D_{BX} - D_{ABX}) + z_B(D_X - D_{AX})] \\ & + [(1 - z_B)(D_{ABX} - D_X)] \times \lambda \end{aligned} \tag{8a}$$

and similarly

$$\begin{aligned} m_B^\lambda = & [(1 - z_A)(D_{AX} - D_{ABX}) + z_A(D_X - D_{BX})] \\ & + [(1 - z_A)(D_{ABX} - D_X)] \times \lambda \end{aligned} \tag{8b}$$

These equations help to assess some properties of the system, which will be discussed based on Eq. 8a for the m_A, but can be fully extended to m_B.

Equation 8a proves that $m_A \leq 0$ for $\lambda = 0$, since by definition $D_{ABX} \geq D_{BX}$ and $D_{AX} \geq D_X$ and hence both $D_{BX} - D_{ABX}$ and $D_X - D_{AX}$ are ≤ 0 and so is the weighted sum.

The slope of the regression $(1 - z_B)(D_{ABX} - D_X)$ is always non-negative since $D_{ABX} \geq D_X$ and $0 \leq z_B \leq 1$. It is interesting to see that the slope of this regression for m_A^λ depends on the extinction probability of the species in concurrence, z_B, and *vice versa*, since due to symmetry arguments the slope of the regression for m_B^λ is $(1 - z_A)(D_{ABX} - D_X)$. This also leads to the conclusion, that the slope of the regression is higher for the species with higher extinction probability (species A in this case), i.e. concurrence will have a more adverse effect on more endangered species than on less endangered species.

Figure 1 also shows the conservation potentials of the two species considered. While the conservation potential of species A is almost twice as high as that of species B without concurrence, the former quickly decreases with increasing values of λ, while CP_B^λ even slightly increases and exceeds CP_A^λ for $\lambda > 0,22$. Although in this illustration the 'crowned crane paradox' (Weitzman, 1993), meaning that the less endangered species has a higher conservation potential than the more endangered species, is not given without concurrence, this is the case for higher values of the concurrence parameter λ.

The conservation potential of a species becomes negative when it's marginal diversity turns positive. By setting $m_A^\lambda = 0$ in Eq. 8a we obtain

$$\lambda_o = \frac{(1 - z_B)(D_{BX} - D_{ABX}) + z_B(D_X - D_{AX})}{(1 - z_B)(D_A - D_{ABX})}$$

as the critical value at which the marginal diversity turns positive. In the primate example, this value is $\lambda_0 = 0.442$ for species A and $\lambda_0 = 0.701$ for species B. Beyond these values of λ conservation measures that reduce the extinction probability of one breed lead to such a reduction of the joint probability $P(AB)$ that both breeds survive, making the overall effect on the expected diversity negative.

Under this model, additional options for conservation activities arise, since expected diversity cannot only be maximized by reducing extinction probabilities of single OTUs, but also by removing the adverse effect of concurrence. In analogy to the marginal diversities shown above this can be quantified by taking the first derivative of expected diversity with respect to the concurrence parameter λ:

$$\frac{\partial E[D(S)]}{\partial \lambda} = (1 - z_A)(1 - z_B)(D_X - D_{ABX})$$

which is negative since by definition $D_X < D_{ABX}$. However, changing λ affects the expected diversity also by changing the effective extinction probabilities, which are a function of λ. For z_A^λ and z_B^λ this

$$\frac{\partial z_A^\lambda}{\partial \lambda} = \frac{\partial z_B^\lambda}{\partial \lambda} = (1 - z_A)(1 - z_B)$$

which has the intuitive appeal, that reducing the concurrence directly increases the conservation probabilities of the involved OTUs. Both changes in extinction probabilities need to be multiplied with the marginal diversities, which reflect the change of expected diversity if extinction probabilities are changed. Hence,

$$\begin{aligned} m_\lambda &= \frac{\partial E[D(S)]}{\partial \lambda} + \frac{\partial z_A^\lambda}{\partial \lambda} m_A^\lambda + \frac{\partial z_B^\lambda}{\partial \lambda} m_B^\lambda \\ &= (1 - z_A)(1 - z_B)(m_A^\lambda + m_B^\lambda + D_X - D_{ABX}) \end{aligned} \tag{9}$$

As was shown in Eq. 8a, b, m_A^λ and m_B^λ are linear functions of λ in the form $m_A^\lambda = c_A + b_A\lambda$ and $m_B^\lambda = c_B + b_B\lambda$, respectively, with

$$c_A = (1 - z_B)(D_{BX} - D_{ABX}) + z_B(D_X - D_{AX})$$

$$c_B = (1 - z_A)(D_{AX} - D_{ABX}) + z_A(D_X - D_{BX})$$

$$b_A = (1 - z_B)(D_{ABX} - D_X)$$

and

$$b_B = (1 - z_A)(D_{ABX} - D_X)$$

Using these results we can rewrite Eq. 9 in the form

$$\begin{aligned} m_\lambda =& (1 - z_A)(1 - z_B)(c_A + c_B + D_X - D_{ABX}) \\ &+ (1 - z_A)(1 - z_B)(b_A + b_B)\lambda \end{aligned} \tag{10}$$

showing that the marginal m_λ is a linear function of λ, which has a positive slope, since b_A and b_B were shown to be positive. Therefore, an increase in concurrence will always reduce the expected diversity.

Analogously to the concept of conservation potential one can ask, how much expected diversity is gained if concurrence was entirely removed. We call this the synergy potential (*SP*) of the breeds in concurrence, defined as

$$SP = -m_\lambda \times \lambda.$$

From Eq. 10 it follows immediately that the synergy potential is a quadratic function of λ in the form

$$\begin{aligned} SP =& -(1 - z_A)(1 - z_B)(c_A + c_B + D_X - D_{ABX})\lambda \\ &- (1 - z_A)(1 - z_B)(b_A + b_B)\lambda^2 \end{aligned}$$

showing that the return of removing concurrence is quadratic and thus the more rewarding, the higher the level of concurrence is.

If we assume in the example discussed before the case where $\lambda = 0.3$, reducing z_A from 0.4 to 0.39 would increase the expected diversity by an increment of +0.74. Reducing z_B from 0.2 to 0.19 would increase the expected diversity by an increment of +1.56. However, reducing λ from 0.3 to 0.29 would increase the expected diversity by an increment of $m_\lambda \times -0.01 = 4.22$, of which 3.11 are directly due to the change of λ and 1.11 are due to the indirect effect by changing z_A^λ and z_B^λ. In Fig. 1, m_λ is also shown as a function of λ, and in contrast to the marginal diversities of the two breeds, this parameter stays negative over the whole parameter space, which means that reducing concurrence always will have a positive effect on expected diversity.

Conservation priorities when OTUs are in synergy

We consider now the case opposite to concurrence, namely a synergistic relation between OTUs. This is the case if the probability of not becoming extinct of one OTU is positively affected by the existence of another OTU. Examples are symbiotic or predator-prey systems. In the case of farm animal breeds this also refers to the synergistic use of breeds in mixed production systems.

In the model used, this phenomenon is reflected by assuming that extinction of one OTU reduces the survival probability of the other OTU. This can be modelled by defining the joint extinction probabilities as follows:

$$P(AB) = (1 - z_A)(1 - z_B)$$

$$P(A, -|\alpha) = (1 - z_A)z_B(1 - \alpha)$$

$$P(-, B|\beta) = z_A(1 - z_B)(1 - \beta)$$

$$\begin{aligned} P(-, -|\alpha, \beta) &= 1 - P(A, B) - P(A, -|\alpha) - P(-, B|\beta) \\ &= z_A z_B + \alpha z_B(1 - z_A) + \beta z_A(1 - z_B) \end{aligned}$$

The parameters $0 \leq \alpha \leq 1$ and $0 \leq \beta \leq 1$ reflect the degree of synergy. For large values of α, the survival of OTU *A* depends heavily on the existence of OTU *B*. Note that with this model, both one-sided dependencies (e.g. A depends on B, but B does not depend on A when $\alpha > 0$ and $\beta = 0$) and symmetric dependencies (both OTUs depend on the existence of the respective other OTU with $\alpha > 0$ and $\beta > 0$) can be modelled.

Using this set of conditional extinction probabilities in Eq. 5 and taking the first derivative with respect to z_A and z_B, respectively, yields the conditional marginal diversities:

$$m_A^{\alpha,\beta} = (1 - z_B)[(1 - \beta)D_{BX} - D_{ABX}] + z_B[(1 - \alpha - \beta)D_X - (1 - \alpha)D_{AX})] + \beta D_X$$

$$m_B^{\alpha,\beta} = (1 - z_A)[(1 - \alpha)D_{AX} - D_{ABX}] + z_A[(1 - \alpha - \beta)D_X - (1 - \beta)D_{BX})] + \alpha D_X$$

In this model, the effective extinction probabilities are

$$z_A^{\alpha} = 1 - P(A, B) - P(A, -|\alpha) = z_A + \alpha z_B(1 - z_A)$$

and

$$z_B^{\beta} = z_B + \beta z_A(1 - z_B),$$

respectively. Both effective extinction probabilities increase linearly with increasing values of α and β, respectively.

The effective conservation potentials based on the effective extinction probability for the given values of α and β are

$$CP_A^{\alpha,\beta} = -m_A^{\alpha,\beta} \times z_A^{\alpha}$$

and

$$CP_B^{\alpha,\beta} = -m_B^{\alpha,\beta} \times z_B^{\beta}$$

and are suggested as the main criterion to judge the relative conservation preference of the OTUs studied.

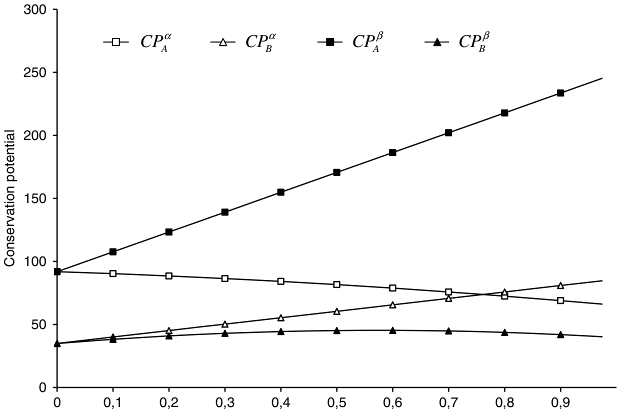

Fig. 2 Conservation potential of OTUs A and B as a function of synergy parameters α and β assuming a one-sided dependency (α is varied with $\beta = 0$ or vive versa) for the example data set

The model is illustrated with the primate example used before, where now a synergistic interdependency between the two gibbon species is assumed. In Fig. 2, the conservation potentials of the two species are depicted for the situation of a one-sided dependency: the curves with open symbols reflect the case where α is varied between 0 and 1 and $\beta = 0$, and the curves with filled symbols reflect the case where $\alpha = 0$ and β is varied between 0 and 1. In the former case, the conservation potential of the originally less endangered species B increases, because it's conservation also increases the probability that species A can be conserved. But it is only with $\alpha \sim 0.75$ that the conservation potential of the less endangered species B exceeds the one of species A. In the other scenario, the conservation potential of species A continuously increases with increasing values of β and therefore species A would always be prioritised for conservation over species B. However, it should be noted that in this scenario the conservation potential of species B also increases slightly with increasing values of β and reaches its maximum with $\beta \sim 0.6$.

Figure 3 shows the difference of conservation potentials $CP_A^{\alpha,\beta} - CP_B^{\alpha,\beta}$ as a function of α and β. Positive values indicate that conservation of species A should be given priority, while negative values suggest priority for species B. As can be seen, species B in this case is only prioritised for high values of α and small values of β, i.e. when existence of species A depends heavily on the presence of species B, but species B is rather independent of species A.

Discussion

The suggested approach provides a systematic and general model to study the impact of non-independence of

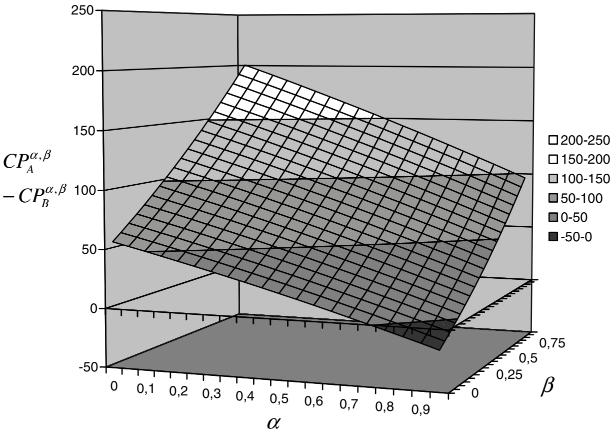

Fig. 3 Difference of the conservation potentials $CP_A^{\alpha,\beta} - CP_B^{\alpha,\beta}$ as a function of α and β for the example data set

extinction or survival probabilities of different OTUs on conservation priorities. It fully stays within the realm of Weitzman's diversity concept and is based on the assumption, that all types of dependencies can be reflected in joint extinction probabilities.

In this study, the conservation potential was used for prioritising breeds for conservation. Other studies base conservation priorities on the 'distinctiveness' of OTUs (van der Heide et al. 2005), expected diversity (Witting et al. 2000), the contribution to actual diversity (Ollivier et al. 2005) or to a 'core set' (Eding et al. 2002) or just the degree of endangerment derived from simple quantities like actual or effective population sizes (for a review see Simianer 2005). The advantage of using the conservation potential as a criterion is, that it combines phylogenetic information, risk of extinction, and economic criteria to a simple quantity. Under the assumption of the same marginal cost to change the extinction probability of two breeds by the same small increment, the conservation potential gives a good guideline as to which OTUs should be prioritised to be included in a conservation program. However, the conservation potential is based on a number of approximations. Simianer (2005) showed that it is based on a linear extrapolation of a concave function and therefore systematically underestimates the true conservation potential. Despite this (often small) bias, the risk of a change of order, i.e. that in a comparison of OTUs i and j $CP_i > CP_j$ while the true conservation potential of OTU i is less than the one of OTU j, is marginal.

The parameterisation suggested in this paper allows a full analytical examination of a given data set. While here, for simplicity, a decision problem of prioritising one out of two OTUs was considered, the approach can easily be generalised to a larger set of interacting OTUs. The critical requirement here will be to define realistic parameters for higher order joint survival or extinction probabilities (for pairs, triplets etc. of OTUs). While Witting et al. (2000) suggest that population viability analysis (Boyce 1992) can be used for this purpose and Bennewitz and Meuwissen (2005) suggested this approach in a farm animal context, it must be doubted that reliable higher order extinction probabilities (reflected by the parameters λ, α and β in this study) will always be available.

Given the computational simplicity due to the reparameterisation in Eq. 5, it even is an option to include uncertainty about the dependency parameters in the model. For the example of the concurrence model, this would mean that we do not assume λ to be known, but we assume a probability density $p(\lambda)$ reflecting our assumption about its most likely value and our prior degree of belief. Since λ lies between 0 and 1, we could assume $p(\lambda)$ to be a Beta-distribution (Box and Tiao 1992). Then Eq. 7a, b can be modified to

$$E_\lambda(CP_A) = \int_0^1 (-m_A^\lambda \times z_A^\lambda) p(\lambda)\, \mathrm{d}\lambda$$

and

$$E_\lambda(CP_B) = \int_0^1 (-m_B^\lambda \times z_B^\lambda) p(\lambda)\, \mathrm{d}\lambda,$$

respectively, and decisions can be made based upon these expected marginal values. Similar approaches can be used to account for uncertainty in other one- and multidimensional parameters of the model.

The results of the illustrative example show, that dependency of extinction probabilities between OTUs can cause substantial changes in conservation priorities. This is especially so in the concurrence situation, where it was shown that under certain conditions conservation activities in one species will reduce the overall expected diversity. A similar argument was used by Witting et al. (2000) who concluded from their study, that optimal conservation schemes in some cases may require an increase of extinction risk, up to an eradication, of species that either compete with, or prey on, other species.

A novel thought resulting from the above considerations is that conservation activities cannot only focus on changing the extinction probability of the considered OTUs, but also on changing the dependency parameters such that the overall expected diversity increases. This appears especially promising in the case of concurrence, where a reduction of λ was observed to be a valid alternative to activities aiming at a reduction of extinction probabilities of single OTUs alone.

In this case, the changes in expected diversity through a reduction of z_A, z_B, or λ need to be seen relative to the cost of the projects required to achieve these changes (Weitzman 1998). Based on arguments from population genetics, Simianer et al. (2003) argued that there is a degression in costs with increasing extinction probabilities, i.e. that it is likely cheaper to reduce z_A from 0.4 to 0.39 than it is to reduce z_B from 0.2 to 0.19. In a case where concurrence is due to a competitive use of the same limited resource (like food) a reduction of the degree of concurrence can be achieved e.g. by increasing the amount or the availability of the limiting resource or by reserving a fixed part of the resource to either of the two (or more) OTUs in concurrence. These different options need to be assessed economically for any specific case, and no general result can be given, which option is optimal in terms of cost efficiency. However, it should be noted, that removing concurrence is a valid option that needs to be taken into account.

Dependency models may be much more complex in reality than outlined here. For instance, in the concurrence situation the concurrence parameter λ may not be a constant but may depend on the relative frequency of the two concurring OTUs. Full competition may only arise if both OTUs are frequent, but may be low if one of the OTUs is low in numbers, i.e. almost extinct. Formally, this could be reflected by assuming λ to be a function of the extinction probabilities, i.e. $\lambda = f(z_A, z_B)$. Further research is needed to examine such models of a higher order of complexity, and the challenge remains to provide reasonable parameters for the application of such models to real conservation problems.

The presented results underline, that Weitzman's diversity concept is a powerful and flexible tool to assess conservation priorities both in a multi-species and a multi-breed context. The suggested approach extends the applicability of the framework significantly and allows a more realistic modelling of interacting systems. The concept also holds if the quantity to maximise is not only expected diversity, but some expected utility being a function of diversity and other desirable properties, like economic, ecological or cultural values.

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