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Large Scale Marine Protected Areas for Biodiversity Conservation Along a Linear Gradient: Cooperation, Strategic Behavior or Conservation Autarky?

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Abstract In this paper we investigate effects of overlap in species between ecosystems along a linear gradient on the location of marine protected areas (MPAs) under full cooperation, strategic behavior and conservation autarky. Compared to the full cooperation outcome, both strategic behavior and conservation autarky lead to under-investment in biodiversity protection. Under strategic behavior, however, we observe the additional problem of “location leakage” i.e. countries invest less in species protected by others. Conservation autarky eliminates location leakage; in ecosystems with partly overlapping species compositions at country borders it even induces MPAs that are too large from a global perspective. We also find that, in our setting of a linear gradient without migrating species, countries focus their conservation efforts on species unique to their own country and that these species are relatively well protected compared to common species.

Keywords Bioeconomic modeling · Biodiversity conservation · Game theory · Marine protected areas · Marine reserves · Reserve site selection · Linear setting

This paper has not been submitted elsewhere in identical or similar form, nor will it be during the first 3 months after its submission to the Publisher.

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Abbreviation

MPA Marine protected area

1 Introduction

International conservation of biodiversity is high on the political agenda, both in terrestrial and marine environments (e.g. see [Convention on Biological Diversity 2010](#)). One of the main tools used for the conservation of biodiversity is the designation of reserves. The literature on reserve site selection has been developed to address the question of where reserves should be located for efficient conservation. Recent work includes considerations of inter alia connectivity, cost-differences, time-constrained budgets, redundancy and persistence ([Polasky et al. 2000, 2001](#); [Cabeza et al. 2004](#); [Costello and Polasky 2004](#); [Beger et al. 2010](#); [Groeneveld 2010](#)).

Biodiversity is heterogeneous across space. Therefore the location of protection has strategic implications. Essentially, the question is whether biodiversity protected in another country is a complement to, or a substitute for biodiversity that is protected domestically. Moreover, different locations have different opportunity costs of conservation. Due to the combination of complement-substitute issues, and differing costs and benefits of protecting different locations, many opportunities arise for countries to either cooperate or defect on protected area size or location decisions.

Only recently has the literature on reserve site selection started to address the question of how the efficient selection of reserves in a region is influenced by the presence of geo-political units, e.g. [Rodrigues and Gaston \(2002\)](#), [Bladt et al. \(2009\)](#), [Kark et al. \(2009\)](#), [Jantke and Schneider \(2010\)](#). These studies, however, compare full cooperation on conservation among a number of countries with a situation where countries designate reserves without considering conservation efforts by others. Following the trade literature, we call the latter setting “conservation autarky”.

On the one hand, conservation autarky seems plausible as countries may value protection in their own domain higher because they do not trust the protection of relevant species in the other country; or they may simply not know about species protection in another country; or they may feel it is their duty to protect species based on moral grounds. Moreover, comparing full cooperation with conservation autarky is looking at the same problem at different scales, where full cooperation represents a regional or global scale involving two or more countries. On the other hand, from an economist’s point of view, it is more likely that countries behave strategically, i.e. countries do less because a species is protected by another country. We refer to this phenomenon as “location leakage”. Both kinds of behavior are observed in practice: e.g. Denmark’s refusal to assign protected area status to the Dogger Bank (a shallow sand bank in the North Sea) can be interpreted as location leakage—she is doing less because Germany, the Netherlands, and the UK are already protecting the area. Conservation autarky is often a result of parochialism: in the Western world much money is spent on protecting species that are relatively safe globally, such as wolves, bald eagles and grizzly bears ([Hunter and Hutchinson 1994](#)).

The model in this paper studies these issues in detail using a general set-up, consisting of a linear gradient of ecosystems with overlapping species compositions. In principle, this set-up could be applied to both the terrestrial and the marine domain. The linear gradient is introduced to reflect the location of ecosystems, e.g. along a coastline including several countries. A detailed description of the setting is given in section 2.2. We choose to focus

on the marine domain, because the strategic issues of biodiversity conservation with large scale Marine Protected Areas (MPAs) along a linear gradient of ecosystems have not yet been discussed in the literature.

MPAs have been modeled in several ways over the last decades. Fisheries economists have considered their use as a fisheries management tool, e.g. [Sumaila \(1998\)](#), [Hannesson \(1998\)](#), [Anderson \(2002\)](#), [Smith and Wilen \(2003\)](#), [Sanchirico \(2004\)](#), [Schnier \(2005\)](#), [Armstrong \(2007\)](#), [Kar and Matsuda \(2008\)](#) and [Ngoc \(2010\)](#), and to a lesser extent, their strategic effects in fisheries ([Sumaila 2002](#); [Ruijs and Janmaat 2007](#); [Punt et al. 2010](#)). Most models consider MPAs as a fisheries management tool only, ignoring other uses; exceptions are [Boncoeur et al. \(2002\)](#), [Dalton \(2004\)](#), [Ngoc \(2010\)](#) and [Punt et al. \(2010\)](#).

Ecologists have considered reserve site selection problems in the marine environment with a focus on biodiversity conservation ([Sala et al. 2002](#); [Richardson et al. 2006](#); [Game et al. 2008](#); [Beger et al. 2010](#)). They have studied connectivity, data scale, uncertainty and persistence, but focus mostly on one country, ignoring the effects of borders which is in contrast to the terrestrial literature.

Many countries have Exclusive Economic Zones (EEZs) that comprise a number of ecosystems providing multiple direct and indirect services. We interpret MPAs as fully protected zones, with biodiversity conservation as their main goal, but with positive spill-over effects on direct uses of the ecosystem such as fisheries. The model developed thus reflects the multiple-use nature that exists in ocean space and that should be considered when making decisions about MPAs ([Punt et al. 2010](#)).

In this paper we formulate a spatial game theoretic model to analyze the issue of strategic behavior versus conservation autarky. MPAs are assigned in one or multiple ecosystems along a gradient. In contrast to most of the MPA literature, we do not cover the movement of species or ecosystems that cross political borders, as this has been covered in-depth by others (e.g. [Beattie et al. 2002](#); [Sumaila 2002](#); [Ruijs and Janmaat 2007](#); [Punt et al. 2010](#)). We assume that if a species occurs in multiple ecosystems, the populations in all ecosystems are separate and independent. This assumption is valid if the scale considered is large enough. Furthermore, we restrict our attention to ecosystems boundaries that coincide with political boundaries.

Our contribution to the literature is therefore twofold: we contribute to the reserve site selection literature by identifying and comparing the three possible scenarios for biodiversity conservation through protected areas, rather than the two scenarios that are usually addressed (i.e. full cooperation and conservation autarky), and we contribute to the MPA literature by drawing the attention to, at this stage, an understudied subject: the strategic aspects of biodiversity conservation through MPAs.

Our paper is the first to explicitly compare a setting of strategic interaction with a setting of conservation autarky in a multiple-use environment. [Bode et al. \(2011\)](#) analyze two trusts buying land parcels under conservation autarky, strategic behavior and cooperation, but their agents have differing conservation objectives. Furthermore, we are the first to describe strategic considerations for biodiversity conservation with large scale MPAs in a setting along a linear gradient, where MPA location and size are endogenously determined.

The basics of our model are similar to economic models on spatial configuration of terrestrial reserves that build on the traditional industrial organization literature, e.g. [Goeschl and Iglori \(2004\)](#), [Albers et al. \(2008\)](#) and [Ando and Shah \(2010\)](#). These models, however, often focus on location only, and on a given number of reserves. In our model, in contrast, location, size and the number of reserves are determined by the preferences for conservation.

We find that for welfare maximization on the one hand conservation autarky implies an inefficiency because conservation efforts by others are ignored, on the other hand autarky

eliminates location leakage. Therefore, our results suggest that in our setting, conservation autarky is still preferred to strategic behavior for the global society.

2 Model Characteristics

2.1 Model Background

We formulate a spatial game theoretic model of MPAs for biodiversity conservation, where two countries decide on the locations and sizes of MPAs. Assigning an MPA not only generates ecological benefits, but also entails opportunity and enforcement costs.

The value of ecological benefits can be disaggregated into direct use values and indirect use values. Direct use values comprise production services, local regulation services, and over-arching support services. Indirect use values comprise cultural services and option-use services (Beaumont et al. 2007).

We would argue that there is a scale issue here, whereby direct use values, such as food or biologically remediated habitats, mainly benefit local exploiters and are less dependent on biodiversity per se. Indirect use values, in contrast, benefit the global society and are heavily dependent on biodiversity. Hence, our game will be at least partly a public goods game.

Because we focus on ecosystems and their services, we need to measure biodiversity at ecosystem level. Consequently, the dissimilarity between ecosystems is a natural starting point.¹ This dissimilarity can be measured by the number of species (Weikard 2002). As we can never be sure that species are fully protected from extinction, we choose to maximize the *expected* total number of species, as in Polasky et al. (2000), Camm et al. (2002) and Arthur et al. (2004). An important issue when maximizing the expected number of species is that the survival probability of a species may be dependent on the survival probability of other species (Mainwaring 2001; van der Heide et al. 2005). Probabilities that ecosystems stay intact (henceforth: persistence probabilities), however, are independent because they are stand-alone entities (Weikard 2002).

The reserve site selection literature also focuses on the number of species. Maximizing the number of species subject to a budget constraint is equal to the Maximum Species Coverage Problem (Church et al. 1996; Ando et al. 1998; Polasky et al. 2000, 2001; Camm et al. 2002; Arthur et al. 2004). Minimizing the number of reserves subject to a biodiversity constraint equals the Minimum Set Cover Problem (Williams and Ara ejo 2000; Sala et al. 2002; Stewart et al. 2003; Cabeza et al. 2004; Richardson et al. 2006). These two problems are the main building blocks of reserve site selection problems. In our framework, however, we opt to use a benefit function approach, maximizing the net benefits of conservation. This approach is more appropriate because we focus on generated ecosystem goods and services and not on species protection per se. Thus, this approach captures the problem in its full extent.

To use the benefits approach, we need:

- (1) An explicit specification of probabilities of ecosystems to stay intact;
- (2) An explicit specification of direct use values.

Therefore we introduce the following assumptions:

¹ Biologists generally measure biodiversity with indices based on relative abundance and species richness (e.g. Hill 1973). Others have proposed to measure biodiversity based on dissimilarity between species (e.g. Faith 1992; Weitzman 1992, 1993, 1998; Solow et al. 1993). Indices that combine dissimilarity, abundance and species richness also exist (e.g. Ricotta 2004; Weikard et al. 2006).

- (a1) The persistence probability of an ecosystem is directly related to share of the ecosystem protected by an MPA (henceforth: MPA share).
- (a2) Increasing the share of the ecosystem protected by an MPA, increases the direct use values of ecosystem services by improving their quality.

The reasoning behind assumption (a1) is as follows: by increasing MPA share, an increasing number of keystone habitats and keystone species, i.e. habitats and species that play a critical role in the ecosystem, are protected. Without the protection of these keystone habitats and species, the essential features of the ecosystem are lost. The system is then transformed into another ecosystem, that still supports some species, but often such a new ecosystem has less value than the original one. Once transformed, it is very difficult to get the ecosystem back to its original state (Folke et al. 2004). In the marine context, an example is the Dutch Wadden Sea. If it were to be impacted too much by human activities such as fishing, dredging and oil and gas exploration, its keystone habitats, undisturbed sandy bottoms and mud flats, would be destroyed, and many species would be lost. A large MPA would protect the ecosystem from damaging activities in this area, and thus the probability of ecosystem destruction becomes smaller.

The keystone habitats and species are not just building blocks of the ecosystem, they are also the main contributors to direct use values and direct ecosystem services, either by providing a home to species that provide these services or by forming the basis for the service itself (assumption (a2)). An example of the former is fish habitat, whereas an example of the latter is sandy beaches that provide tourism services. As the MPA gets bigger, more keystone habitats and species are protected and direct services have higher quality. In the case of fishing, for example, protection of fish habitat could improve the growth rate and carrying capacity² of the fish stocks. Of course, harvest would be restricted to a smaller area, which is reflected in the cost function of MPAs.

2.2 A Biodiversity Conservation Model

In our MPA model, we consider two countries $k \in \{1, 2\}$ that share a common sea. This common sea comprises the set E of ecosystems. Ecosystems are characterized by a number of keystone habitats and keystone species, and their destruction would imply the destruction of that ecosystem. Collectively in all ecosystems, a set S of species exists, consisting of $|S|$ species, denoted i . Each ecosystem $e \in E$ is characterized by a subset $s_e \subseteq S$ of species, and consequently each of the i species occurs in a subset $N_i \subseteq E$ ecosystems. Set E is subdivided over countries k into E_1 and E_2 . See Fig. 1 for an example of our set-up.

The intersection of two sets of species in ecosystems e and e' , $s_e \cap s_{e'}$, decreases with distance. In this paper we will use a simple exponential decay function to describe this relationship:

$$X = X_o \exp^{-r\delta} \quad (1)$$

with X describing the set intersection, X_o the set intersection between two neighboring areas, r the decay rate, and δ the distance between the two ecosystems under consideration (Nekola and White 1999). This implicitly assumes a uniform decay gradient in all directions. The reasoning is that many ecosystems are located along environmental gradients. Species that are very common occur in (nearly) all ecosystems. Other species occur only in specific habitats of ecosystems, and their specific habitats occur and disappear as we go on along the gradient.

² The carrying capacity of a fish stock is the size of the stock that it will reach in the absence of fishing.

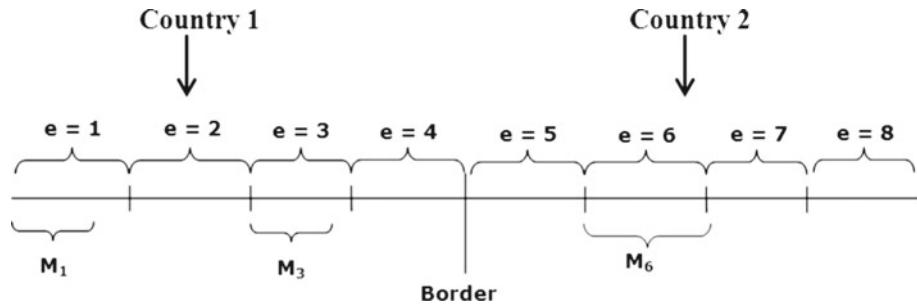


Fig. 1 A schematic presentation of the nature protection model. Each of the two countries 1 and 2 own four ecosystems. In every ecosystem a share can be designated as MPA of size $0 \leq M_e \leq 1$. Ecosystems 1 and 3 in country 1 are partially protected; ecosystem 6 in country 2 is fully protected

We can think of this setting as a long coastline shared by two or more countries where a natural gradient, such as temperature, or benthos conditions, or salinity, defines the ecosystems occurring along this coastline, as with the large marine ecosystems on the western coastline of North America from the USA to Canada, or the Baltic and the North Sea along the coasts of Denmark, Germany and the Netherlands. Alternatively, we can think of a transect between the coasts of two or more countries where an increasing depth gradient defines the different ecosystems. As an example, consider the Dutch coast as starting point. The Dutch Wadden Sea area would then be the first ecosystem. The next ecosystem along the gradient would be the North Sea itself, and through the Norwegian Sea we end up in the Barents Sea as the fourth ecosystem.³ The gradient is then defined by a combination of depth and temperature. Another gradient is that of the Baltic Sea via the Kattegat into the North Sea, where salinity is the defining element. As stated earlier, we restrict our attention to ecosystem boundaries that (nearly) coincide with political boundaries, as is the case with the aforementioned gradients.

Each country can decide to protect a share M_e ($0 \leq M_e \leq 1$) of ecosystem e , i.e. M_e is set apart as an MPA.

The gradient defines the distribution of species over ecosystems, and as such is the most important factor determining the spatial configuration of MPAs. Along a line, a uniformly decaying gradient will imply large numbers of unique species in ecosystems at the edges. The central ecosystems all have a lower number of unique species, as a larger number of their species is shared with their neighbors.⁴

We calculate the expected number of species in the following way: persistence probability of a single ecosystem e is an increasing function of the area protected in that ecosystem, M_e :

$$\text{Prob}(e \text{ persists}) = f(M_e), \quad f'(M_e) > 0, \quad \forall e \in E. \tag{2}$$

If species i occurs in ecosystem e , then the probability that species i becomes extinct in ecosystem e , is one minus the probability that ecosystem e persists, i.e. $(1 - f(M_e))$. Species i is found in the subset of ecosystems N_i , hence the probability that species i becoming

³ The boundaries between ecosystems are in reality not rigid. Moreover, an implication of the assumption of independence of ecosystems is that there are no highly migratory species that travel between ecosystems, such as tuna and whales. These species, however, although of great importance to certain ecosystems, are exceptions. Most species stay within one ecosystem during their life cycle. Species that occur in multiple ecosystems are therefore considered to be independent populations.

⁴ Had we chosen a circle instead of a line, then all ecosystems would have had the same number of species in common. The line mimics the fact that ecosystems at the edges of gradients often have a large number of unique species.

extinct in all N_i ecosystems is equal to: $\prod_{e \in N_i} (1 - f(M_e))$. The survival probability of a species is then equal to the probability that it does *not* become extinct in all its ecosystems:⁵

$$\pi_i = 1 - \prod_{e \in N_i} (1 - f(M_e)) \quad \forall i \in S \tag{3}$$

The sum of all survival probabilities of species is the expected number of species.

2.2.1 Full Cooperation Among Countries

Under full cooperation, countries maximize the value V of their joint net benefits. Let M_E denote the vector of all MPAs in the set E of ecosystems, and M_{E_k} the vector of all MPAs in the subset E_k of ecosystems. Countries benefit from direct use values from preservation and from indirect use values through biodiversity. They maximize:

$$V(M_E) = D_E(M_E) + B \left(\sum_{i \in S} \pi_i \right) - C_E(M_E) \tag{4}$$

with D_e the direct benefits from protecting area M_e in ecosystem $e \in E$, B are the indirect benefits from biodiversity, and $C_E(M_E)$ is the cost of protection. $\sum_{i \in S} \pi_i$ is the total expected number of species. Substituting (3) in (4), the maximization problem is:

$$V(M_E) = D_E(M_E) + B \left(\sum_{i \in S} \left(1 - \prod_{e \in N_i} (1 - f(M_e)) \right) \right) - C_E(M_E). \tag{5}$$

The first order condition (FOC) for an interior solution is:

$$\frac{\partial V}{\partial M_e} = \frac{\partial D_e(M_e)}{\partial M_e} + \frac{\partial B \left(\sum_{i \in S} (1 - \prod_{e \in N_i} (1 - f(M_e))) \right)}{\partial M_e} - \frac{\partial C(M_e)}{\partial M_e} = 0 \quad \forall e \in E. \tag{6}$$

Marginal benefits consist of the marginal benefits from direct services and marginal benefits from biodiversity services. Marginal costs of MPAs are the marginal opportunity and enforcement costs.

This problem can be solved analytically for small problems with only a few ecosystems and species, and simple specifications of benefit, cost and probability functions. The problem becomes rapidly complicated when large numbers of variables and parameters are involved. We present border cases, and a simple example that can still be solved analytically in section 3, as well as a more complex example where simulations are needed in section 4.

2.2.2 Strategic Behavior Among Countries

Under strategic behavior (or Nash equilibrium), each country takes the decision of the other country as given when maximizing its own net benefit function. Countries reap the direct benefits of their ecosystems E_k , and bear the costs of MPAs in their own ecosystems. Additionally

⁵ The survival probability of a species is consequently a function of the persistence probabilities of the ecosystems it occurs in. As a referee has already correctly pointed out, even though persistence probabilities are independent, the survival probabilities of species may still be interdependent because species occur in the same ecosystem. By protecting an ecosystem, we protect multiple species and hence their survival probabilities are linked.

the value of the biodiversity services accrues to both countries in equal shares. Consequently, each country maximizes:

$$V_k(M_{E_k}) = D_{E_k}(M_{E_k}) + 1/2B \sum_{i \in S} \left(1 - \prod_{e \in N_i} (1 - f(M_e)) \right) - C_{E_k}(M_{E_k}), \quad \forall k \in \{1, 2\}. \tag{7}$$

First order conditions for an interior solution are:

$$\begin{aligned} \frac{\partial V_k}{\partial M_e} &= \frac{\partial D_e(M_e)}{\partial M_e} + 1/2 \frac{\partial B \sum_{i \in S} (1 - \prod_{e \in N_i} (1 - f(M_e)))}{\partial M_e} \\ &\quad - \frac{\partial C(M_e)}{\partial M_e} = 0, \quad \forall k \in \{1, 2\}, \quad \forall e \in E_k. \end{aligned} \tag{8}$$

In contrast to full cooperation, marginal benefits now consist of the marginal benefits from direct services within a country and half of the total biodiversity services. Marginal costs are the marginal costs of domestic MPAs only.

2.2.3 Conservation Autarky

In the previous section we have implicitly assumed that from an individual country’s perspective it does not matter where a species is protected. This gives rise to location leakage, causing countries to free-ride on the protection of species by others. In a situation of conservation autarky, it is assumed that the protection of species in one country is not a substitute for its protection in another country. Countries only account for biodiversity protected in their own country. Under conservation autarky each country maximizes its perceived benefits:

$$V_k(M_{E_k}) = D_{E_k}(M_{E_k}) + 1/2B \sum_{i \in S_k} \left(1 - \prod_{e \in N_{ik}} (1 - f(M_e)) \right) - C(M_{E_k}), \quad \forall k \in \{1, 2\} \tag{9}$$

where S_k denotes the set of species in country k , and N_{ik} denotes the set of ecosystems where species i occurs in country k . The associated first order conditions for a maximum are:

$$\begin{aligned} \frac{\partial V_k}{\partial M_e} &= \frac{\partial D_e(M_e)}{\partial M_e} + 1/2 \frac{\partial B \sum_{i \in S_k} (1 - \prod_{e \in N_{ik}} (1 - f(M_e)))}{\partial M_e} \\ &\quad - \frac{\partial C_e(M_e)}{\partial M_e} = 0 \quad \forall k \in \{1, 2\}, \quad \forall e \in E_k. \end{aligned} \tag{10}$$

These first order conditions differ from the conditions derived for strategic behavior in the second term only: marginal benefits of species protection are restricted to species occurring domestically.

3 Analytic Benchmarks and Example

In this section we explore two benchmark cases and a simple example of a species gradient, that are analytically tractable. We derive first order conditions and MPA shares and

investigate the main effects of the species gradient under full cooperation, strategic behavior and conservation autarky, both in the benchmark cases and the variant in between.

3.1 Benchmarks of the Gradient

We consider the outcomes of full cooperation, strategic behavior, and conservation autarky for two benchmark cases: in the equal ecosystems case, all ecosystems contain all species in set S , consequently we have E equal and independent ecosystems. In the unique ecosystems case, all ecosystems are unique, i.e. no species occurs in more than one ecosystem. First order conditions for the two cases under the three scenarios are given in Table 1.

If $f(M_e)$ is equal for all ecosystems, then the form of the solutions for equal independent ecosystems would be fully symmetric, both for full cooperation and strategic behavior, and MPA share would be dictated only by the distribution of direct benefits and costs in the different ecosystems. Free-riding occurs for strategic behavior, i.e. MPA shares are smaller than under full cooperation, but there is no location leakage: countries do not invest less in species that are protected by others because of the symmetry. In conservation autarky, countries ignore contributions by others, and because they have all species in their domain, they will assign larger MPAs than under strategic behavior. These MPAs are not as large as under full cooperation because countries only account for the services in their own country.

If all ecosystems are unique, and no species occurs in multiple ecosystems, there are no trade-offs in location choice. Consequently, MPA share is determined solely by biodiversity within an ecosystem, and direct benefits and costs on the spot. Again, MPA shares are smaller under strategic behavior and conservation autarky because they only account for services generated in their own country. Note that due to the absence of interdependence, the solutions for strategic behavior and conservation autarky are the same.

3.2 Simple Gradient Example

As a simple illustrative example, suppose we have two countries and three ecosystems, where each ecosystem has one species in common with its neighbor, as in Table 2. Furthermore, assume linear benefits (d_e), quadratic costs with cost parameter c_e , and persistence probabilities linear in MPA share. Finally, let us assign ecosystems 1 and 2 to country 1, and ecosystem 3 to country 2.

The net benefit functions under full cooperation, strategic behavior and conservation autarky are respectively:

$$\begin{aligned}
 V(M_E) &= d_1M_1 + d_2M_2 + d_3M_3 \\
 &\quad + ((1 - (1 - M_1)) + (1 - (1 - M_1)(1 - M_2)) + (1 - (1 - M_2)(1 - M_3)) \\
 &\quad + (1 - (1 - M_3))) - \frac{1}{2}c_1M_1^2 - \frac{1}{2}c_2M_2^2 - \frac{1}{2}c_3M_3^2. \tag{11}
 \end{aligned}$$

$$\begin{aligned}
 V_1(M_{E_1}) &= \sum_{e \in E_1} d_e M_e + 1/2 \sum_S \left(1 - \prod_{e \in N_i} (1 - M_e) \right) - \sum_{e \in E_1} \frac{1}{2} c_e M_e^2 \\
 V_2(M_{E_2}) &= d_3M_3 + 1/2 \sum_S \left(1 - \prod_{e \in N_i} (1 - M_e) \right) - \frac{1}{2} c_3 M_3^2. \tag{12}
 \end{aligned}$$

Table 1 First order conditions for full cooperation, strategic behavior, and conservation autarky in the border cases of the gradient

	Equal independent ecosystems	Unique ecosystems
Full cooperation	$\left(\frac{\partial D_e(M_e)}{\partial M_e} + \frac{\partial B(M_e) \left(\frac{\partial C(M_e)}{\partial M_e} - S \prod_{h \neq e} (1-f(M_h)) \right)}{\partial M_e} \right) = \frac{\partial C(M_e)}{\partial M_e} \quad \forall e \in E$	$\left(\frac{\partial D_e(M_e)}{\partial M_e} + \frac{\partial B(M_e) \left s_e \right \frac{\partial f(M_e)}{\partial M_e}}{\partial M_e} \right) = \frac{\partial C_e(M_e)}{\partial M_e} \quad \forall e \in E$
Strategic behavior	$\left(\frac{\partial D_e(M_e)}{\partial M_e} + \frac{1}{2} \frac{\partial B(M_e) \left(\frac{\partial C(M_e)}{\partial M_e} - S \prod_{h \neq e} (1-f(M_h)) \right)}{\partial M_e} \right) = \frac{\partial C(M_e)}{\partial M_e} \quad \forall k \in \{1, 2\}, e \in E_k$	$\left(\frac{\partial D_e(M_e)}{\partial M_e} + \frac{1}{2} \frac{\partial B(M_e) \left s_e \right \frac{\partial f(M_e)}{\partial M_e}}{\partial M_e} \right) = \frac{\partial C_e(M_e)}{\partial M_e} \quad \forall k \in \{1, 2\}, e \in E_k$
Conservation autarky	$\left(\frac{\partial D_e(M_e)}{\partial M_e} + \frac{1}{2} \frac{\partial B(M_e) \left(\frac{\partial C(M_e)}{\partial M_e} - S \prod_{h \in E_k, h \neq e} (1-f(M_h)) \right)}{\partial M_e} \right) = \frac{\partial C(M_e)}{\partial M_e} \quad \forall k \in \{1, 2\}, e \in E_k$	$\left(\frac{\partial D_e(M_e)}{\partial M_e} + \frac{1}{2} \frac{\partial B(M_e) \left s_e \right \frac{\partial f(M_e)}{\partial M_e}}{\partial M_e} \right) = \frac{\partial C_e(M_e)}{\partial M_e} \quad \forall k \in \{1, 2\}, e \in E_k$

$|s_e|$ denotes the number of species occurring in ecosystem e

Table 2 Example of ecosystem configuration

Country	Ecosystem	Species
1	$e = 1$	1, 2
1	$e = 2$	2, 3
2	$e = 3$	3, 4

Table 3 First order conditions and solutions to MPA shares of the analytical example

	First order conditions	Solutions
Full cooperation	$d_1 + (2 - M_2) = c_1 M_1$	$M_1 = \frac{d_1(c_2 c_3 - 1) + c_3(2c_2 - d_2) + d_3 - 2c_3}{c_1 c_2 c_3 - c_1 - c_3}$
	$d_2 + (2 - M_1 - M_3) = c_2 M_2$	$M_2 = \frac{c_1 c_3(d_2 + 2) - d_1 c_3 - d_3 c_1 - 2c_1 - 2c_3}{c_1 c_2 c_3 - c_1 - c_3}$
	$d_3 + (2 - M_2) = c_3 M_3$	$M_3 = \frac{d_3(c_1 c_2 - 1) + (2c_2 - d_2)c_1 + d_1 - 2c_1}{c_1 c_2 c_3 - c_1 - c_3}$
Strategic behavior	$d_1 + 1/2(2 - M_2) = c_1 M_1$	$M_1 = \frac{d_1(4c_2 c_3 - 1) + 2c_3(2c_2 - d_2) + d_3 - 2c_3}{4c_1 c_2 c_3 - c_1 - c_3}$
	$d_2 + 1/2(2 - M_1 - M_3) = c_2 M_2$	$M_2 = \frac{4c_1 c_3(d_2 + 1) - 2d_1 c_3 - 2c_1 - 2d_3 c_1 - 2c_3}{4c_1 c_2 c_3 - c_1 - c_3}$
	$d_3 + 1/2(2 - M_2) = c_3 M_3$	$M_3 = \frac{d_3(4c_1 c_2 - 1) + 2c_1(2c_2 - d_2)c_1 + d_1 - 2c_1}{4c_1 c_2 c_3 - c_1 - c_3}$
Conservation autarky	$d_1 + 1/2(2 - M_2) = c_1 M_1$	$M_1 = \frac{4c_2(1 + d_1) - 2(1 + d_2)}{4c_1 c_2 - 1}$
	$d_2 + 1/2(2 - M_1) = c_2 M_2$	$M_2 = \frac{4c_1(1 + d_2) - 2(1 + d_1)}{4c_1 c_2 - 1}$
	$d_3 + 1 = c_3 M_3$	$M_3 = \frac{1 + d_3}{c_3}$

$$\begin{aligned}
 V_1(M_{E_1}) &= \sum_{e \in E_1} d_e M_e + 1/2 \sum_{i \in S_1} \left(1 - \prod_{e \in N_{i_1}} (1 - M_e) \right) - \sum_{e \in E_1} \frac{1}{2} c_e M_e^2 \\
 V_2(M_{E_2}) &= d_3 M_3 + \sum_{i \in S_2} \left(1 - \prod_{e \in N_{i_2}} (1 - M_e) \right) - \frac{1}{2} c_3 M_3^2
 \end{aligned}
 \tag{13}$$

The relevant FOCs and the solutions are given in Table 3. Because survival probabilities are linear in MPA share, the resulting survival probabilities of the different species are:

$$\begin{aligned}
 \pi_1 &= M_1 \\
 \pi_2 &= M_1 + M_2 - M_1 M_2 \\
 \pi_3 &= M_2 + M_3 - M_2 M_3 \\
 \pi_4 &= M_3.
 \end{aligned}
 \tag{14}$$

Survival probabilities of species 1 and 4 are equal to the MPA share in ecosystem 1 and 3 because they only occur in those ecosystems. Species 2 and 3 have a weighted sum of MPA shares as survival probabilities.

The sum of marginal benefits of direct use (d_e), and the marginal change in the expected number of species, equal the marginal costs of an additional unit of MPA, $c_e M_e$. The FOCs show the effect of the distribution of species on the optimal location and share of MPAs. Both species 2 and 3 can be protected in multiple ecosystems, hence the negative effect of M_2 in the FOCs for M_1 and M_3 , and vice-versa, except in the case of conservation autarky, where this effect only occurs within a country (i.e. for species 2 in country 1), but not between countries.

In an interior solution, a country introduces at least a small MPA in all ecosystems. This can be seen from the FOCs: an interior solution requires $0 \leq M_e \leq 1 \forall e$, consequently $2 - M_e$ is always positive, and we get a positive MPA for each ecosystem.

The solutions show that the effects of parameters are ambiguous, and depend on the value of other parameters, in particular cost parameters. If the denominator is positive and $c_1 c_2 c_3 > 1$ direct benefits of an ecosystem (d_e) increase the MPA in that ecosystem. Interestingly, for full cooperation and strategic behavior, there is also a positive effect of d_1 on M_3 , and vice-versa, whereas d_2 affects MPA shares in the other two ecosystems in a negative way. A similar effect is present in the solutions for conservation autarky, but only within country 1: the d_e 's of its respective ecosystems have a negative influence on the MPA share chosen in the other ecosystem. This occurs because ecosystem 2 is partly a substitute for the other two (or one in the case of conservation autarky). If M_1 increases, M_2 can be decreased. Under full cooperation and strategic behavior, this has a domino effect causing a protection loss for some of the species in ecosystem 3, where, consequently M_3 has to be raised to make up for this loss. This domino effect does not occur in conservation autarky where protection in other countries is ignored.

The cost parameters determine the sign of the denominator; if the denominator is positive, M_e is decreasing in c_e . Furthermore it can be seen that c_2 has a positive effect on the numerators and denominators of M_1 (and M_3 for full cooperation and strategic behavior). How an increase in c_2 changes M_1 and M_3 , depends on relative parameter values.

The reaction functions for the three MPAs under strategic behavior facilitate a further comparison. These curves are described by the following equations:

$$\begin{aligned}
 M_1 &= \frac{2(d_1 + 1)c_2 - d_2 - 1 + 1/2M_3}{2c_1c_2 - 1/2} \\
 M_2 &= \frac{2(d_2 + 1)c_1 - d_1 - 1 - c_1M_3}{2c_1c_2 - 1/2} \\
 M_3 &= \frac{d_3 + 1 - 1/2M_2}{c_3}.
 \end{aligned}
 \tag{15}$$

The first order conditions in Table 3 and (15) show two strategic effects that will induce smaller MPAs: free-riding and location leakage. Free-riding occurs because countries do not account for biodiversity benefits in the other country. This can be seen from the factor $1/2$ in the FOC. Location leakage is clear from (15): if country 1 increases its MPA in ecosystem 2, country 2 will reduce its MPA share in ecosystem 3, and vice-versa. Another interesting effect of location leakage is that even though M_3 did not play a role in the original FOC with respect to M_1 , it has a positive influence on the equilibrium outcome of M_1 . The intuition is that if country 2 invests in the species of ecosystem 3, location leakage applies in ecosystem 2. This in turn also decreases the protection of species shared between ecosystem 1 and 2, and therefore the MPA in ecosystem 1 is increased. This effect also runs the other way, even though it cannot be seen directly from the reaction curves.

The solutions of full cooperation and strategic behavior do not simply differ by a factor of $1/2$ because benefits comprise more than just the public good, and the distribution of ecosystems and species is not fully symmetric. Conservation autarky is less complex because countries ignore species' presence in other countries. The absence of interdependence in the solutions for conservation autarky is indicated by the absence of parameters relevant to the share of M_1 and M_2 in the solution for M_3 , and vice-versa. M_1 and M_2 are still interdependent because they both lie within the same country.

Table 4 Difference in MPA shares between the different outcomes

	Full cooperation— strategic behavior	Full cooperation— conservation autarky	Strategic behavior— conservation autarky
Difference in MPA share in ecosystem 1	$\frac{c(2c^2-3c+2)}{(c^2-2)(2c^2-1)}$	$\frac{2(c^2-c+1)}{(2c+1)(c^2-2)}$	$\frac{1}{(2c+1)(2c^2-1)}$
Difference in MPA share in ecosystem 2	$\frac{2c(c^2-3c+1)}{(c^2-2)(2c^2-1)}$	$\frac{2c(c-3)}{(2c+1)(c^2-2)}$	$\frac{-2c}{(2c+1)(2c^2-1)}$
Difference in MPA share in ecosystem 3	$\frac{c(2c^2-3c+2)}{(c^2-2)(2c^2-1)}$	$\frac{c^2-2c+2}{c(c^2-2)}$	$\frac{1-c}{c(2c^2-1)}$

To show differences in MPA shares between full cooperation, strategic behavior and conservation autarky, we further simplify MPA shares in Table 3 by assuming zero direct benefits (i.e. $d_1 = d_2 = d_3 = 0$) and symmetric costs for all ecosystems (i.e. $c_1 = c_2 = c_3 = c$). The results are displayed in Table 4.

An interior solution for all M_e requires $c > 2$. In that case, under full cooperation, MPAs in ecosystems 1 and 3 are always larger than those under strategic behavior. The MPA in ecosystem 2 under full cooperation is smaller for $2 < c < \frac{\sqrt{5+3}}{2} \approx 2.6$, and larger for $c > 2.6$. The differences between full cooperation and conservation autarky are also generally positive, implying that full cooperation assigns larger MPAs than under conservation autarky, except in ecosystem 2 for $2 \leq c \leq 3$. Here, free-riding is outweighed by the fact that a country considers certain species as unique (although they are not), and therefore overprotects these species relative to the global optimum. By comparing MPA shares under strategic behavior and conservation autarky, we find that the MPA in the first ecosystem is larger under strategic behavior, but the others are larger under conservation autarky. In general, because countries only consider protection in their own ecosystems, species that occur on both sides of the border receive more protection than under strategic behavior, but not as much as under full cooperation. Hence, from the global perspective, inefficiencies still occur, even though the situation is an improvement over strategic behavior.

4 Simulation Model

4.1 Species Distribution and Ecosystem Persistence

We will now explore the effects of a more realistic probability distribution, as well as larger numbers of ecosystems and species. For the simulation, we will consider a coastline of ecosystems with a universal decay rate and an equal maximum number of species in each ecosystem.⁶

From a matrix of distances between ecosystems and the maximum number of species, a distribution of species over ecosystems can be calculated. This distribution is exogenous to our model. Its calculation is explained in Appendix I.

⁶ A non-universal decay rate would result in more abrupt changes in species composition between ecosystems. An example would be that ecosystems that are neighbors have no species in common. A specification in two dimensions with a non-universal decay rate would be a more realistic setting, but is more difficult to solve and adds little to the results found here, except from a richer set of possible solutions and configurations.

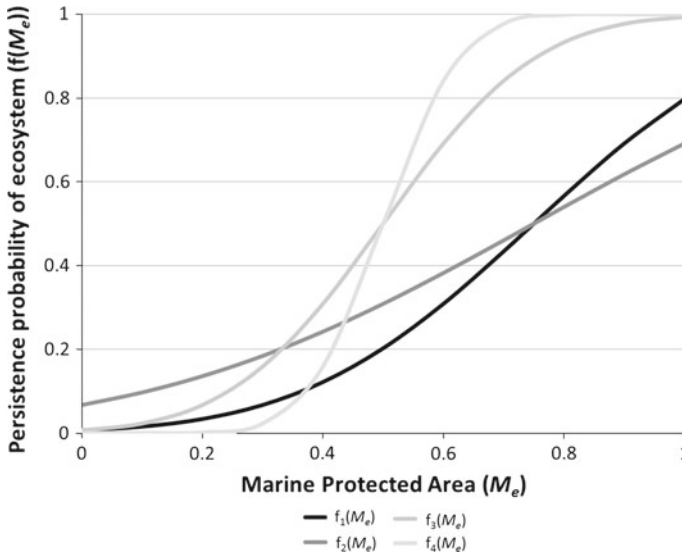


Fig. 2 Examples of possible persistence probability functions of the ecosystem ($f(M_e)$) as a function of MPA share. The used parameters are for $f_1(M_e)$: mean (μ) = 0.75, standard deviation (σ) = 0.3, for $f_2(M_e)$: $\mu = 0.75$, $\sigma = 0.5$, for $f_3(M_e)$: $\mu = 0.5$, $\sigma = 0.2$ and for $f_4(M_e)$: $\mu = 0.5$, $\sigma = 0.1$

The persistence probability function is assumed to be a cumulative normal distribution with a mean (μ) between zero and one, and a small standard deviation (σ) to keep the relation between the minimum and maximum survival probabilities, and MPA share between zero and one. Furthermore, it is assumed that the persistence probability function is equal across ecosystems. Examples of persistence probability functions for several parameter combinations are shown in Fig. 2. The first two functions f_1 and f_2 are examples of ecosystems where the keystone species or habitat respond directly to protection; their probability of survival goes up for every extra unit of protected area. Moreover, no minimum area is required for their survival. An example is plankton in the Antarctic Ocean. Function f_4 represents an example where a minimum area is required for protection, for example for more sedentary species such as mussel banks or coral reefs. Function f_3 represents an intermediate case, where the keystone habitats or species benefit from protection in general, but they benefit more quickly once a threshold is crossed. Furthermore, f_2 does not cross the origin which represents a case where the ecosystem has a positive persistence probability even without protection. While under f_3 and f_4 ecosystems can be fully secured, f_1 and f_2 represent cases where ecosystems can be lost even at the maximum size of the MPA.

4.2 The Economic Model

For the economic part of the model, we have to specify a benefit function and a cost function. For the direct benefits and the costs, we use the same functions as in the analytic example. As described in the previous section, the persistence probabilities in the biodiversity part now follow a cumulative normal distribution. We assume linear benefits

from the expected number of species. Hence, for full cooperation the value function becomes:

$$V(M_E) = \sum_{e \in E} d_e M_e + b \sum_{i \in S} \left(1 - \prod_{e \in N_i} \left(1 - \left(\frac{1}{2} \left(1 + \operatorname{erf} \left(\frac{M_e - \mu}{\sqrt{2\sigma^2}} \right) \right) \right) \right) \right) - \frac{1}{2} \sum_{e \in E} c_e M_e^2 \tag{16}$$

where erf is the error function used for calculations of the cumulative normal distribution, μ is the mean of the distribution, σ is its standard deviation, and b are the benefits of biodiversity. The equivalent formulation under strategic behavior is:

$$V_k(M_{E_k}) = \sum_{e \in E_k} d_e M_e - \frac{1}{2} \sum_{e \in E_k} c_e M_e^2 + \frac{1}{2} b \sum_{i \in S} \left(1 - \prod_{e \in N_i} \left(1 - \left(\frac{1}{2} \left(1 + \operatorname{erf} \left(\frac{M_e - \mu}{\sqrt{2\sigma^2}} \right) \right) \right) \right) \right), \quad \forall k \in \{1, 2\}. \tag{17}$$

In (17) some of the M_e are exogenous to the decision maker as they are controlled by the other country. For conservation autarky, the specification is:

$$V_k(M_{E_k}) = \sum_{e \in E_k} d_e M_e - \frac{1}{2} \sum_{e \in E_k} c_e M_e^2 + \frac{1}{2} b \sum_{i \in S_k} \left(1 - \prod_{e \in N_{ik}} \left(1 - \left(\frac{1}{2} \left(1 + \operatorname{erf} \left(\frac{M_e - \mu}{\sqrt{2\sigma^2}} \right) \right) \right) \right) \right), \quad \forall k \in \{1, 2\}. \tag{18}$$

4.3 Simulations

We simulate a coastline with ten ecosystems and two countries; each country has the jurisdiction over five ecosystems. Parameter values for the simulations are given in Table 5. Parameters were chosen arbitrarily such that interior solutions were produced in all cases. The effects of parameters are later explored in a sensitivity analysis. With these parameters we calculate a species distribution over the ten ecosystems that matches the patterns in exponential decay (see Appendix I). The resulting pattern is shown in Tables 6 and 7.

Next, we solve the economic model given this species distribution and other parameters, for full cooperation, strategic behavior and conservation autarky.

To overcome the non-convexities of this problem, we used a hybrid evolutionary algorithm for full cooperation and conservation autarky, and a hybrid co-evolutionary algorithm for the strategic equilibrium as described in Son and Baldick (2004). We used an adapted version of the continuous genetic algorithm described by Haupt and Haupt (2004).

The results for full cooperation, strategic behavior and conservation autarky are shown in Fig. 3. The ecosystems with the highest number of unique species (ecosystems 1 and 10) get the highest priority in protection. However, under strategic behavior, a smaller area is protected than under full cooperation. The differences between the two are not too large because of the S-shape of the persistence probability.

Table 5 Arbitrary parameter and set values of the simulation in the base case

Sets	Range on elements
E	Ecosystems 1–10
E_1	Ecosystems 1–5
E_2	Ecosystems 6–10
S	Species 1–255
S_1	Species 1–149
S_2	Species 33, 71, 78, 86, 97, 100–104, 118–255
Parameters	Values
Maximum number of species in ecosystem (S_e^{max})	50
X_o	1
r	0.9
δ	1 (per ecosystem)
μ	0.75
σ	0.3
d_e	2 (k€/ share protected)
b	0.2 (k€/expected species)
c_e	10 (k€/share protected)

Table 6 Initial distribution of species over ecosystems

Ecosystem	Species
1	(1–50)
2	(1–20), (51–80)
3	(21–28), (51–70), (81–102)
4	(29–31), (51–54), (71–74), (81–96), (103–125),
5	(32), (75–77), (81–85), (97–99), (103–117), (126–148)
6	(33), (78), (97), (100–101), (103), (118–124), (126–143), (149–167)
7	(71), (86), (104), (126–131), (144), (149–162), (168–193)
8	(102), (125), (145–147), (149–154), (163–164), (168–181), (194–216)
9	(125), (145), (163), (165–166), (168), (182–188), (194–209), (217–237)
10	(148), (167), (189–191), (194), (210–235), (238–255)

There are two main reasons for assigning smaller MPAs under strategic behavior: free-riding and location leakage. Free-riding can be generally observed in Fig. 3. All MPAs are smaller than under full cooperation when countries do not account for the benefits generated in the other country.

Location leakage is also visible in Fig. 3, but it mainly occurs near the border. Moreover it causes two strategic equilibria. In equilibrium 1, country 1 is the country that exploits the leakage, and in equilibrium 2, country 2 exploits the leakage, the result being a much smaller MPA in the exploiting country and a larger MPA in the exploited country.

From Fig. 3, we can see that most MPA shares under conservation autarky are comparable to those under strategic behavior, except for MPA shares in ecosystems at borders between

Table 7 Overlap in number of species between ecosystems

	1	2	3	4	5	6	7	8	9	10
1	50									
2	20	50								
3	8	20	50							
4	3	8	20	50						
5	1	3	8	20	50					
6	1	1	3	8	20	50				
7	1	1	1	3	8	20	50			
8	0	1	1	1	3	8	20	50		
9	0	0	1	1	1	3	8	20	50	
10	0	0	0	1	1	1	3	8	20	50

The matrix is symmetric and therefore only the lower half is shown

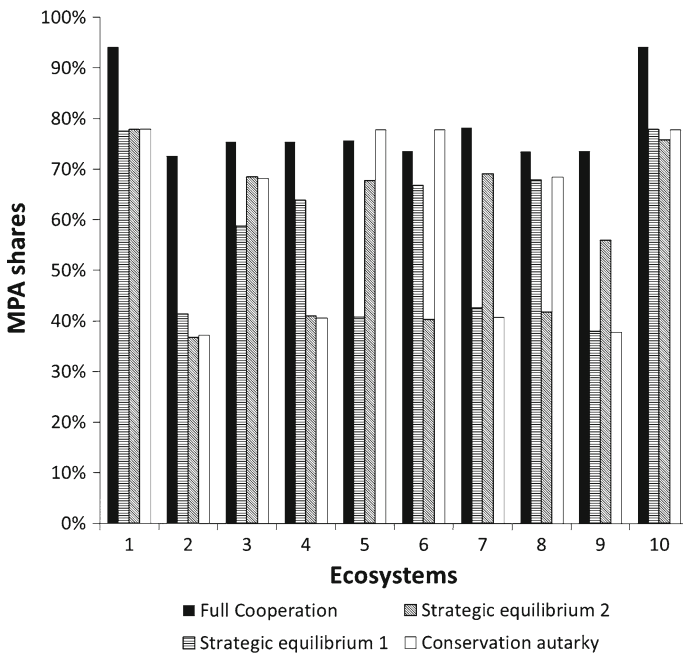


Fig. 3 MPA shares in ecosystems under full cooperation, strategic equilibrium (twice) and conservation autarky

countries. The similarity is due to the remaining free-riding problem. Ecosystems at the borders are more strongly protected because countries do not account for protection of species in other countries. This eliminates location leakage, and introduces an inefficiency from the perspective of full cooperation because the substitution of protection across countries is ignored.

Table 8 shows the total net benefits, and benefits to individual countries. It clearly illustrates the occurring inefficiencies with the associated equilibria. Total net benefits to the global society are highest under full cooperation, and lower under both the strategic equilibria and

Table 8 Net benefits to the global society and separate countries under full cooperation, strategic equilibria and conservation autarky

	Full cooperation	Strategic equilibrium 1	Strategic equilibrium 2	Conservation autarky
Total net benefits	24.58	20.32	20.39	21.45
Net benefits country 1	12.29	10.42	9.94	3.86 ^a
Net benefits country 2	12.29	9.90	10.45	3.87 ^a
Expected number of species	200.38	132.36	132.97	145.97

Total net benefits are calculated using (16) and the MPA shares from the solutions; expected no. of species is calculated assuming substitution. Net benefits to countries are calculated using (17) for full cooperation and strategic behavior, and (18) for conservation autarky. ^a Net benefits to countries for the conservation autarky scenario ignore substitution possibilities and cannot be compared to the net benefits in the other scenarios

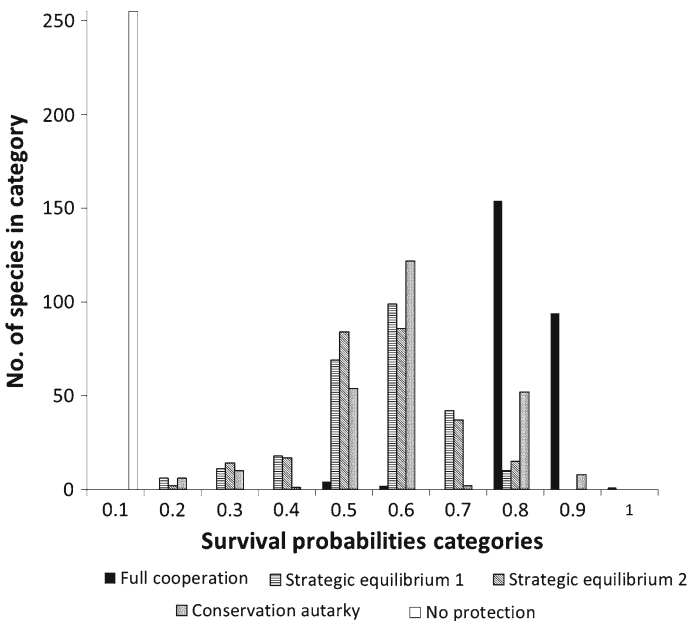


Fig. 4 Histogram of the number of species in survival probabilities categories of species under full cooperation, strategic equilibrium 1 and 2, conservation autarky, and when no protection is applied (i.e. no MPAs are assigned). The size of each category is 0.1

conservation autarky. The inefficiency under conservation autarky is smaller for our parameter values. In general, conservation autarky is probably preferred to strategic behavior.

These distinct differences are also found in the survival probabilities of individual species. In Fig. 4 we show histograms of survival probabilities of species under full cooperation, both strategic equilibria, conservation autarky and the original survival probabilities in the absence of MPAs (no protection).

Figure 4 shows that under full cooperation, the survival probability of most species is between 0.7 and 0.9. In both strategic equilibria, in contrast, the survival probability of the majority of species is between 0.4 and 0.7. Compared with full cooperation, species are protected less than necessary. Under conservation autarky, most species have survival

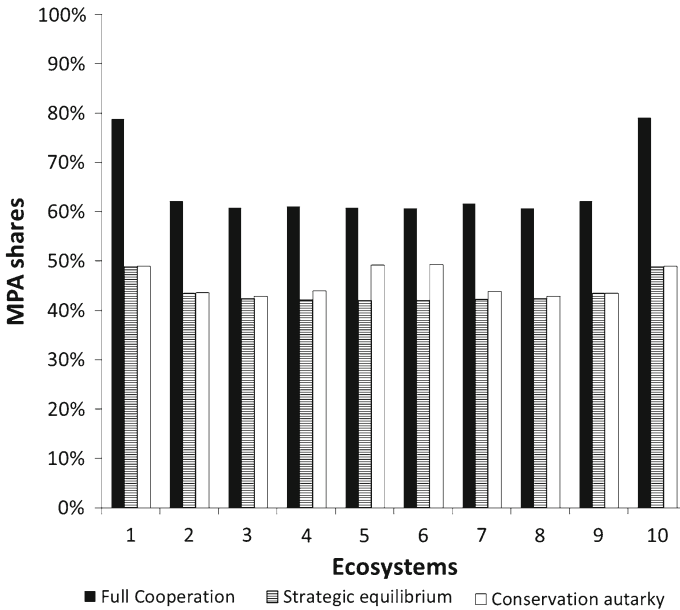


Fig. 5 MPA share under full cooperation, strategic equilibrium and conservation autarky when $\mu = 0.75$ and $\sigma = 0.5$

probabilities between 0.5 and 0.9. This is an improvement compared to both strategic equilibria, but it is still not as good as full cooperation. In the no protection case, all species have a very low (below 0.02) survival probability.

4.4 Sensitivity Analysis

Our sensitivity analysis is limited to the effect of the ecological parameters of the model, because the effects of economic parameters are in line with intuition. Their effects are explained in detail in Appendix II.

The ecological parameters describing the persistence probability mainly affect the conservation pattern in the ecosystems that contain common species. A low σ , indicating a very steep probability curve (cf. Fig. 2), induces a conservation pattern where conservation is concentrated in a few ecosystems with large MPAs and small MPAs in the neighboring ecosystems. A higher σ induces a more even spread pattern with overall smaller MPAs. The MPAs in ecosystems 1 and 10 are always larger than MPAs in other ecosystems, and in the conservation autarky case, ecosystem 5 and 6 also have large MPAs. This is clearly shown in Fig. 5, where we show full cooperation, strategic behavior and conservation autarky for $\mu = 0.75$ and $\sigma = 0.5$ Changing μ does not alter the pattern of MPA designation, but it mainly changes the level. Increasing μ raises MPA levels, and decreasing μ decreases them.

The decay rate r determines the overlap between ecosystems and hence the number of unique species in each ecosystem. An increase in r induces a smaller overlap between ecosystems and hence more unique species. Given that we fix the number of species per ecosystem, it also increases the total number of species needed to generate a species distribution over ecosystems, because each ecosystem now requires a higher number of unique species.

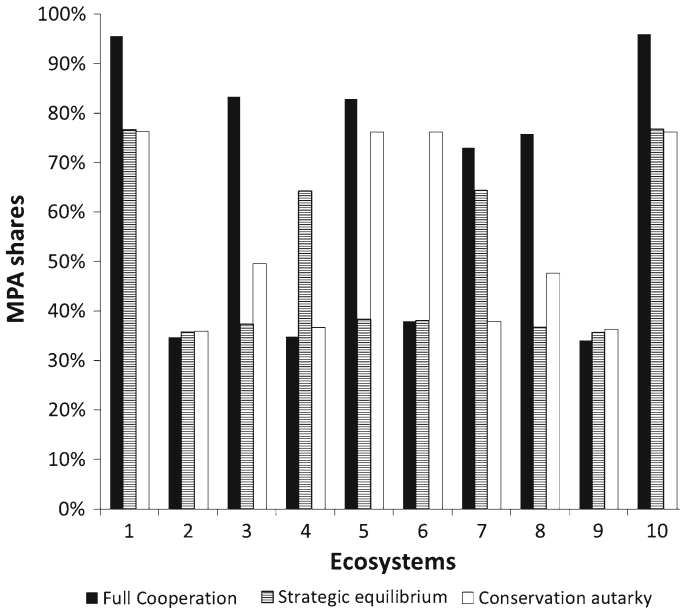


Fig. 6 MPA share under full cooperation, strategic equilibrium, and conservation autarky, when $r = 0.65$ and number of species = 200

A decrease in r lowers the MPA share for two reasons: firstly, fewer species exist, and secondly, fewer unique species exist. Figure 6 shows the MPA shares under the three scenarios with $r = 0.65$ and 200 species. The ecosystems with the (perceived) unique species are still almost fully protected, but other ecosystems have much smaller MPAs under these parameter values. Some ecosystems have become increasingly valuable, because the complete species distribution has changed and more unique species occur elsewhere. This also results in a different conservation pattern.

5 Discussion and Conclusions

In this paper we have presented a game theoretic model for the allocation of MPAs along a linear gradient, where ecosystems have overlapping species compositions. We have investigated the full cooperation case, and compared it with strategic behavior and conservation autarky. In both cases, compared to full cooperation, ecosystems and species are under-protected due to free-riding. However, while under strategic behavior, all ecosystems are generally under-protected, under conservation autarky, species at the border receive a higher level of protection. The fundamental difference between these two scenarios is whether or not countries consider species protection in another country a substitute for domestic protection.

Conservation autarky is generally inefficient because biodiversity conservation in one country can be a substitute for conservation in another country. However, in our analysis conservation autarky is less inefficient than strategic behavior. Ignoring a species existing elsewhere may actually be beneficial in a global perspective. Conservation autarky eliminates location leakage, and species are no longer under-protected at the borders, but rather over-protected compared to full cooperation. Free-riding, however, remains.

An important result from our simulations is that even when a country chooses to behave strategically, most unique species are still relatively well protected compared to common species. It can be observed from Figs. 3, 5 and 6 that the largest differences in MPA shares under strategic behavior compared to full cooperation, are found in ecosystems with species that occur in both countries. This finding makes sense from a valuation point of view: unique species are the most valuable and therefore most heavily protected. Location leakage cannot occur for these species precisely because they are unique. Common species, in contrast, can be protected elsewhere, and therefore countries under-protect these species and ecosystems, compared to full cooperation. Exceptions are those unique species occurring only in ecosystems next to heavily protected ecosystems. These species become less protected, because neighboring ecosystems are heavily protected. They suffer from “local location leakage” and are “forgotten unique species”.

In contrast to most of the reserve site selection literature on conservation across borders we focused on the marine domain. However, our model approach can also be used in a terrestrial setting, if the basic assumptions hold, most importantly if the effect of migration is small. The qualitative results of the model remain the same.

Also in contrast to the reserve site selection literature we have used a benefits approach rather than the Maximum Species Coverage Problem or the Minimum Set Cover Problem. If we had we used these methods, the difference between the three scenarios would probably be larger because these methods value species protection and costs only and ignore direct benefits. Using these approaches the game becomes a pure public goods game, rather than a partly public goods game as it is in our model.

A well-known question in ecology, related to the substitution effect, is whether we should select a Single Large Or Several Small (SLOSS problem) reserves. In our model, the answer to this question is shown to be dependent on the distribution of species over ecosystems and the persistence probability of ecosystems. If the persistence probability curve is the same in all ecosystems, species have a large range, and the persistence probability curve of ecosystems is sufficiently steep, then a single large reserve is better. This is because a large reserve is needed to reach a decent level of protection, and a lot of species can be protected in that single area. If many rare species exist and the curve is sufficiently flat, several small reserves are better because only small reserves are needed for a decent level of protection, and each added reserve adds extra protected species. These results, however hinge on the similarity of the persistence probability curve across ecosystems. A general answer to the SLOSS problem cannot be given.

In our study of international cooperation on MPA allocation at the ecosystem level we assume that all services and the distribution of the effects of the MPA are accounted for. As shown by Punt et al. (2010), accounting fully for all services is an important condition for the optimal allocation of MPAs because cooperating on a single issue, and ignoring another, can produce worse outcomes than behaving strategically and taking all effects into account.

We have shown how the distribution of species over ecosystems affects the assignment of MPAs in neighboring ecosystems through location leakage. Location leakage induces preferences to spread MPAs. This is similar to the analysis for terrestrial conservation as, for instance, in Albers et al. (2008).

Although we have shown how the location of MPAs across ecosystems matters, the distribution of MPAs within an ecosystem is also very important, especially if an ecosystem crosses the border between countries. In the latter case, the movement of species determines who bears the cost and who reaps the benefits (Ruijs and Janmaat 2007). We do not consider such movements in this paper, but conjecture that trans-boundary migration of species would increase free-riding and location leakage.

In our simulations most of the parameters are symmetric, except the distribution of species. This asymmetry is the reason that two strategic equilibria exist, showing different distributions for the gains. Asymmetry in other aspects than distribution of species would alter spatial conservation patterns, but our general conclusions remain.

This paper is the first to investigate the effect of strategic behavior in biodiversity conservation across marine ecosystems. We conclude that strategic behavior is an important, yet ignored effect in conservation planning. In the past, the emphasis may have been too much on conservation autarky, neglecting the dangers of free-riding and location leakage. As we have shown, conservation autarky may be preferable if it is compared with strategic behavior.

In the light of our analysis, international cooperation efforts on the protection of species should focus on three areas:

- Common species. Species that are known to occur in ecosystems on both sides of the borders will most likely be under-protected through location leakage.
- “Forgotten” unique species. Some unique species may suffer from local location leakage, i.e. their ecosystem is not well protected either because of location leakage or because neighboring ecosystems are well protected.
- Species that occur in ecosystems that have low direct benefits of protection (or high costs). These are likely to be under-protected if countries do not cooperate. Free-riding on indirect benefits will have a relatively large impact if direct benefits are small.

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Appendix I: Calculation of the Distribution of Species Over Ecosystems

Given a set of species and ecosystems, a universal decay rate, a matrix of distances between ecosystems and the maximum number of species in each ecosystem a distribution of species over ecosystems, $Distribution_{i,e}$, can be calculated with a simple mathematical model. Starting from a dummy objective:

$$DUM = \sum_{e \in E} \sum_{i \in S} Distribution_{i,e} \tag{19}$$

where DUM is a variable used for the maximization, and $Distribution$ is a binary matrix denoting species i 's presence (1) or absence (0) in ecosystem e , and is the actual variable of interest.

Each ecosystem e has a number of species, $|s_e|$, and this number is exogenously given. In the distribution we want all ecosystems to contain that number of species, therefore we require:

$$|s_e| = \sum_{i \in S} Distribution_{i,e} \quad \forall e \in E. \tag{20}$$

Consider the number of species common to two ecosystems. The similarity $Sim_{e,h}$ (in number of species) between two ecosystems $e, h \in E$, is calculated with the distance decay function as follows:

$$Sim_{e,h} = (X_o \exp^{-r\delta}) \min(S_e^{\max}, S_h^{\max}) \quad \forall e, h \in E, e \neq h \tag{21}$$

with X_0 the maximum similarity (usually one), r the decay rate, and δ the distance between ecosystem e and h . The minimization term adjusts the similarity for the number of species present in each area.

Given a distribution of species over ecosystems, *Distribution*, we can check whether this distribution matches the required similarity, $Sim_{e,h}$, by calculating the similarity implied by this distribution. This similarity $Overlap_{e,h}$ is calculated as follows:

$$Overlap_{e,h} = Distribution^T \times Distribution \tag{22}$$

with $Distribution^T$ denoting the transpose of the distribution matrix. Thus the full model becomes:

$$\begin{aligned} \max DUM &= \sum_{e \in E} \sum_{i \in S} Distribution_{i,e} \\ \text{s.t. } S_e^{\max} &= \sum_{i \in S} Distribution_{i,e} \quad \forall e \in E \\ Sim_{e,h} &= Overlap_{e,h} \quad \forall e, h \in E. \end{aligned} \tag{23}$$

Although the model sketched above is strictly speaking a Mixed Integer Non-Linear Problem, it can be approximated with a normal Non-Linear Problem (NLP) by letting *Distribution* be continuous over the interval [0,1]. Through rounding of $Sim_{e,h}$ to the nearest integer, and equalizing it with $Overlap_{e,h}$ we have constraints consisting of integers only, thus the solution of the NLP will coincide with the mixed integer variant. The solution to (23) is usually not unique as many configurations satisfy the constraints and the maximum value of the objective variable is the same for all those configurations.

Appendix II: Sensitivity Analysis of Economic Parameters

The parameters describing locations in terms of costs and benefits have opposite effects. Raising direct benefits of MPAs in a certain ecosystem increases the MPA share in that ecosystem and decreases the MPA in adjoining ecosystems for full cooperation, strategic behavior, and conservation autarky. In the case of conservation autarky however, the effect is limited to a country, as countries only consider their own species and ecosystems. Raising the costs in one location has the opposite effect. This can be seen from Fig. 7, where we doubled the costs in ecosystem 6. Compared with Fig. 3, the MPA is lower in ecosystem 6 and MPAs in neighboring ecosystems are larger, except under conservation autarky where cross-border effects do not exist. The effect of an increased cost of conservation is clearest in neighboring ecosystems, and decreases with distance. Ecosystems 1 and 10 for example, are hardly affected (cf. Fig. 3).

Incidentally, the introduction of the sharp asymmetry in costs also removes one of the strategic equilibria. Country 2 now always assigns a small MPA in ecosystem 6 because of the high costs. This decision in turn reduces the possibilities for location leakage.

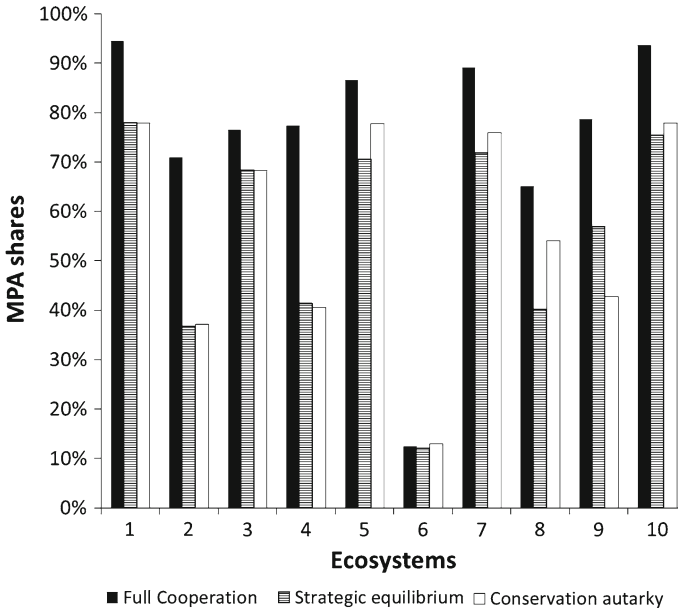


Fig. 7 MPA shares in ecosystems under full cooperation, strategic equilibrium and conservation autarky when the costs in ecosystem 6 are increased by 100 %

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