Bioeconomics and biodiversity in harvested metacommunities: a patch-occupancy approach

EMILY A. MOBERG,† JULIE B. KELLNER, AND MICHAEL G. NEUBERT

Biology Department, MS 34, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543 USA

Abstract.   We develop a coupled economic-metacommunity model to investigate the trade-off between diversity and profit for multispecies systems. The model keeps track of the presence or absence of species in habitat patches. With this approach, it becomes (relatively) simple to include more species than can typically be included in models that track species population density. We use this patch-occupancy framework to understand how profit and biodiversity are impacted by (1) community assembly, (2) pricing structures that value species equally or unequally, and (3) the implementation of marine reserves. We find that when local communities assemble slowly as a result of facilitative colonization, there are lower profits and optimal harvest rates, but the trade-off with diversity may be either large or small. The trade-off is diminished if later colonizing species are more highly valued than early colonizers. When the cost of harvesting is low, maximizing profits tends to sharply reduce biodiversity and maximizing diversity entails a large harvesting opportunity cost. In the models we analyze, marine reserves are never economically optimal for a profit-maximizing owner. However, management using marine reserves may provide low-cost biodiversity protection if the community is over-harvested.

Key words: ecosystem-based management; fisheries management; marine reserves; metacommunity; multispecies interactions.

† **E-mail:** emoberg@whoi.edu

INTRODUCTION

There is growing evidence that biologically diverse ecosystems provide services to society that are more valuable than the sum that would be provided by isolated individual species (Boehlert 1996, Worm et al. 2006); that is, biodiversity has real value (Halpern et al. 2012). It follows that natural and anthropogenic threats to biodiversity, including over-harvesting and habitat destruction, have real biodiversity costs (Halpern et al. 2008). As a result, and particularly in marine systems, interest has begun to move from the management of single species or populations, and toward 'ecosystem-based man-agement' in which the conservation of biodiversity is typically one of the explicit goals (Kellner et al. 2011).

Of course, the conservation of biodiversity will have costs. In harvested systems, maximizing biodiversity may come at the cost of reduced economic productivity or employment (Cheung and Sumaila 2008). In order for managers and policy makers to strike a reasoned balance between economic productivity and biodiversity conservation they must be able to estimate those costs, typically with the aid of mathematical models.

Although bioeconomic modeling studies have considered the management of several interact-

ing species (e.g., Finnoff and Tschirhart 2003, Fleming and Alexander 2003, Kellner et al. 2011), these are typically limited in the number of species that they consider. A model complex enough to capture all of the interactions both within and between its biological and economic components, for realistically large communities, is difficult to construct and often needs an prodigious amount of environmental, biological, and economic data in order to estimate its parameters (Fulton et al. 2011, Fogarty 2014). In most cases, such data is simply not available. In addition, ecosystem-based management is "place-based" (McLeod et al. 2005, Crowder and Norse 2008) and so requires models with a spatial component. Spatial management has become an ubiquitous part of the marine conservation toolbox (Neubert and Herrera 2008, Botsford et al. 2009, Rassweiler et al. 2012) and, in a variety of conditions, has been shown to improve management outcomes (e.g., Thrush et al. 1998, Sanchirico and Wilen 1999, Neubert 2003, Kellner et al. 2007, Neubert and Herrera 2008, Moeller and Neubert 2013). Marine reserves—spatial management in which some areas are closed to fishing—have garnered interest as a way to potentially increase biodiversity, population sizes, resilience of communities to perturbations (including climate change), and spillover of biomass into fishable areas.

How, then, could one include multiple species in a mathematically-tractable bioeconomic framework that is complex enough to address questions of spatial management? Here we present one possibility, and demonstrate how it could be used to understand the trade-offs (or synergies) between biodiversity conservation and economic productivity. Our approach has, at its foundation, a so-called patch-occupancy model (e.g., Levins and Culver 1971, Hastings 1980, Caswell and Cohen 1991, Leibold et al. 2004). Such models have been used to investigate how species-specific differences in dispersal and colonization ability affect local and regional diversity patterns (Levins and Culver 1971, Gouhier et al. 2011), as well as the role of disturbance in maintaining or eroding biodiversity (Nee and May 1992, Prakash and de Roos 2004).

Here we develop a patch-occupancy metacommunity framework in order to understand how profit and biodiversity are impacted by (1) the process of community assembly, (2) pricing structures that treat species harvest values either equally or unequally, and (3) the implementation of marine reserves.

In general, we are concerned with the trade-off between diversity and profit over a range of harvest rates and reserve fractions. The curves in Fig. 1 are intended to illustrate the different diversity and profit quantities discussed in the paper. Two quantities are useful for summarizing this trade-off: the change in diversity—the 'diversity gain'—and the change in profit—the 'foregone profit'—that accompany a change in harvest rate or reserve fraction relative to their profit maximizing levels (Fig. 1). These quantities are useful for comparing the trade-off under different management scenarios. If no reserves are implemented, the diversity gain and forgone profit result solely from a decrease in harvest rate (Fig. 1a). When reserves are added (as in Fig. 1b), the changes in diversity and profit can result from a combination of the effects of the reserve and harvest rate changes. With reserves, we also introduce the concept of 'protected diversity,' which is the increase in diversity at open access that results from implementing a reserve. The shape of these trade-off curves is determined by the biotic interactions within the community; the shape shown here was anticipated from biomass versus profit for single-species models and serves as a comparison for the shape we may obtain when plotting diversity versus profit. One objective of this study is to characterize and understand how biotic interactions influence the shape of these trade-off curves. Table 1 details the relevant quantities that we calculate in our two illustrative models.

Patch Occupancy Framework

Patch occupancy models have several advantages over alternative approaches. First, by using spatial models, we can incorporate ecologically important processes such as dispersal and habitat disturbance. Second, because they are spatially implicit, and only consider species' presence or absence (rather than population density), patch-occupancy models tend to be more amenable to analysis than their spatially explicit counterparts. Finally, coupling the patch-occupancy model with a simple economic model enables us to
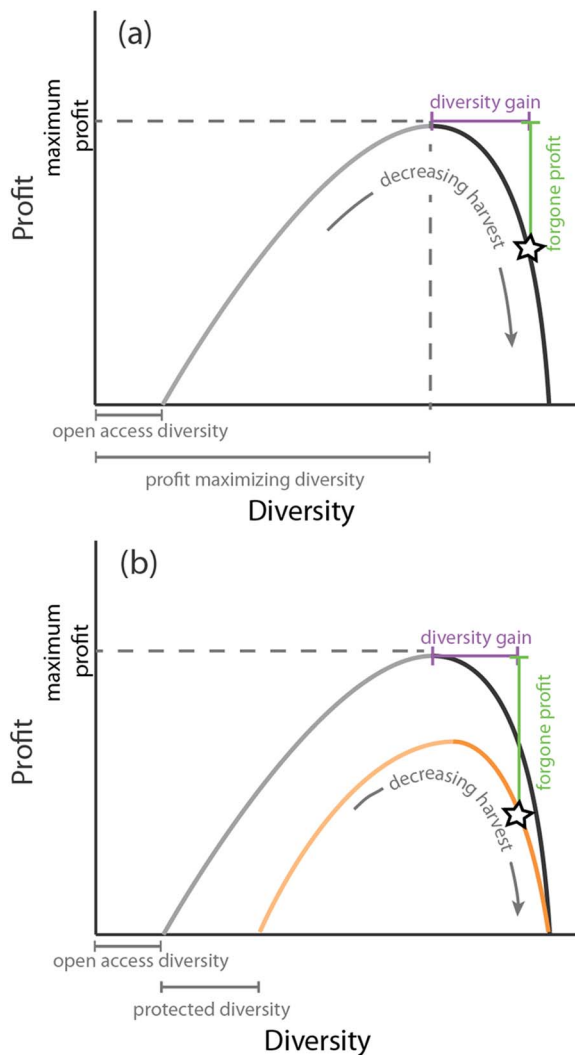
Fig. 1. Schematic of the quantities related to profit-diversity trade-offs with (a) effort regulation and (b) effort regulation plus marine reserves. In each panel, the grey and black curve represents the profit-diversity trade-off for a community with no marine reserve. The orange curve indicates this trade-off for a community where some habitat is protected by a marine reserve. The diversity gain (purple, horizontal bar) and forgone profit (green, vertical bar) are calculated for a particular harvest rate (star). They are measured relative to the diversity and profit at the profit maximizing harvest rate. Descriptions of 'open access diversity,' 'profit maximizing diversity,' and 'protected diversity' are provided in the text and Table 1. For each profit-diversity curve, the lighter portion of the curve indicates where profit and diversity can be simultaneously increased by harvesting less.

optimize profit or diversity and gain insights into the trade-offs between different management objectives.

The first step in formulating a patch occupancy model is to divide a site (e.g., a bay, reef, or fishing ground) into a set of patches. Each of these patches is described by its state, as defined by the identities of the species present. Patches can change state either because they are colonized by individuals of a new species dispersing from other patches or by losing species via local extinction. The dynamics of community assembly are determined by the rules governing the colonization process—in particular how the state of a patch determines which species may invade—and the rules governing species replacement (or coexistence) after a colonization event.

In the following sections, we construct two illustrative models that capture two extreme community assembly mechanisms. In the first, null model, we assume that the species do not interact and may colonize any habitable patch at which they are not already present. The simplicity of this model makes it a useful baseline against which to compare more complicated and realistic processes. Such models are commonly used in community assembly studies (e.g., Weiher and Keddy 1995, Neubert et al. 2006). In the facilitation model we assume that species may only colonize patches already inhabited by a facilitating species. This type of obligate facilitation operates, for example, when one species provides habitat for another (e.g., anemones and clownfish (Dunn 1981), which may be targeted for aquarium trade, or crabs in mussel beds (Silliman et al. 2011)); for other examples, see Bruno et al. (2003). In the facilitative model section below, we demonstrate the trade-offs that might be present in these communities. The facilitation model is simple and readily compared with a null model; in the discussion, we suggest possible model extensions to incorporate more complex community assembly dynamics.

In the framework we develop here, local extinction is the result of harvesting that can be regulated by a resource manager. Harvest causes extirpation of all species within a patch and renders the patch uninhabitable until the patch habitat recovers. Fishing frequently damages habitat (for example, through trawling) and has been shown to have strong effects on community

Table 1. Definitions and concepts.

Term	Units	Definition
Diversity (α)	no. spp.	average number of species in a patch at equilibrium
Profit (Π)	$ per time	revenue from selling fish minus harvest costs of fish at equilibrium
Profit (π)	$ per patch per time	revenue from selling fish minus harvest costs of fish at equilibrium, per patch
Diversity gain	no. spp.	change in diversity relative to that at profit maximizing harvest level
Forgone profit	$ per time	change in profit relative to maximum profit
Open access	no units	unregulated state in which profit is zero
Open access diversity	no. spp.	diversity at open access harvest level
Profit maximizing diversity	no. spp.	diversity at the profit maximizing harvest level
Protected diversity	no. spp.	difference between diversity at open access with and without a reserve

composition (e.g., Thrush et al. 1998, Thrush and Dayton 2002). In addition, previous studies that have incorporated destruction of habitat have found it to be an important driver of interspecies interactions (Caswell and Cohen 1991, Klausmeier 2001, Prakash and de Roos 2004) and optimal management (Moeller and Neubert 2013). Below we present a case in which harvesting is the only source of disturbance in the community; we discuss the implications of this assumption in the discussion.

The structure of this model, the simplicity of which we exploit to facilitate analysis over these broad ranges of ecological and economic parameters and relationships, comes in the form of strong assumptions. For instance, we assume that harvesters do not know the state of any particular patch—including one that they just harvested. Harvester avoidance of recently fished areas would increase the effective fishing pressure applied to other areas. The model is also spatially implicit, which means that the survival of relict populations in space, as can occur with cellular automaton models, cannot occur. Our study of equilibrium conditions also means that the study of systems that are perturbed or far from equilibrium are not accommodated. However, as detailed below, many of these assumptions make this framework suitably tractable to be coupled with a simple economic model in order to address the role of community assembly, pricing structure, and profit-diversity trade-offs under different types of management.

Null Model

In the null model, species do not interact and are identical in colonizing ability. Species may colonize any habitable patch at which they are not already present; the rate of colonization is independent of the presence or absence of other species. Some patches are also uninhabitable until they recover.

Imagine S species which are distributed among a large set of N patches. A simple way of defining the state of a particular habitable patch is to label it with a $1 \times S$ vector, ψ, composed of zeros and ones. The ith element of ψ, ψ_i, is one if species i is present and zero if it is absent. An uninhabitable patch is in state ϕ. We will keep track of the number of patches in these states with the variables X_ψ and X_ϕ. In general, there will be $2^S + 1$ state variables. Table 2 lists the variable and parameter names for reference.

It will be notationally convenient to define Ψ as the set of all possible ψ, and Ψ_i as the subset of Ψ whose members have ith element equal to one. Thus Ψ is the set of all possible habitable states and Ψ_i is the set of all states where species i is present (regardless of other inhabitants). It will also be useful to define the state where only species i is present as $\mathbf{e}_i$.

The state of an individual patch is changed when it is colonized, harvested, or recovers from harvest. Patches are harvested at rate h, causing the patch to become temporarily uninhabitable. These patches recover at rate r, becoming habitable, but empty. Thus, the number of uninhabitable patches changes at the rate

$$\frac{dX_\phi}{dt} = h\left(\sum_{\psi \in \Psi} X_\psi\right) - rX_\phi. \qquad (1)$$

Next, let us consider the rate of change of the number of habitable patches that are in state ψ. These patches change state when they are

Table 2. Null model parameters and variables.

Term	Units	Definition
r	time^{-1}	rate of recovery for uninhabitable patches to become habitable
c	time^{-1}	rate of propagule production from a single patch
w	\$ patch^{-1}	cost of effort
ε	...	efficiency of harvest
N	no.	number of patches in the community
S	no. spp.	number of species in the community
h	time^{-1}	rate of harvest; this renders the harvested patch uninhabitable
X_ϕ	no. patches	number of uninhabitable patches
X_ψ	no. patches	number of patches in state ψ
x_ϕ	...	proportion of patches in the uninhabitable state
y_i	...	proportion of patches with species i (regardless of other inhabitants)
x_f	...	proportion of patches in reserve, with all S species present

Note: An ellipsis indicates a unitless quantity.

colonized or harvested. In a given patch, colonization by species i occurs only when species i is absent; i.e., when $\psi_i = 0$. Propagules of species i are produced in state Ψ_i patches. There are $\sum_{\eta \in \Psi_i} X_\eta$ such patches. Because all species are identical in this null model, these propagules are generated at constant per-patch rates, c. Each of these propagules lands on a patch in state ψ with probability X_ψ/N. We now sum over all species to obtain the rate of colonization of patches in state ψ as

$$\sum_{i=1}^{S} \left((1 - \psi_i) \frac{X_\psi}{N} c \sum_{\eta \in \Psi_i} X_\eta \right). \quad (2)$$

New state-ψ patches are created by the colonization of patches that, by the addition of a single species, become a state-ψ patch. Let us focus on one such patch that is missing species i; it is in state $\psi - \mathbf{e}_i$. At any time, there are $c \sum_{\eta \in \Psi_i} X_\eta$ propagules of species i being produced to colonize our focal patch. Only a fraction of these propagules, $1/N$, will land on it to possibly recruit. Summing over all species that are eligible to colonize patches in state $\psi - \mathbf{e}_i$ (those with $\psi_i = 1$) gives us the total rate of addition of new state-ψ patches

$$\sum_{i=1}^{S} \left(\psi_i \frac{X_{\psi - e_i}}{N} c \sum_{\eta \in \Psi_i} X_\eta \right). \quad (3)$$

Combining the effects of harvest and colonization, we obtain

$$\frac{dX_0}{dt} = rX_\phi - \sum_{i=1}^{S} \left(\frac{X_0}{N} c \sum_{\eta \in \Psi_i} X_\eta \right) - hX_0 \quad (4)$$

and

$$\frac{dX_\psi}{dt} = -\sum_{i=1}^{S} \left((1 - \psi_i) \frac{X_\psi}{N} c \sum_{\eta \in \Psi_i} X_\eta \right)$$
$$+ \sum_{i=1}^{S} \left(\psi_i \frac{X_{\psi - e_i}}{N} c \sum_{\eta \in \Psi_i} X_\eta \right) - hX_\psi \quad (5)$$

for $\Psi \neq 0$. By defining

$$x_\phi = X_\phi/N, \text{ and } x_\psi = X_\psi/N \quad (6)$$

(so that x_ϕ and x_ψ track the fraction of patches in these states) and rearranging we further simplify the null model to

$$\frac{dx_\phi}{dt} = h \left(\sum_{\psi \in \Psi} x_\psi \right) - rx_\phi \quad (7)$$

$$\frac{dx_0}{dt} = rx_\phi - \sum_{i=1}^{S} \left(x_0 c \sum_{\eta \in \Psi_i} x_\eta \right) - hx_0 \quad (8)$$

$$\frac{dx_\psi}{dt} = c \left(\sum_{i=1}^{S} \sum_{\eta \in \Psi_i} x_\eta [\psi_i x_{\psi - e_i} - (1 - \psi_i) x_\psi] \right) - hx_\psi. \quad (9)$$

Eqs. 7–9 comprise the biological and harvesting component of our null model. A simple example of this model, with only two species, is illustrated in Fig. 2; we show the corresponding equations, for the reader's entertainment, in Appendix A.

A manager of such a multispecies fishery might choose h to maximize profit. The profit depends on the cost of harvesting, the price for the harvested fish, and the intra-and interspecific interactions that determine the dynamics of the metacommunity. In the section 'Null model: diversity and profit,' we focus on a manager who wants to understand the potential trade-off between long-term, sustainable profit (i.e, the profit at equilibrium) and biodiversity. Before this, we explore how the equilibrium configuration of the metacommunity depends upon the control variable h, which we will take to be a constant. This allows us to formulate relatively simple static optimization problems and facilitates
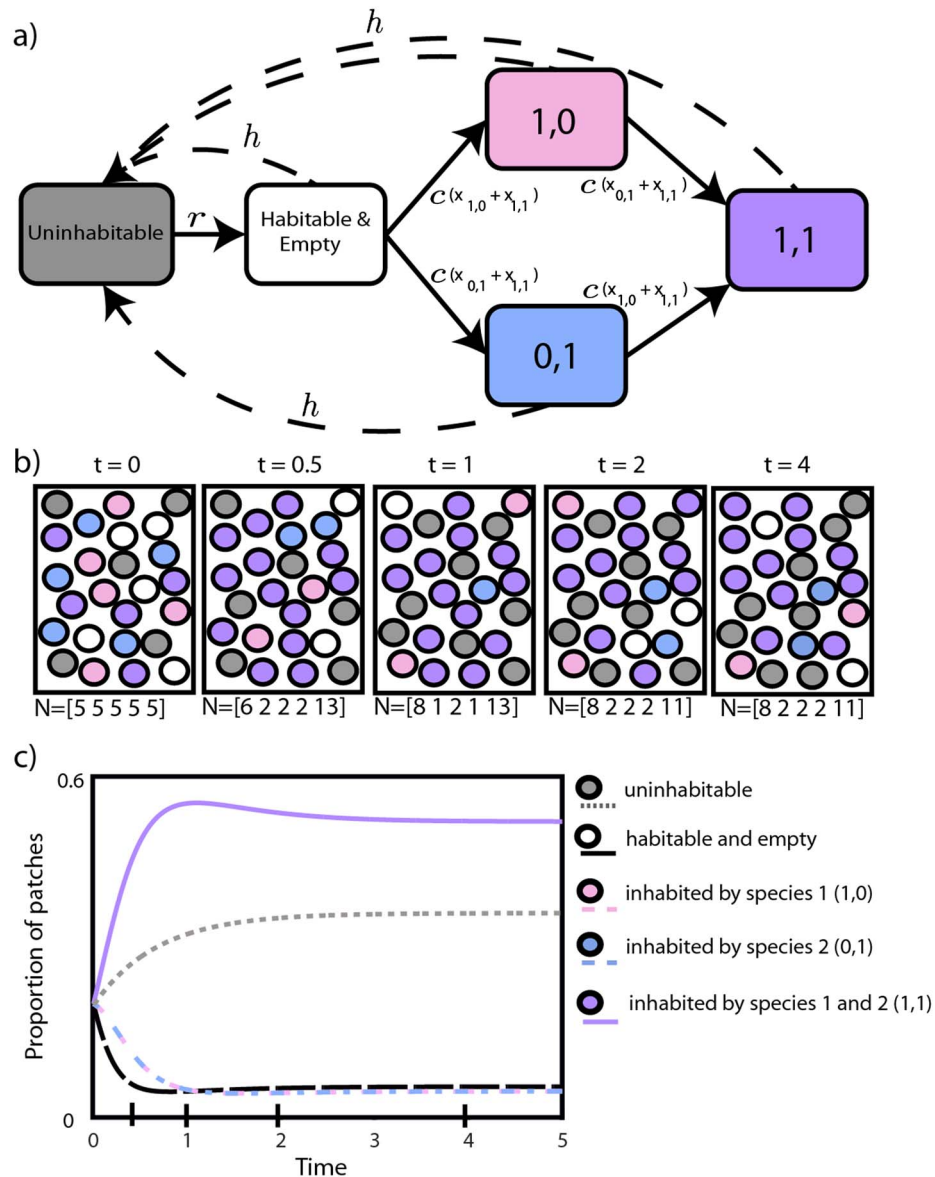
Fig. 2. (a) Schematic of null model states (boxes) and transitions (arrows; solid lines are colonization, dashed lines are harvest, labels are rates) for a community with 2 species. The model equations are described in Appendix A. Uninhabitable patches (gray box) can recover to become habitable (white boxes) at rate r. These empty patches can then be colonized by either species 1 or 2 (pink and blue boxes) at a rate proportional to the number of patches producing propagules and the number of patches being colonized. Finally, these patches may transition to a patch with both species (purple box). All patches may become uninhabitable through harvest. (b) Schematic of how the transitions in (a) manifest for many patches. The circles represent patches in various states using the same color scheme as in (a). Each panel corresponds roughly to the time steps marked in (c). Note that in the last two time steps, an equilibrium has been reached where the overall number of patches in each state is the same, but the state of individual patches may have changed. (c) Plot showing the simulations of the system of equations from Appendix A through time. While the proportion of patch states was initialized with an even distribution, the proportions differ once the equilibrium has been reached.

identification of profit-diversity trade-offs. An alternative approach, and an ambitious next step, might include the consideration of the dynamic control of harvest in time and the stability of solutions to imperfect control; the importance of such analyses in understanding fisheries collapse is illustrated for a single species by Roughgarden and Smith (1996).

Null model: equilibria

The dynamics of our null model are dominated by equilibria. While the state of any particular patch will continue to change as it is harvested, recovers, and is colonized, the proportion of patches in those states converges to a set fraction determined by the parameter values. Thus, at any time the patches are in a mosaic with some patches containing all species, some uninhabitable, et cetera. As long as all S species are initially present in the community, the fraction of patches in the uninhabitable state will converge to the equilibrium value x_ϕ^*, and the fraction of patches in the various habitable states will converge to x_ψ^*. An easy way to calculate the equilibria is to introduce the new variable $y_i = \sum_{\eta \in \Psi_i} x_\eta$ which gives the fraction of all patches that contain species i. The dynamics of y_i are given by

$$\frac{dx_\phi}{dt} = h(1 - x_\phi) - rx_\phi, \qquad (10)$$

$$\frac{dy_i}{dt} = cy_i(1 - x_\phi - y_i) - hy_i, \text{ for } 1 \leq i \leq S. \quad (11)$$

We can solve for the proportions of patches in these states at equilibrium as

$$x_\phi^* = \frac{h}{r + h} \qquad (12)$$

and

$$y_i^* = y^* = \frac{r}{r + h} - \frac{h}{c}. \qquad (13)$$

All S species persist as long as the harvest rate satisfies $c \geq h(r + h)/r$. At higher harvest levels, all species are extirpated and $y^* = 0$. We show that this solution is stable in Appendix B.

To calculate x_ψ^*, we take advantage of the symmetry among species' equilibrium values and use the binomial formula. Specifically,

$$x_\psi^* = \left(\frac{y^*}{1 - x_\phi^*}\right)^k \left(1 - \frac{y^*}{1 - x_\phi^*}\right)^{(S-k)} (1 - x_\phi^*) \quad (14)$$

where k is the number of species present in state ψ (i.e., the sum of the elements of ψ). The proportion of patches with exactly i species, z_i, is

$$z_i = \frac{S!}{i!(S-i)!} \left(\frac{y^*}{1 - x_\phi^*}\right)^i \left(1 - \frac{y^*}{1 - x_\phi^*}\right)^{(S-i)} (1 - x_\phi^*).$$
$$(15)$$

At low harvest rates, most patches have all species, although there are some patches in every state (Appendix D: Fig. D1). At sufficiently high harvest levels, when $c < h(r + h)/r$, all species are extirpated from the system.

Null model: diversity and profit

We use the equilibrium values (Eqs. 14–15) to calculate diversity and profit. We focus on α diversity, or the expected number of species at a patch

$$\alpha = \sum_i iz_i = Sy^*. \qquad (16)$$

For the null model, Eqs. 10–11, α diversity declines monotonically with harvest rate in all cases (Fig. 3a). Higher colonization rates or recovery rates increase the diversity at a particular harvest level. When the diversity curve intersects the h-axis, all species are extirpated.

To calculate profit, we need to specify the monetary value of the harvest from a patch in each state. Because species are identical and do not interact, each contributes the same amount of biomass and value to a patch. Without loss of generality then, we set the value of the harvest from a patch equal to the number of species that are present. Any unoccupied (or uninhabitable) patch is worth 0. We call the price of a patch with i species present p_i; for the null model, $p_i = i$.

There is also a cost to harvest. We will assume the per patch harvest cost is w. The revenue gained from all inhabited patches, which are harvested with efficiency ε, minus the effort costs is the equilibrium profit, Π

$$\Pi = \varepsilon Nh\left(\sum_i z_i p_i\right) - whN. \qquad (17)$$
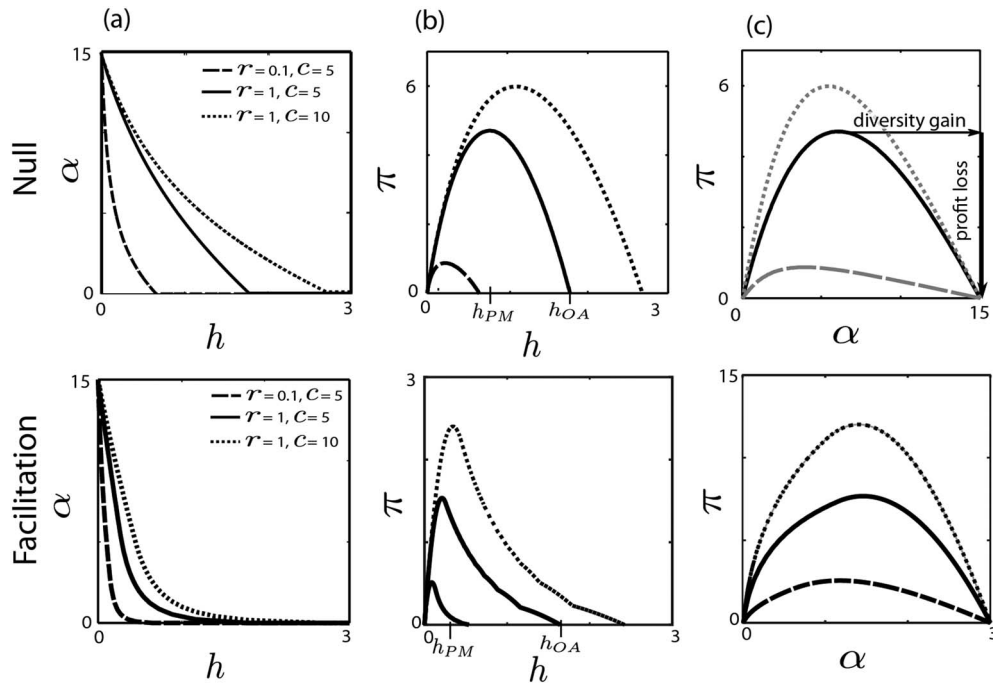
The per patch profit rate $\pi = \Pi/N$ gives the

Fig. 3. For the null model (top row; Eqs. 10 and 11) and facilitation model (bottom row; Eqs. 25–28), α diversity (a) and profit (b) depend upon the harvest rate. Together these determine the trade-off between profit and diversity at equilibrium (c). For the parameter values $r = 1$ and $c = 5$ (solid curve), the profit maximizing harvest rate is marked h_{PM} and the open access harvest rate is marked h_{OA}. The diversity gain (relative to profit maximizing harvest level) and profit loss (when diversity is maximized) are labelled in (c). For all panels, $S = 15$, $w = 0.5$, and $\varepsilon = 1$.

average profit obtained from harvest of an individual patch and is obtained by dividing Eq. 17 by N.

A manager who can regulate the harvest level is able to maximize the profit rate. Without such oversight, we will assume the system is at open-access, i.e., profits are driven to zero (Clark 1973). Profit is maximized at an intermediate harvest level, h_{PM}. The open access harvest level, h_{OA}, is higher (Fig. 3b).

We can now compare the diversity and profit at different harvest levels or among fisheries with different biological or economic parameters (Fig. 3c). α diversity is maximized when $h = 0$, thus $\pi = 0$ as well. We focus on the maximal diversity gain (recall Fig. 1)—the increase in diversity from the profit maximizing harvest rate relative to the diversity at no harvest. The monetary cost of maximizing diversity is the difference in profit at h_{PM} and at the diversity maximizing level. In the null model, $h = 0$ maximizes diversity, so the

'profit loss' or cost to maximize diversity is equivalent to the maximal profit.

As can be seen in Fig. 4, if propagule production rates, c, are high relative to the recovery rate, both the profit lost (a) and the diversity gained (b) by maximizing diversity are more sensitive to variation in harvest costs, w, than propagule production rates. Higher propagule production rates and lower effort costs (northwest in both plots) boost the maximum profit attainable in a given community, which incentivizes a heavy harvest and thus reduces diversity.

However, the trade-off is not always large. Both low costs or high propagule production rates can make a community profitable to harvest; however, they do not impact the trade-off between diversity and profit in identical ways. For example, when propagule production rates are low, the profit loss is very low, whereas the diversity gain may still be large. When
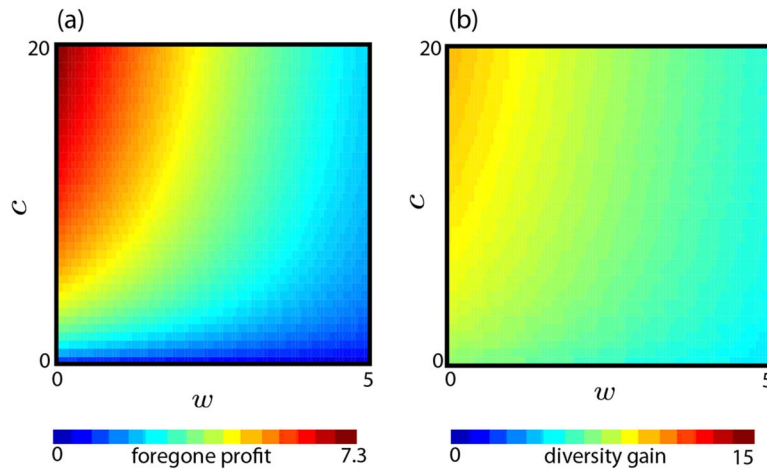
Fig. 4. (a) Potential profit lost from harvesting at the diversity maximizing level ($h = 0$); i.e., the maximum profit. For a particular combination of harvest cost (w) and propagule production rate (c), this value is represented by the vertical profit-loss arrow in Fig. 3c. (b) Diversity gain at no harvest relative to harvesting at the profit maximizing level ($h = h_{PM}$). For a particular w and c combination, this value is represented by the horizontal diversity gain arrow in Fig. 3c. For both panels, $S = 15$, $r = 1$ and $\varepsilon = 1$.

propagule production rates are low, a small increase in harvest rate increases the proportion of empty patches dramatically. As a result, even the small profit-maximizing harvest levels can cause large diversity losses. A community with low propagule production rates and high harvest costs will still face high diversity losses when harvesting occurs, but the high harvest cost reduces optimal harvest rates, so this potential diversity loss is not realized. However, it is important to note that these results are for a profit-maximizer; the costs associated with managing an open-access fishery may be very different.

Null model: spatial management

To investigate the cost of conserving diversity using marine reserves we modify our models to keep track of the proportion of patches that cannot be harvested. Since harvest is the only source of disturbance, we will assume that protected patches harbor all species. These reserves have the potential to provide the maximum benefit to biodiversity. Let us call the fixed fraction of patches that are set aside as protected reserves x_f . The dynamics are governed by the following systems of equations, which modify Eqs. 10 and 11:

$$\frac{dx_\phi}{dt} = h(1 - x_\phi - x_f) - rx_\phi \tag{18}$$

$$\frac{dy_i}{dt} = c(y_i + x_f)(1 - x_\phi - y_i - x_f) - hy_i. \tag{19}$$

The equilibria are then

$$x_\phi^* = \frac{h(1 - x_f)}{r + h} \tag{20}$$

$$y_i^* = y^*$$
$$= \frac{-h + A - cx_f + \sqrt{(h - A + cx_f)^2 + 4cx_f A}}{2c} \tag{21}$$

where $A = c(1 - x_\phi^* - x_f)$. This is the equilibrium as long as y^* is positive (otherwise $y_i^* = 0$).

We calculate α diversity and profit, which are now

$$\alpha = S(y_i^* + x_f) \tag{22}$$

$$\pi = \varepsilon h\left(\sum z_i p_i\right) - wh \tag{23}$$

where z_i is modified from Eq. 15 as

$$z_i = \frac{S!}{i!(S - i)!}\left(\frac{y^*}{1 - x_\phi^* - x_f}\right)^i\left(1 - \frac{y^*}{1 - x_\phi^* - x_f}\right)^{(S-i)}$$
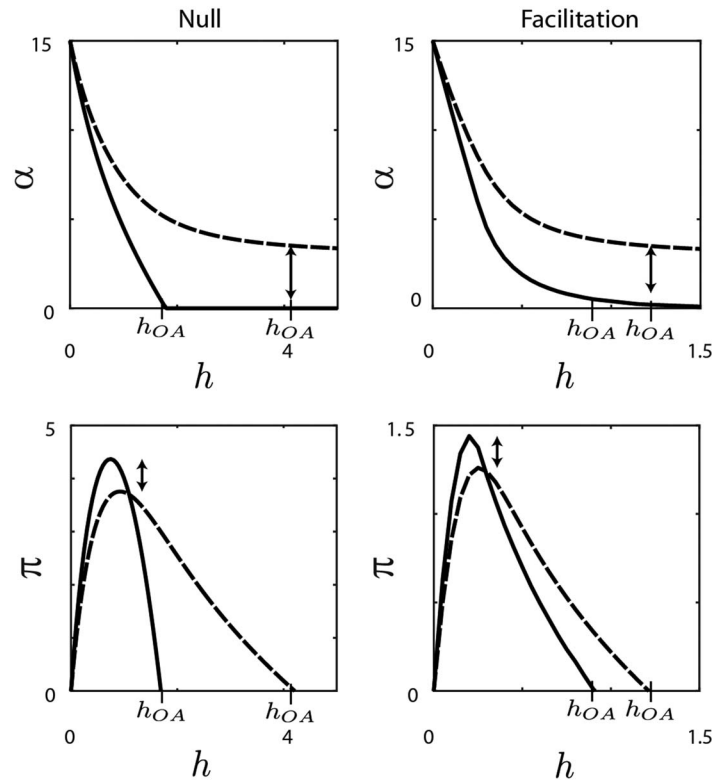$$\times (1 - x_\phi^* - x_f). \tag{24}$$

Fig. 5. Fifteen-species versions of the null model (left panels, Eqs. 18–19) and facilitation model (right panels, Eqs. 25–28) with parameter values $c = 5$, $r = 1$, $\varepsilon = 1$, and $w = 0.5$. The black, dashed line indicates a community with 20% in reserve and the solid line indicates a community with no reserves. (top) α diversity as a function of harvest rate. The open access harvest rates are marked. The vertical arrow shows the 'protected diversity', which is the difference between the diversity at open access with no reserves and at open access with a reserve. (bottom) Profit as a function of harvest rate. The vertical arrow shows the difference in maximal profit rate without and with a reserve.

We use these to compare the trade-off between diversity and profit (Fig. 5, left column).

At a particular harvest level, α diversity is always higher when reserves are present, as a set of patches with all species present is preserved. The maximum profit attainable is, however, lower if reserves are implemented (Fig. 5). Hart (2006) found a similar pattern in a single-species model, maximizing yield. The harvest rate that maximizes profit and the harvest rate at open access both increase. Consistent with this finding, Halpern et al. (2004) showed that concentrated effort outside reserves could not produce comparable harvest to a community without reserves, unless there is a compensatory increase to the production rate.

In addition to increased diversity at all harvest rates, reserves provide an additional benefit: a diversity buffer. Whatever the harvest rate, diversity cannot fall below a lower limit (equal to $x_f S$). Even when the community is harvested at extreme (open-access) harvest levels, some diversity is preserved. We define 'protected diversity' as the difference in diversity in the community at open-access when no reserve is present and when it is. At very high harvest rates, the diversity gain is almost entirely due to the diversity of patches in the reserve state; outside the reserves, most patches will be in uninhabitable states.

We can calculate the forgone profit necessary to achieve different combinations of the two types of diversity: protected diversity and the realized diversity gain. In Fig. 6, we show that
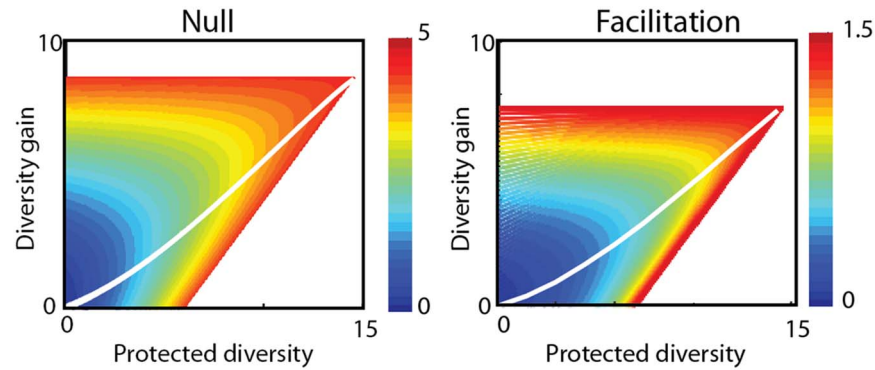
Fig. 6. The cost, in forgone profit, necessary to achieve different levels of protected diversity and diversity gain for a 15-species version of the null model (Eqs. 18 and 19) and facilitation model (Eqs. 25–28) with parameter values $c = 5$, $r = 1$, $w = 0.5$ and $\varepsilon = 1$. Since α diversity is positive at $h = h_{\mathrm{PM}}$, the diversity gain does not extend to $S = 15$. The white line shows the profit-maximizing diversity gain for each level of protected diversity. Points below this line are sub-optimal in both diversity and profit.

the cost of adding relatively large amounts of protected diversity is consistently low (i.e., the iso-cost curves are approximately flat over large ranges of protected diversity). The white line shows the diversity at the profit-maximizing harvest rate for a given amount of protected diversity. Above the white line, one can often gain protected diversity without sacrificing much profit by increasing the reserve fraction. Below the white line, for a fixed protected diversity, one can always increase the diversity gain and profit by decreasing the harvest rate. Overall, while increasing the diversity in a community (relative to the profit maximizing level) has a cost, the cost of using marine reserves to do so—which provides a degree of guaranteed diversity even if over-harvested—is relatively cheap. These patterns are consistent for other parameter values.

FACILITATION MODEL

Real communities are more complicated than our null model: species interact, have different life-history traits, and are differentially valuable when harvested. In this section we present a model in which interspecies interactions are strong, as a contrast to the null model.

As in the null model, species accumulate in a patch as they colonize, but in this "facilitation" model, species colonize in sequential order, (i.e., species 2 cannot colonize unless species 1 is present, and species 3 cannot colonize without species 2, etc.). Once a species has colonized, it does not displace the previous inhabitants, so a patch with species 5 necessarily will contain species 1 through 4 as well. Uninhabitable patches, which are created by harvest, must recover from this disturbance before they can be colonized by the first species.

Because of this strong facilitative interaction, the number of states is tremendously reduced compared to the null model with the same number of species. One can now specify the state of a patch with a scalar quantity indicating the number of species in a patch. We call the proportion of patches in state i, x_i. As before, we write a system of differential equations to track how colonization, harvest, and recovery change the proportion of patches in these states. (For parameters and variables, see Table 3.)

We again imagine N patches inhabited by S species. x_ϕ indicates the fraction of patches that are uninhabitable. These are created through harvest (at rate h) and recover at rate r:

$$\frac{dx_\phi}{dt} = h\left(\sum_{i=0}^{n} x_i\right) - rx_\phi. \qquad (25)$$

Let us focus on patches in state i. The proportion of such patches changes when propagules from species i colonize state $i - 1$ patches, propagules from species $i + 1$ colonize state i patches, or state i patches are harvested and

Table 3. Facilitation model parameters and variables.

Term	Units	Definition
r	time^{-1}	rate of recovery for uninhabitable patches to become habitable
c	time^{-1}	rate of propagule production from a single patch
w	\$ patch^{-1}	cost of effort
ε	...	efficiency of harvest
N	no.	number of patches in the community
S	no. spp.	number of species in the community
h	time^{-1}	rate of harvest; this renders the harvested patch uninhabitable
x_ϕ	...	proportion of patches in the uninhabitable state
x_i	...	proportion of patches with species 1 through i
x_f	...	proportion of patches in reserve, with all S species present
ρ_j	\$	the value of species j
κ	...	constant that relates the value of patches in state $j-1$ to those in state j

Note: An ellipsis indicates a unitless quantity.

rendered uninhabitable. Colonization by species i occurs via propagules which are produced at a per patch rate of c_i. Combining these, we obtain (cf. Fig. 7)

$$\frac{dx_0}{dt} = rx_\phi - c_1 x_0 \left(\sum_{i=1}^{S} x_i \right) - hx_0, \tag{26}$$

$$\frac{dx_i}{dt} = -c_{i+1}x_i \left(\sum_{j=i+1}^{S} x_j \right) + c_i x_{i-1} \left(\sum_{j=i}^{S} x_j \right) - hx_i, \tag{27}$$

$$\frac{dx_S}{dt} = c_S x_S x_{S-1} - hx_S. \tag{28}$$

Facilitation model: equilibria

As in the null model, while individual patches continue to change state, the proportions of patches in different states equilibrate. These equilibria are straightforward to calculate for arbitrary parameter values (Appendix C). Here we focus on the case when the propagule production rate is equal among species (i.e., $c_i = c$ for all i). We illustrate this case for comparison with the null model.

For the model given by Eqs. 25–28, the number of species that can persist is given by

$$S^* = \min\left(S, \left\lfloor \frac{cr}{h(r+h)} \right\rfloor \right) \tag{29}$$

where $\lfloor \; \rfloor$ indicates the floor function.

If the harvest rate is high relative to the propagule production and recovery rates, all S species cannot coexist in the community at equilibrium. Thus, species 1 through S^* occupy positive proportions of the habitat, while species above S^* are absent. The stable solution when S^* is positive (Appendix C) is

$$x_\phi^* = \frac{h}{r+h}, \tag{30}$$

$$x_i^* = \frac{h}{c}, \text{ for } i = 0, \dots, S^* - 1, \tag{31}$$

$$x_{S^*}^* = \frac{r}{r+h} - \frac{S^* h}{c}, \quad \text{and} \tag{32}$$

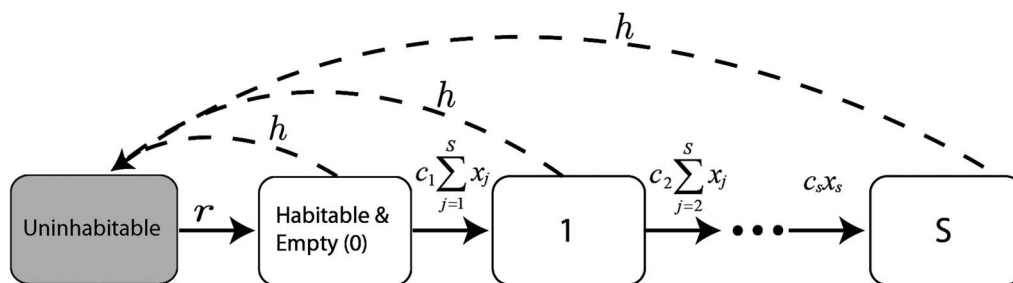$$x_j^* = 0, \text{ for } j > S^*. \tag{33}$$

Fig. 7. Schematic of facilitation model (Eqs. 25–28) states (boxes), transitions (arrows), and rates (arrow labels). As in the null model, patches can transition from being uninhabitable to habitable and empty at rate r, but subsequent colonization can only be initiated by species 1. Those patches may then be colonized by species 2, etc. at rates that are proportional to the propagule production rate c, the number of patches able to be colonized, and the number of patches producing colonizing propagules. All patches may be harvested at rate h.

The proportion of patches in the uninhabitable state is the same as in the null model. In the null model, all species are extirpated when $h(r + h)/r > c$. In contrast, in the facilitation model, species are sequentially extirpated from the community as harvest rate increases from zero, with the late colonizers being the most vulnerable to overfishing (Appendix D: Fig. D2). The earliest colonizer (species 1), which is the most resilient in the face of harvesting, is eliminated at the same harvest rate that would eliminate all species in the null model.

Facilitation model: diversity and profit

Using Eqs. 30–33, we can calculate equilibrium diversity and profit. The expected number of species in a patch, or α diversity is

$$\alpha = \sum_{i=1}^{S} i x_i, \tag{34}$$

$$= \left(\frac{r}{r+h} - \frac{h(S^* + 1)}{2c} \right) S^*, \tag{35}$$

since a patch in state i has i species present and $c_i = c$.

Diversity declines monotonically with harvest in the facilitation model, but more precipitously at low harvest levels than in the null model (Fig. 3a). Diversity vanishes (i.e., all species are extirpated) at the same harvest rate for both types of communities.

In the facilitation model, species are not identical. It is reasonable then to allow different species to have different economic value. Let ρ_j be the value of species j. A simple model for species values is the geometric series:

$$\rho_j = \rho_1 \kappa^{j-1}. \tag{36}$$

If the constant κ is less than 1, early colonizing species are worth more than later colonizers; $\kappa > 1$ indicates the opposite. We use $\rho_1 = 1$, and $\kappa = 0.9$, 1, and 1.1 to explore different value relationships.

The value of a patch in state i is then

$$p_i = \sum_{j=1}^{i} \rho_j, \tag{37}$$

and the total harvest value is

$$\pi = h \left[\left(\varepsilon \sum_{i=1}^{S} x_i p_i \right) - w \right]. \tag{38}$$

As in the null model, profit is maximized at an intermediate harvest rate (Appendix D: Fig. D3). At open-access, profit is zero and the harvest rate is higher. As might be expected, profits are larger, and profit-maximizing harvest rates are smaller, if later colonizing species are more valuable relative to early colonizers (i.e., for larger κ). Profit is maximized at lower harvest rates than in the null model (compare Appendix D: Fig. D3 with Fig. 3b). At sufficiently high harvest levels, when only early colonizing species persist, the profit is essentially independent of κ.

We can now compare the diversity and profit among fisheries with different biological or economic parameterizations (Fig. 8). Diversity is again maximized at $\alpha = S$ when $h = 0$ and $\pi = 0$. Fig. 8b shows the potential profit that is lost by maximizing diversity. Fig. 8c shows the diversity that is gained by not harvesting, relative to harvesting to maximize profit; this is the difference between maximum diversity, S, and the diversity at the profit maximizing-harvest level. Below, we highlight several qualitative patterns in the trade-off between diversity and profit.

First note that low harvest costs (w) and high propagule production rates (c) increase profits. In such profitable systems, the trade-off between diversity and profit is relatively large; however, as later colonizers become more valuable (higher κ), the trade-off between diversity and profit is diminished. In contrast, communities with high effort costs and low propagule production rates do not tend to have a large trade-off, as both the profit loss and diversity gain are low.

One interesting case to consider is a low κ community (first column of Fig. 8) with low w and low c. While the monetary loss from maximizing diversity is low, the diversity gain is still high. In this case, even though the profit maximizing harvest level is low (and thus profits are low), diversity declines even more rapidly (as the community re-builds species slowly), making the profit maximizing diversity level low. As κ increases, and the trade-off between diversity and profit decreases, this low w, low c region ceases to have such high diversity costs.

Facilitation model: spatial management

Let x_f be the proportion of patches that are designated as a reserve. These patches cannot be fished and we assume they are in the unharvest-
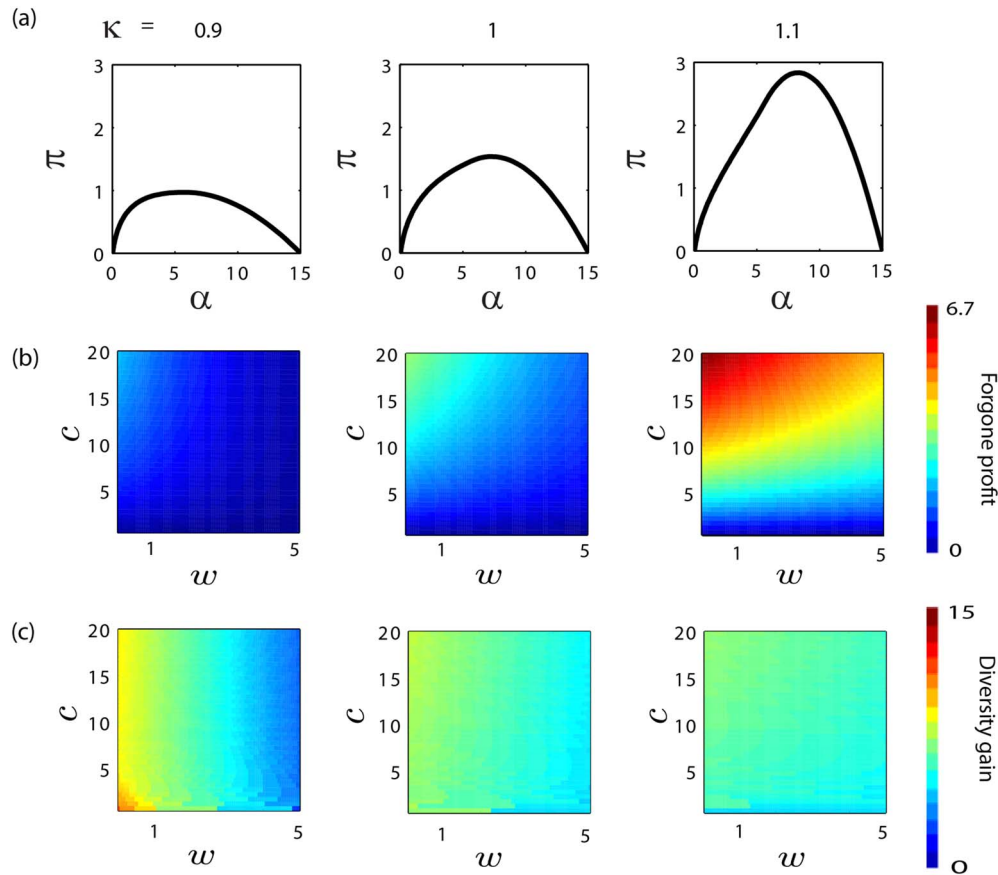
Fig. 8. (a) α versus π for a 15-species version of the facilitation model (Eqs. 25–28), with $w=0.05$, $r=1$, $\varepsilon=1$, and $c=5$. Price per patch was determined by κ, as marked. (b) Potential profit lost from harvesting at the diversity maximizing level ($h=0$). (c) The diversity gain from no harvest relative to harvesting at the profit maximizing level ($h=h_{PM}$). For all panels, $S=15$, $r=1$, $\rho_1=1$, and $\varepsilon=1$.

ed equilibrium state with all species present. We modify Eqs. 25–28 to obtain a set of $S+2$ differential equations that describe the dynamics of a facilitation system with reserves:

$$\frac{dx_\phi}{dt} = h(1 - x_\phi - x_f) - rx_\phi, \qquad (39)$$

$$\frac{dx_0}{dt} = rx_\phi - c_1 x_0 \left(\sum_{j=1}^{S} x_j \right) - hx_0, \qquad (40)$$

$$\frac{dx_i}{dt} = -c_{i+1}x_i \left(x_f + \sum_{j=i+1}^{S} x_j \right) + c_i x_{i-1} \left(x_f + \sum_{j=i}^{S} x_j \right)$$
$$- hx_i, \qquad (41)$$

$$\frac{dx_S}{dt} = c_S(x_f + x_S)x_{S-1} - hx_S. \qquad (42)$$

Using a modification of Eq. 35 to calculate

diversity:

$$\alpha = Sx_f + \sum_{i}^{S} ix_i \qquad (43)$$

and Eq. 38 along with the (numerically derived) equilibria of this system, we can calculate diversity and profit for communities with and without reserves (Fig. 5).

As in the null model, diversity is always higher in communities with reserves, and at high harvest levels the diversity is almost entirely within the reserves. The implementation of reserves reduces the maximum profit rate (Fig. 5), but higher harvest levels can still be profitable. In these instances, the open-access harvest rate is larger.

We again calculate the 'protected diversity,'

'forgone profit,' and 'diversity gain' for all combinations of harvest rates and reserve fractions. These quantities are calculated in the same way as in the null model and are shown schematically in Fig. 1b. The cost in forgone profit of different levels of protected diversity and diversity gain is shown in Fig. 5.

Qualitatively, the trade-offs among cost and the two diversity metrics are the same as in the null model, although the maximum foregone profit and maximum diversity gains are lower in the facilitation model. For a given reserve fraction, the protected diversity is the same between the two models. The cost of adding protected diversity to a given level of diversity gain is still minimal and is generally cheaper than in the null model.

DISCUSSION

The coupled metacommunity-economic modeling framework we have described provides a way to examine the ecological and economic factors that influence profit-diversity trade-offs. The quantities we highlighted—foregone profit, diversity gain, and protected diversity—are useful for structuring thinking about the trade-offs in a complex bioeconomic system (Fig. 1).

Our framework is, perhaps, best suited for identifying the types of harvested communities that are cost-effective to manage. For example, our analysis showed that in communities structured by facilitative colonization dynamics, a manager could often increase diversity without sacrificing much profit from reduced harvest, especially when propagule production rates and harvest costs are low.

An advantage of the framework is that it permits inclusion of a variety of ecological rates and types of interactions. This is important, because such variation exists in real marine systems. For example, strongly competitive systems that exhibit trophic cascades have been observed (Casini et al. 2008), while other systems show strong facilitative interactions (Silliman et al. 2011). These communities may change at vastly different rates. Recovery from harvest disturbance may take a long time—hundreds of years for deep water corals, which grow on the order of a few millimeters per year (Lartaud et al. 2013)—or a short time—for habitats which are

not damaged by fishing, such as long-line fished systems or those with muddy substrates. Additionally, colonization rates can vary widely in marine metacommunities and may depend upon oceanographic features, the distribution of habitat, and species' attributes. Strategic models of the kind we developed here can accommodate this ecological variability and complement the system-specific analyses that model the interactions and management of a particular community (e.g., Rassweiler et al. 2012).

In our analysis, we compared a null community with no interactions to one with strong, facilitative colonizing interactions. The facilitative interaction results in a community that is more sensitive to harvest; it loses species sequentially as harvest rates increase. In contrast, all species persist in the null model until the harvest rate exceeds a threshold value. Facilitative community assembly also reduces profits and profit-maximizing harvest rates. Both the magnitude and shape of the profit-diversity trade-off are changed by the type of ecological interaction (Figs. 4 and 8). Decreasing propagule production rates or colonization rates affect the diversity-profit trade-off in similar ways in both the null and facilitation models; the magnitude of the trade-off is changed, but not the shape.

The reader should not expect that the relationship between profit and diversity will always be as simple as the curves depicted in Figs. 1, 3c, and 8a; other types of ecological interactions will produce even more interesting, complicated trade-offs. For example, in a competitive metacommunity where species displace each other at a patch (modeled by Hastings 1980), there is a non-monotonic relationship between the harvest rate and the number of species that persist. Our preliminary analysis of optimal harvest in this type of community suggests that the relationship between diversity and profit is more complex. In addition, other measures of diversity (e.g., beta-diversity or species richness) may be better suited to capturing these trade-offs.

The models we formulated can include potentially large numbers of species. The extensive literature on two species metacommunities has illustrated how important interspecies interactions are for species persistence and diversity patterns (e.g., Caswell and Cohen 1991, Nee and May 1992, Klausmeier 2001, Prakash and de Roos

2004, Gouhier et al. 2011). When these models are extended to include marine reserves, species interactions may change the optimal reserve size and configuration (Baskett 2007, Baskett et al. 2007). We extended these results by showing that such interactions continue to be important in much larger communities. Our results comport with those of Matsuda and Abrams (2006) who studied yield in multispecies fisheries and found, as we did, that few species are driven to extinction at yield (or in our case, profit) maximizing harvest levels. In addition, the authors found that constraining the harvest to prevent species extinction could be done without substantially reducing yield, which is analogous to our result for the cost of protected diversity.

We also investigated the cost of using marine reserves as a diversity-preserving management technique. In particular, we highlighted differences in the diversity gains achieved when the harvest rate maximizes profit or dissipates it at open access. For both the null and facilitation models, we found that that the cost of achieving some protected diversity tends to be low. At least for the theoretical communities we studied, marine reserves are an efficient way to prevent the erosion of diversity at high harvest levels.

In contrast with some previous results, we found that marine reserves are not economically optimal in this model (i.e., reserves never increase the maximum profit attainable). Different per patch pricing methods that we examined did not reverse this result. Other, single-species models (e.g., Neubert 2003, Sanchirico et al. 2006, Neubert and Herrera 2008, White et al. 2008, Moeller and Neubert 2013) have found reserves to be economically optimal; these models incorporate spatial heterogeneity, which our models do not.

Our models also neglect natural disturbance. Thus, the inclusion of marine reserves here shows the maximum diversity benefit of reserves, as reserves have all species present. Natural disturbance primarily affects the role of marine reserves (in the non-reserve section, a disturbance rate that reduces all patches to being uninhabitable is additive with harvest and can be easily separated), as an additional $S + 2$ equations to track the natural destruction and re-building of non-fished patches would be required. The magnitude of natural disturbance relative to the colonization, harvest, and recovery rates will determine whether natural disturbance is critical to the trade-offs we described here.

We assume that harvesters do not know the state of a particular patch, but rather only know the mean conditions of the entire metacommunity. They are additionally harvesting all fish present at a patch. In reality, harvesters with modern technology are increasingly able to target specific species of fish at specific locations. Allowing fishermen to target either species (species-specific harvest rates) or areas in space would dramatically increase the number of states and/or controls. This would certainly make harvesters more economically efficient and likely qualitatively change the shape of the trade-off between profit and diversity.

This framework allowed us to investigate broad scale patterns of diversity-profit trade-offs and identify regions where conservation would be cost-effective. We believe there are many interesting directions to extend this work. For example, our model is spatially implicit and does not allow us to investigate spatial patterns in connectivity (for colonization) or in harvest (such as 'fishing the line around marine reserves'). The inclusion of spatial complexity allows for spatial variation in harvest, which can result in non-intuitive configurations of harvesting effort (Wilen et al. 2002, Neubert 2003, Kellner et al. 2007, Costello and Polasky 2008). These analyses show that complicated patterns that are not intuitively obvious may appear when harvester behavior in space is accounted for. Spatial variation in harvest may mitigate the trade-off between harvest and biodiversity objectives.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

Appendices A–D and the Supplement are available online: http://dx.doi.org/10.1890/ES14-00503.1.sm