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- Biodiversity may increase with dispersal or be maximized at an intermediate level
- Dispersal-diversity relationship depends on ecological and economic parameters
- Inclusion of non-consumptive benefits changes harvest regime

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Species dispersal and biodiversity in human-dominated metacommunities

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ABSTRACT

The concept of the Anthropocene is based on the idea that human impacts are now the primary drivers of changes in the earth's systems, including ecological systems. In many cases, the behavior that causes ecosystem change is itself triggered by ecological factors. Yet most ecological models still treat human impacts as given, and frequently as constant. This undermines our ability to understand the feedbacks between human behavior and ecosystem change. Focusing on the problem of species dispersal, we evaluate the effect of dispersal on biodiversity in a system subject to predation by humans. People are assumed to obtain benefits from (a) the direct consumption of species (provisioning services), (b) the non-consumptive use of species (cultural services), and (c) the buffering effects of the mix of species (regulating services). We find that the effects of dispersal on biodiversity depend jointly on the competitive interactions among species, and on human preferences over species and the services they provide. We find that while biodiversity may be greatest at intermediate levels of dispersal, this depends on structure of preferences across the metacommunity.

Keywords: bioeconomics, biodiversity, dispersal, non-consumptive benefits, spatial insurance

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1. INTRODUCTION

In the age of the Anthropocene, humans have impacted almost all of the world's ecosystems (Crutzen and Stoermer, 2000; Lewis and Maslin, 2015; Steffen et al., 2007). Among the most important anthropogenic drivers of ecosystem change is globalization, or the closer integration of the world economy (Perrings, 2014). Trade and travel have connected ecosystems far beyond the natural dispersal of species (Costello et al., 2007; Hulme, 2009; Lenzen et al., 2012; Mack et al., 2000). At the same time, the way people have exploited ecosystems has fundamentally altered their vulnerability to introduced species (Dalmazzone, 2000; Hanspach et al., 2008; Pyšek et al., 2010; Vila and Pujadas, 2001). Yet most ecological models abstract from human impacts, treating them as given, constant, or ignoring them completely. There is a need for a "new ecology" that treats people's actions as part of the system (Schmitz, 2016). In this article we revisit the theory of species dispersal in metacommunities to take into account the feedbacks between dispersal, biodiversity, and human exploitation in model systems. In particular, we revisit the theoretical link between dispersal and species diversity in metacommunities subject to human exploitation.

A central result in the theory of species dispersal is that very low or very high rates of dispersal tend to reduce diversity, whereas intermediate rates of dispersal tend to increase diversity (Amarasekare and Nisbet, 2001; Loreau and Mouquet, 1999; Loreau et al., 2003; Mouquet and Loreau, 2003). Intermediate dispersal provides source-sink and rescue effects that replenish locally threatened populations, so maintaining species diversity without leading to the competitive exclusion that drives down diversity when dispersal rates are extreme (Brown and Kodric-Brown, 1977; Holt, 1985; Pulliam, 1988). There are some exceptions to this. For

example, Haegeman and Loreau (2014) identify conditions in which resource and consumer dispersal can exhibit strictly increasing relationships with diversity.

Results from experimental and field research are not decisive. Some experimental studies have found support for the intermediate dispersal hypothesis (Howeth and Leibold, 2010; Kneitel and Miller, 2003; Venail et al., 2008), but others conclude that the relationship between diversity and dispersal depends on the type of organism and spatial scale of the study (Cadotte, 2006; Cadotte and Fukami, 2005; Cadotte et al., 2006). For example, in a meta-analysis of experimental studies of the impact of dispersal on species diversity, Cadotte (2006) argues that the "hump" shaped relationship between dispersal and diversity is specific to the animal kingdom. Other research supports a strictly increasing relationship between dispersal and diversity, such as in microcosm communities (Gilbert et al., 1998; Gonzalez and Chanton, 2002; Gonzalez et al., 1998; Holyoak, 2000; Thompson and Shurin, 2012; Warren, 1996). In contrast, field studies often find that dispersal has only negative effects on species diversity. Invasion biologists, for example, routinely document cases where the effect of dispersal is strongly negative, even at large spatial scales (Chisholm, 2012; Ehrenfeld, 2010; McKinney and Lockwood, 1999; Rhymer and Simberloff, 1996a; Vilà et al., 2011).

An important omission in the understanding of species dispersal is the role of human intervention. Seemingly natural systems are subject to a range of interventions that alter their responses to dispersal. Crops are promoted while crop competitors, predators, and pathogens are suppressed. Charismatic mega-fauna are often protected while inconspicuous plants or insects are ignored. People indirectly select for or against species as in, for example, the consequences of nutrient deposition from agriculture into aquatic ecosystems or the accidental introduction of invasive species (Chisholm, 2012). The observed mix of species in actual ecosystems reflects the

joint effects of human control and natural ecological dynamics (Horan et al., 2011; Liu et al., 2007).

We consider interactions between dispersal, competition, predation, and species diversity in the presence of human preferences for particular ecological states. We take metacommunities that are subject to anthropogenic predation (e.g. harvest) and ask how dispersal affects species diversity when humans alter relative abundances by promoting or suppressing species. We build on the metacommunity models of Loreau et al. (2003) and Gonzalez et al. (2009) to investigate the relationship between biodiversity and dispersal when people derive consumptive benefits from harvesting individual species and non-consumptive benefits from species abundance and richness (mix of species) (Barbier, 2007; Bertram and Quaas, 2016). Non-consumptive benefits from species abundance refer to benefits arising directly from species' biomass, such as carbon sequestration or aesthetic and spiritual values. Non-consumptive benefits from richness or the mix of species refer to benefits such as the regulation of water quality or soil erosion.

We hypothesize that the relationship between diversity and dispersal depends not only on the competitive interactions between species, but also on patterns of harvest/control that reflect human preferences for species and the benefits that they provide. We expect harvest/control to alter the ecological dynamics of the system, resulting in a different diversity-dispersal relationship than occurs in an ecological model that ignores (or assumes fixed) human behaviors. Human harvest alters species abundances, and this can change the source-sink dynamics created by species dispersal between patches. If people value one species over another, we expect harvest/control to promote more preferred species while suppressing less preferred species. Similarly, if people derive non-consumptive benefits from species we expect harvest/control to increase the biomass of preferred species in the patch or maintain even abundances. We find that

while the intermediate dispersal hypothesis holds in some cases, diversity can be monotonically increasing in dispersal depending on ecological competition parameters and human preferences across species.

2. THE ECOLOGICAL MODEL

We adapt the model developed by Loreau et al. (2003) and Gonzalez et al. (2009) which has a metacommunity comprising three communities, each initially made up of three species. Within each ecological community, all species compete for a single limiting resource. Species consume a deterministically variable quantity of resource depending on environmental conditions, and time. Communities are coupled together through dispersal.

Changes in species biomass N and resource biomass R in the j th community are described by the equations:

$$[1] \quad \frac{dN_{ij}}{dt} = N_{ij}(t)(ec_{ij}(t)R_j(t) - m) - aN_{ij}(t) + \frac{a}{M-1} \sum_{k \neq j}^M N_{ik}(t)$$

$$[2] \quad \frac{dR_j}{dt} = I - lR_j(t) - R_j(t) \sum_{i=1}^S c_{ij}(t)N_{ij}(t)$$

for species $i=1,2,3$ and communities $j=1,2,3$ at time t . Species are assumed to consume resources at rate $c_{ij}(t)$, convert resources to new biomass with efficiency e , and die at rate m .

The limiting resource is assumed to increase in all communities by a fixed amount, I , and be lost at a constant rate l . The system assumes a Holling type I predator response, where all

species have the same conversion efficiency but differ in their consumption (predation) rates.

Species disperse among communities at a constant proportion or rate a .

Species consumption of the resource is a non-linear function of species-specific competitive ability and environmental variation fluctuating over time for each species in each community such that:

$$[3] \quad c_{ij}(t) = \frac{1.5 - |H_i - F_j(t)|}{10}$$

$$[4] \quad F_j(t) = \frac{1}{2} \left[\sin(x_j + 2\pi t/T) + 1 \right]$$

Consumption rates are constrained to lie within the range [0.05, 0.15]. H_i is a dimensionless, species-dependent competition parameter such that $H_1 = 1$, $H_2 = 1/2$, and $H_3 = 0$. It is assumed that environmental conditions, F_j , fluctuate over time as a sinusoidal function. A phase parameter ($x_1 = \pi/2$, $x_2 = 0$, $x_3 = -\pi/2$) shifts the environmental variation along its horizontal axis (Figure 1). The period of environmental variation and hence consumption rates is given by T . Depending on the length of each phase T , in the absence of human intervention or dispersal a single species will exclude all others in a given community. If T is sufficiently large, this will be the set of species that possess the highest initial consumption rate, $c_{ij}(t)$. If T is small, this will be the set of species whose consumption rates are closest to the average across all communities (a "generalist" species). In our model, having consumption rates closest to the average across communities is equivalent to the characteristics of generalist species in ecology -

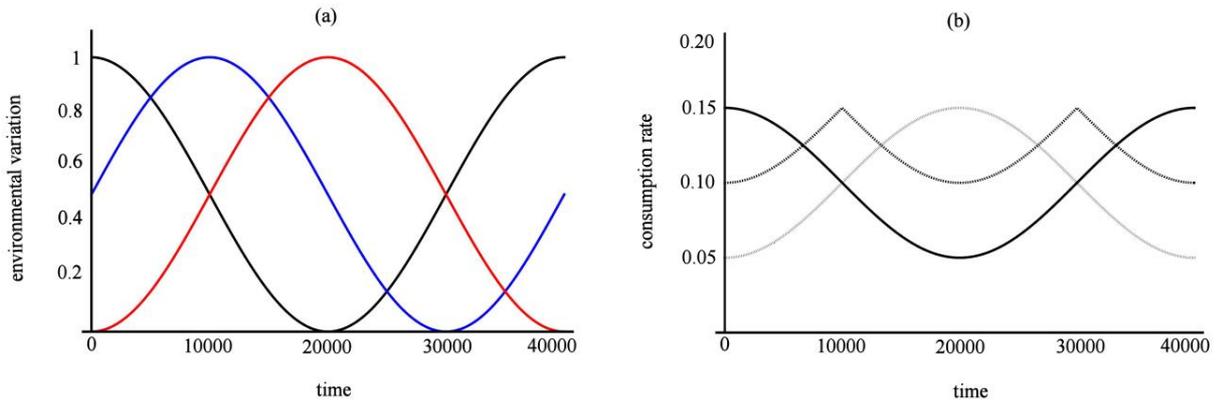


Figure 1. Community environmental variation (a) and species consumption (b) curves over time. In (a), color denotes community number: black (community 1, $x_1 = \pi/2$), blue (community 2, $x_2 = 0$), red (community 3, $x_3 = -\pi/2$). The phase parameter, x_j , shifts environmental variation along its x-axis. In (b), species consumption rates are for community 1 and species is indicated by color: black ($H_1 = 1$), charcoal ($H_2 = 1/2$), and light gray ($H_3 = 0$). Consumption rate is determined by the interaction by the species competition parameter and environmental variation. Reproduced from Shanafelt et al. (2015).

1 the ability to occupy a broad range of environments (Futuyma and Moreno, 1988; Poisot et al.,
2 2012; Schluter, 2000).¹

3 The ecological model depends on several assumptions. First, it is assumed that
4 communities initially contain the same set of species and differ only in their environmental
5 variation over time as defined by the phase parameter x_j . Second, species differ only in their
6 consumption rates, which vary by community as a function of H_i and x_j . This implies that
7 species are more or less similar in their ecological function and exist within a single trophic
8 level. Third, species compete for a single limiting resource whose natural influx and loss rates
9 are constant and independent across time and communities. Fourth, species competition arises
10 solely from resource consumption. There is no direct interaction between individuals within and
11 across patches (e.g. local competition for light or nutrients in plant systems). Finally, we assume
12 that dispersal is density-independent and occurs at a constant rate of dispersal. These
13 assumptions, while restrictive, simplify the analysis while providing a structure for analyzing
14 competition over a range of environmental conditions, and the effect of harvest on species
15 composition. These assumptions, and how they relate to the economic model, are discussed in
16 more detail in Appendix A. For a detailed analysis and extension of the Loreau spatial insurance
17 model, see Loreau et al. (2003), Gonzalez et al. (2009), Urban (2006), Shanafelt et al. (2015),
18 and Thompson and Gonzalez (2016).

¹ We would expect our results to hold in a time-invariant environment, e.g. in the absence of temporal variability in environmental conditions. Loreau et al. (2003) and Gonzalez et al. (2009) use temporal variability in species biomass as a mechanism for local species coexistence, sensu the paradox of the plankton (Hutchinson, 1961). However, other models of the intermediate dispersal hypothesis find non-monotonic relationships between biodiversity and dispersal in systems where species growth rates are held constant (Haegeman and Loreau, 2014; Haegeman and Loreau, 2015; Wang and Loreau, 2016).

21 3. THE BIOECONOMIC MODEL

22 Consider a managed ecosystem of three communities, where each patch can be thought of as an
 23 independent management area containing three species. We assume that people obtain benefits
 24 from the direct consumption of species (harvest), from non-consumptive benefits arising from
 25 species abundance (stocks), and from biodiversity (the composition of those stocks). The benefits
 26 from consumption include the provisioning services of the ecosystem (e.g. the production of
 27 foods, fuels, fibers etc). The non-consumptive stock benefits of species abundance include, for
 28 example, cultural and regulating services such as the value of biomass for carbon sequestration,
 29 and the aesthetic, totemic or spiritual values of species. The non-consumptive stock benefits of
 30 diversity include the stabilizing effects of biodiversity on ecosystem functioning and the
 31 subsequent flow of ecosystem services (regulating services) (Millennium Ecosystem
 32 Assessment, 2005). We assume that all species are positively valued in consumption, and so do
 33 not consider cases where species are a direct source of disutility (e.g. pests or pathogens).

34 We may rewrite [1] and [2] to reflect the impact of harvest, equal to $qE_{ij}(t)N_{ij}(t)$, on the
 35 abundance of species and the resource:

36

37 [5]
$$\frac{dN_{ij}}{dt} = N_{ij}(t)(ec_{ij}(t)R_j(t) - m) - qE_{ij}(t)N_{ij}(t) - aN_{ij}(t) + \frac{a}{M-1} \sum_{k \neq j}^M N_{ik}(t)$$

38 [6]
$$\frac{dR_j}{dt} = I - lR_j(t) - R_j(t) \sum_{i=1}^S c_{ij}(t)N_{ij}(t)$$

39

40 where effort in harvesting species i on patch j is given by E_{ij} ($0 \leq E_{ij} \leq E_{\max}$) and q is the
 41 constant efficiency of effort. This is a Schaefer harvest function, common in economics and

42 fisheries science (Schaefer, 1957). We arbitrarily set the maximum harvest effort such that it is
43 possible to maintain species biomass at any chosen level.²

44 We further assume that in each community a resource manager harvests species in that
45 community in order to maximize an index of net social benefits, ignoring the actions of managers
46 in other communities connected by species dispersal. That is, managers act independently, and
47 do not condition their decisions on the harvest decisions of others. Formally, we define the j^{th}
48 manager's problem as:

49

² Our choice of harvest function assumes perfect targeting of species - a standard assumption in the literature (Clark, 2010; Conrad and Clark, 1987). In reality managers face problems with imperfect selection. For example, in fisheries different types of fishing practices - hook lines, nets, or trawling - result in different rates of by-catch (the capture of non-target species) (Davies et al., 2009; Hall et al., 2000). This means that the effect of harvest between species need not always be independent, e.g. the harvest of one species may directly affect the abundance of another species. In general this idea is treated implicitly. For example, in a fisheries context Abbott and Wilen (2009) utilize a separate function to account for by-catch in setting stock quotas. Mesteron-Gibbons (1988), Fenichel and Horan (2007), and Fenichel et al. (2010) explicitly take into account the indirect effects of harvesting one or more interacting species in predator-prey, host-pathogen, and invasive species contexts.

Traditional optimal control problems in economics generally assume the existence of control variables for each state variable and that each control variable perfectly controls a different state variable at every moment in time (Conrad and Clark, 1987; Clark, 2010). Violating this assumption results in an "imperfect control", which has been shown to lead to complex feedback rules for efficient management (Fenichel et al., 2010; Fenichel et al., 2011; Horan and Fenichel, 2007; Horan and Wolf, 2005). Indeed, in our context relaxing this assumption will result in a complex interplay between ecological, economic, and spatial dynamics to determine the relationship between biodiversity and dispersal. We leave this for future work.

$$\begin{aligned}
 & V_j(N_j, R_j, t) = \\
 50 \quad [7] \quad & \max_{E_{ij}} \int_0^\tau \left[\sum_{i=1}^S (p_{ij} q E_{ij}(t) N_{ij}(t) - w q E_{ij}(t) + \alpha_{ij} N_{ij}(t)) + \beta_j \left(1 - \sum_{i=1}^S \left(\frac{N_{ij}(t)}{N(t)} \right)^2 \right) \right] e^{-\delta t} dt
 \end{aligned}$$

51

52 subject to:

52

53 [5] and [6]

53

54 $N_{ij}(0), R_j(0)$

54

55 $N_{ij}(t) \geq 0, R_j(t) \geq 0$

55

56

57 where p_{ij} is the unit price of each species harvested (a measure of the marginal social benefit of
 58 harvest of species i) and w is the marginal cost of harvest effort. The marginal non-
 59 consumptive benefits of species abundance are given by the parameter α_{ij} . The total social non-
 60 consumptive benefit of species biomass is taken to be a non-saturating, linear function which - as
 61 is the case for an ecosystem service such as carbon sequestration - scales with the biomass of
 62 species i on patch j . The parameter β_j is a measure of the non-consumptive benefits of
 63 biodiversity. It represents the value of ecosystem functioning and regulating services that
 64 increase with biodiversity. For simplicity β_j is taken to be a weighted Simpson's index of
 65 diversity (Simpson, 1949).³ Total benefits from biodiversity are maximized when there is an
 66 even number of species abundances. $N(t)$ measures the biomass of all species in the
 67 community. δ is the discount rate, and τ is the time horizon over which harvest is determined.

³ The Simpson's index can be interpreted as the probability that two individuals selected at random with replacement from a population will not belong to the same type. A number of indices exist to measure biodiversity, many of which are strongly correlated (Bandeira et al. 2013). See Humphries et al. (1995) for a review of diversity metrics used in conservation ecology. In using a Simpson's index, as opposed to species richness, we assert that people value species abundances as well as species presence or absence.

68 In addition, at the terminal time, the transversality condition requires that the social (shadow)
 69 value of an extra unit of each species and the resource are constrained to zero.

70 The full optimal solution to the system [5], [6], and [7] is set of feedback responses that
 71 approach the optimal harvest at the most rapid rate possible (Clark, 2010; Conrad and Clark,
 72 1987). This approach path is optimal because the system is linear in the control variables and
 73 there exists a separate control for each state variable. We may formally write the complete
 74 solution of the optimal choice of harvest as a feedback rule dependent on the stock of each
 75 species:

76

$$77 \quad [8] \quad E_{ij} = \begin{cases} E_{\min} & \text{if } N_{ij} < N_{ij}^* \\ E_{ij}^* & \text{if } N_{ij} = N_{ij}^* \\ E_{\max} & \text{if } N_{ij} > N_{ij}^* \end{cases}$$

78

79 If the marginal net benefit of harvest effort is positive for a species, then harvest effort is set to
 80 its maximum level, E_{\max} . If the marginal net benefit of harvest effort for a species is negative,
 81 then harvest effort is set to zero. If the marginal net benefit of harvest effort is zero, then harvest
 82 effort is equal the ‘singular solution’ - the optimal level of harvest effort at equilibrium, E_{ij}^* .

83 At the singular solution, E_{ij}^* , harvest balances the marginal benefits and costs of a change
 84 in stock size (Clark, 2010; Conrad and Clark, 1987):

85

$$\begin{aligned}
 & \left[\frac{ec_{ij}R_j \sum_{k=1}^S (p_{kj}N_{kj}c_{kj} - wc_{kj})}{l + \sum_{k=1}^S (c_{kj}N_{kj}) + \delta} + \left(p_{ij} - \frac{w}{N_{ij}} \right) (m + a - ec_{ij}R_j + \delta) \right] \\
 86 \quad [9] \quad E_{ij}^* &= \frac{N_{ij}}{wq} \left[-\alpha_{ij} - \beta_j \left(\frac{2 \left(\sum_{k \neq i} N_{kj}^2 - N_{ij} \sum_{k \neq i} N_{kj} \right)}{\left(\sum_{k=1}^S N_{kj} \right)^3} \right) \right]
 \end{aligned}$$

87

88 Equation [9] implies that if the optimal solution is jointly optimal for all species, then there are
 89 separate optimal harvest policies for each species and patch in each moment of time (Fenichel
 90 and Horan, 2007a; Fenichel et al., 2011). The first term in the square brackets is the present
 91 value of marginal benefits from preserving the resource to be consumed by species in the future
 92 (Melstrom and Horan, 2013). The second term represents the marginal user cost of harvest: the
 93 forgone future growth in the abundance of all species as a result of harvesting now. The final two
 94 terms are the marginal non-consumptive benefits of species abundance and biodiversity,
 95 respectively. See Appendices B-D for its derivation and more detailed discussions of the
 96 economic model.⁴

97 It is worth re-emphasizing that the decision-maker in each social-ecological community
 98 focuses only on conditions in that social-ecological community. They do not take into account
 99 the harvest of species in other patches, nor is there trade of harvested resources among social-
 100 ecological systems. Decision-makers also take the dispersal of species between communities as
 101 given and at a constant proportion. Thus the harvest regime in a particular community is optimal
 102 only with respect to conditions in that community. Any impacts that local decisions have on

⁴ Note that the singular solution in [9] is a simplification. Due to the complex nature of the problem, we assume a global interior solution of the state variables. We evaluate the validity of this assumption in Appendices C and D.

103 other communities are ‘external effects’ of those decisions. This is in contrast to the aggregate
104 social-planner problem in which an overarching decision-maker coordinates local decisions and
105 selects harvest rates of species across all communities to maximize aggregate system-level social
106 welfare (Clark, 2010; Conrad and Clark, 1987). However, solving the social-planner problem
107 requires restructuring the maximization problem in equation [7] and is left for future work.

108 We consider three preference structures: 1) people derive utility from the direct
109 consumption of species only (provisioning services secured by harvest), 2) people derive utility
110 from the direct consumption of species and from the non-consumptive use of aggregate biomass
111 (provisioning services from harvest plus regulating services from standing biomass), and 3)
112 people derive utility from the direct consumption of species and from the non-consumptive
113 benefits of the composition of species (provisioning services from harvest plus cultural and/or
114 regulating services from biodiversity).

115 We solve the general version of the maximization problem numerically in [7] using the
116 forward-backward sweep method of Lenhart and Workman (2007). This method exploits the
117 fact that the optimal control problem is constrained to a set of initial conditions for the state
118 variables, and a set of terminal conditions for the co-state variables (transversality conditions) -
119 variables accounting for the value of an extra unit of each species and the resource. Given initial
120 conditions for species and resource biomass and an initial guess as to the harvest trajectory, the
121 state variables are solved forward to the terminal time. Using the transversality conditions and
122 the values of the state and control variables, the co-state variables are solved backwards to the
123 origin. Harvest is updated, and the procedure repeated until the solution converges.⁵ We adopted

⁵ The system of equations was solved numerically using a 4th order Runge-Kutta ODE estimator with an adjustable step size. It should be noted that this estimator allows for infinitely small population sizes. A species population will never reach zero and be extirpated from the patch or system. Further, a species cannot be eradicated by harvest because of the nature of the Schaefer harvest function.

124 a time horizon of 100 time steps. We allowed environmental variation to cycle with a period of
125 25 time steps. For a full list of parameter values, see Table 1.

126

127

128 4. RESULTS

129 We present our findings as a progression – reporting the results of models of increasing
130 complexity. We begin by describing the behavior of the system without people. This most
131 closely tracks the case discussed by Loreau et al. (2003) and Gonzalez et al. (2009). We then
132 present the results of the bioeconomic model, starting with the case in which all species respond
133 to environmental conditions in the same way, and concluding with the case in which all species
134 are different. Our results are summarized in Table 2.

135

136

137 *4.1. Dispersal in the absence of human predation*

138

139 Our baseline is a system without humans. The main finding of Loreau et al. (2003) and
140 Gonzalez et al. (2009) is that intermediate rates of species dispersal between communities
141 maximize community-level (local) and metacommunity-level (global) biodiversity, productivity,
142 and stability. At low dispersal rates, each community functions as a separate closed system, and
143 the species with the highest initial consumption rate competitively excludes all others. At high
144 dispersal rates, the system functions as a single community and the species with the highest
145 average consumption rate dominates. At intermediate dispersal rates immigration maintains local

146 Table 1. Ecological and economic model parameters.

147

Ecological parameters

Variable	Value	Interpretation
S	3	Total number of species
M	3	Total number of patches (communities)
$c_{ij}(t)$	variable [0, 0.15]	Species consumption rate of resource biomass
e	0.2	Resource to species biomass conversion efficiency
m	0.2	Natural mortality rate
I	165	Patch resource influx
l	10	Rate of resource loss
a	variable [0, 1]	Species dispersal rate
H_i	variable 1, 1/2, 0	Species competition parameter
x_j	variable 1, 0, -1	Environmental phase parameter
T	25	Period of environmental variation

Economic parameters

Variable	Value	Interpretation
p_{ij}	variable 14, 15, 16 25, 5, 1	Price per unit species harvested
q	0.2	Efficiency of harvest effort
w	variable 45, 65	Cost per unit of species harvest
α_{ij}	variable [0, 1.5]	Marginal social benefits of species abundance
β_j	variable [0, 50]	Social benefits of biodiversity
δ	0.01	Discount rate
τ	100	Terminal time

148

149 Note that "ij" indicate species i on patch j where $i = 1, 2, 3$ and $j = 1, 2, 3$.

150 Table 2. Summary of results.
 151

species	benefits	dispersal	prices between patches	result
same $H_i = 1/2$	harvest	no	-	<ul style="list-style-type: none"> • harvest of all species • suppression of lesser valued species
	harvest abundance	no	-	<ul style="list-style-type: none"> • harvest declines with benefits from abundance • if benefits from abundance greatly exceed benefits from harvest, then harvest ceases
	harvest biodiversity	no	-	<ul style="list-style-type: none"> • as benefits from biodiversity increase, species are harvested to maintain more even abundances • levels of biomass depend on the set of relative prices
	harvest	yes	same	<ul style="list-style-type: none"> • quantity and evenness of species harvested increases with dispersal • diversity increases with dispersal
	harvest	yes	different	<ul style="list-style-type: none"> • harvest rates for each species converge at intermediate dispersal, then diverge at high dispersal • quantity of species harvested increases with dispersal • diversity maximized at intermediate dispersal
different $H_i = 1, 1/2, 0$	harvest	yes	same	<ul style="list-style-type: none"> • at low (high) dispersal, the generalist (least valuable) species dominates • diversity maximized at intermediate dispersal
	harvest	yes	different	<ul style="list-style-type: none"> • at low dispersal, the generalist species dominates • initial suppression of species increase with dispersal, leading to greater coexistence but lower biomass • diversity increases with dispersal

152 biodiversity while preserving global biodiversity and maximizing ecological productivity and
153 stability of productivity.

154 We assume the same structure of three communities in the coupled system, each
155 composed of three species. The species with the greatest average consumption rate in each
156 community and across all three communities (the "generalist" species) competitively excluded
157 other species in the system regardless of the natural dispersal rate. This is because populations of
158 the generalist species were never driven down enough in adverse environmental conditions to
159 prevent them from suppressing other species under favorable environmental conditions.

160

161

162 *4.2. No dispersal - Harvest of functionally **identical** species for consumptive and non-*
163 *consumptive benefits in isolated communities*

164

165 We next considered the impact of anthropogenic predation or harvest in each community without
166 dispersal. All species within each patch were assumed functionally identical. All species
167 experienced the same response to environmental conditions and possessed the same resource
168 consumption rate curves. We present results for $H_i = 1/2$ for $i = 1, 2, 3$. See Appendix E for the
169 outcomes under other species competition parameters and environmental conditions. We take
170 three cases.

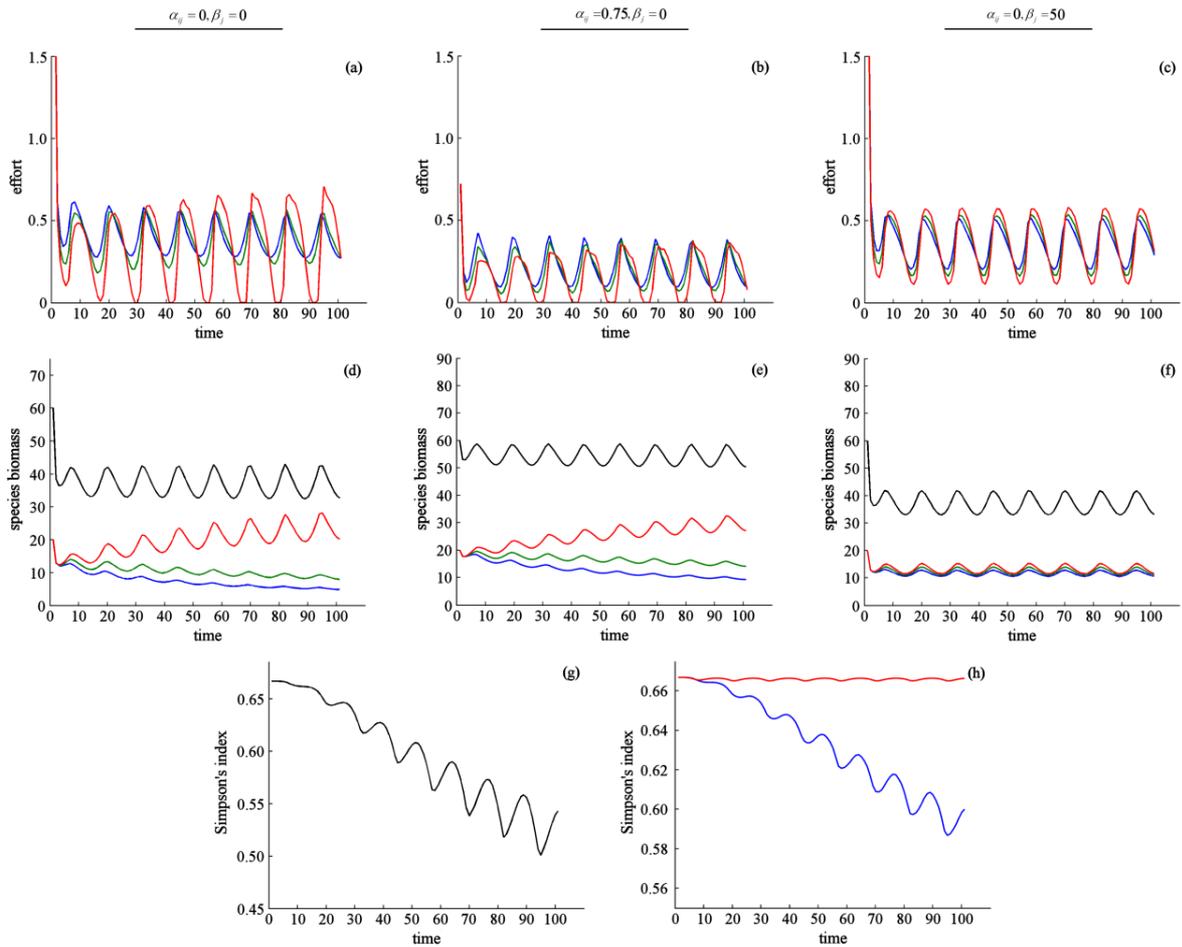
171 *4.2.1. Case 1: Harvest for consumptive benefits*

172

173 When benefits were obtained solely through species harvest ($p_{ij} > 0$, $\alpha_{ij}, \beta_j = 0$), managers
174 initially drove the stock to its equilibrium value by setting harvest effort to the maximum.
175 Managers then maintained the equilibrium stock via harvest effort at the singular solution, which
176 fluctuated over time by species and patch. In our case the equilibrium was a stationary cycle that
177 oscillated deterministically according to a sine function. As in other studies of stochastic (Clark,
178 1976; Parma, 1990; Reed, 1979) and fluctuating (Carson et al., 2009; Costello et al., 1998;
179 Costello et al., 2001) growth rates, we found that species harvest rates fluctuated with species
180 consumption rates, with more valuable species being extracted at higher rates than less valuable
181 species (Figure 2a; Appendix G).

182 In choosing the level of harvest, managers balanced current net benefits of harvest against
183 the benefits of future harvests. Since species compete for resources within the ecological
184 community, managers suppressed less valuable species in order to relieve competitive pressure
185 on more valuable species. This effect involved a high initial pulse of harvest that drove down the
186 biomass of all species, but particularly the biomass of the least valued species. The result was
187 that abundance of the least valued species was reduced, and abundance of the more valued
188 species was increased (Figure 2d; Appendix G). The lower the price of a species, the greater its
189 initial suppression. See Appendix F for examples when the price is low or negative (a pest
190 species).

191 While suppression of the less valued species increased growth of the most profitable
192 species, it also reduced biodiversity (Figure 2g; Appendix G). Biodiversity, as measured by a



193
 194 Figure 2. Effect of harvest price when benefits are obtained from harvest only (a, d), harvest and
 195 and abundance (b, e), and harvest and the mix of species (c, f). Harvest effort (a-c), species biomass
 196 (d-f), and biodiversity (g, h). In (a-f) color indicates harvest effort and species biomass for
 197 species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest
 198 price). Black shows aggregate species biomass. In (g, h) color indicates the types of benefits:
 199 harvest only (black), harvest and abundance (blue), harvest and the mix of species (red). Note
 200 the difference in the y-axes in (g) and (h). The dynamics when benefits are derived solely from
 201 harvest take longer to reach equilibrium than when benefits are also derived from abundance and
 202 the mix of species, or when the system is coupled via dispersal. For the sake of comparison we
 203 present results for a 100 step time horizon here (a, d, g). We present results for a longer
 204 timescale in Appendix G. The dynamics follow the same trajectory, saturating and settling into a
 205 persistent, fluctuating equilibrium.
 206

207 Simpson's index, declined and became more variable over time. As less profitable species were
208 suppressed, fluctuations in the proportion of species biomasses reside increasingly in the single,
209 most profitable species.

210

211

212 *4.2.2. Case 2: Harvest for consumptive and non-consumptive benefits (abundance)*

213

214 If people derived benefits from both harvest (a flow benefit) and abundance (a stock benefit)
215 ($p_{ij}, \alpha_{ij} > 0$; $\beta_j = 0$), managers harvested less at lower rates and more evenly across species
216 (Figure 2b, e; Appendix G), and biodiversity increased (Figure 2h). As stock benefits exceeded
217 market prices, species became more valuable if left in the "wild" than for consumption. Holding
218 harvest price constant and increasing α_{ij} resulted in the aggregate benefit of all species
219 approaching the same value. Managers maximized net benefits by balancing the marginal net
220 benefits of harvesting and abundance - which depends on the ratio of p_{ij} to α_{ij} . A given species
221 was harvested only if harvest benefits exceeded abundance benefits, and harvest decreased when
222 a species was valued for other, non-consumptive benefits (Hartman, 1976). If a desirable species
223 was threatened by competitive exclusion, and the benefits from suppressing the competing
224 species exceeded benefits from its abundance, then the competing species would be suppressed.

225 4.2.3. Case 3: Harvest for consumptive and non-consumptive benefits (biodiversity)

226

227 When people derived benefits both from harvest and from the mix of species ($p_{ij}, \beta_j > 0$;
 228 $\alpha_{ij} = 0$), we found that harvest effort resulted in an even distribution of species abundances
 229 (Figure 2c, f; Appendix G). The Simpson's biodiversity index increased with the benefits from
 230 biodiversity, though differences were found to be negligible at high values of β_j (Figure 2h;
 231 Appendix G). While the most desirable species stock was maintained at a higher level than other
 232 species, we did not observe suppression of less valuable species.

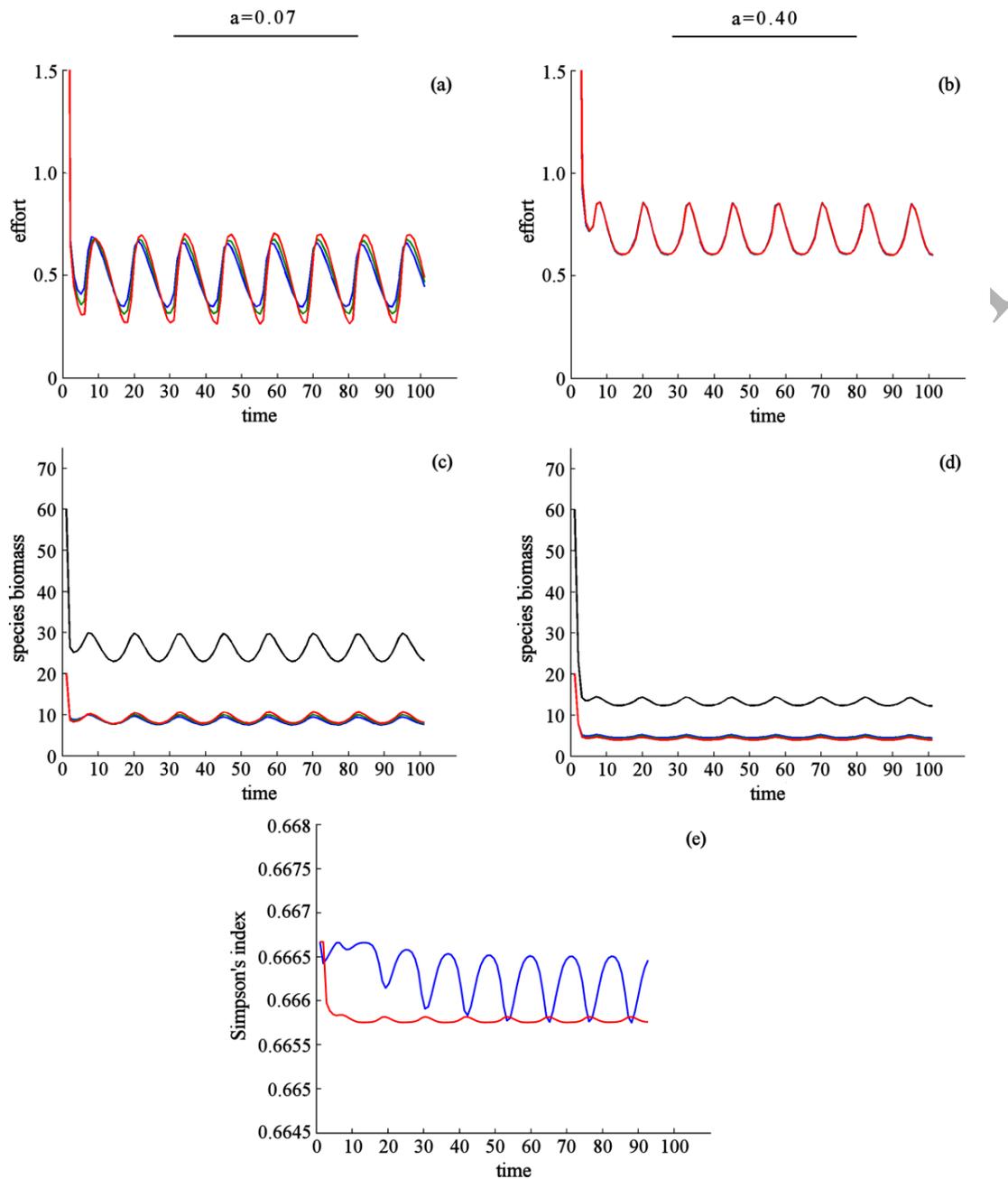
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235 4.3. Dispersal - Harvest of functionally **identical** species for consumptive benefits

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237 Beyond the baseline we considered two additional scenarios. In the first we assumed species in
 238 the different communities to be functionally identical, and explored the implications of uniform
 239 and non-uniform preferences over species. If preferences are uniform, the value of each species
 240 is identical across communities ($p_{i,1} = p_{i,2} = p_{i,3}$ for all i). This means that in the absence of
 241 dispersal, each community would harvest species in the same fashion. Differing environmental
 242 conditions affect fluctuations in species biomass but not harvest decisions (Appendix E). In the
 243 presence of dispersal, optimal harvest patterns change. As dispersal rates increase we observed a
 244 shift in harvest away from the suppression of less valuable species and towards identical harvest
 245 rates for all species (Figure 3a, b). As a consequence, species populations converged to similar
 246 levels of biomass (Figure 3c, d). As expected the Simpson's index also increased with dispersal
 247 (Figure 3e). The increase in harvest with dispersal is due to the fact that the marginal benefits of



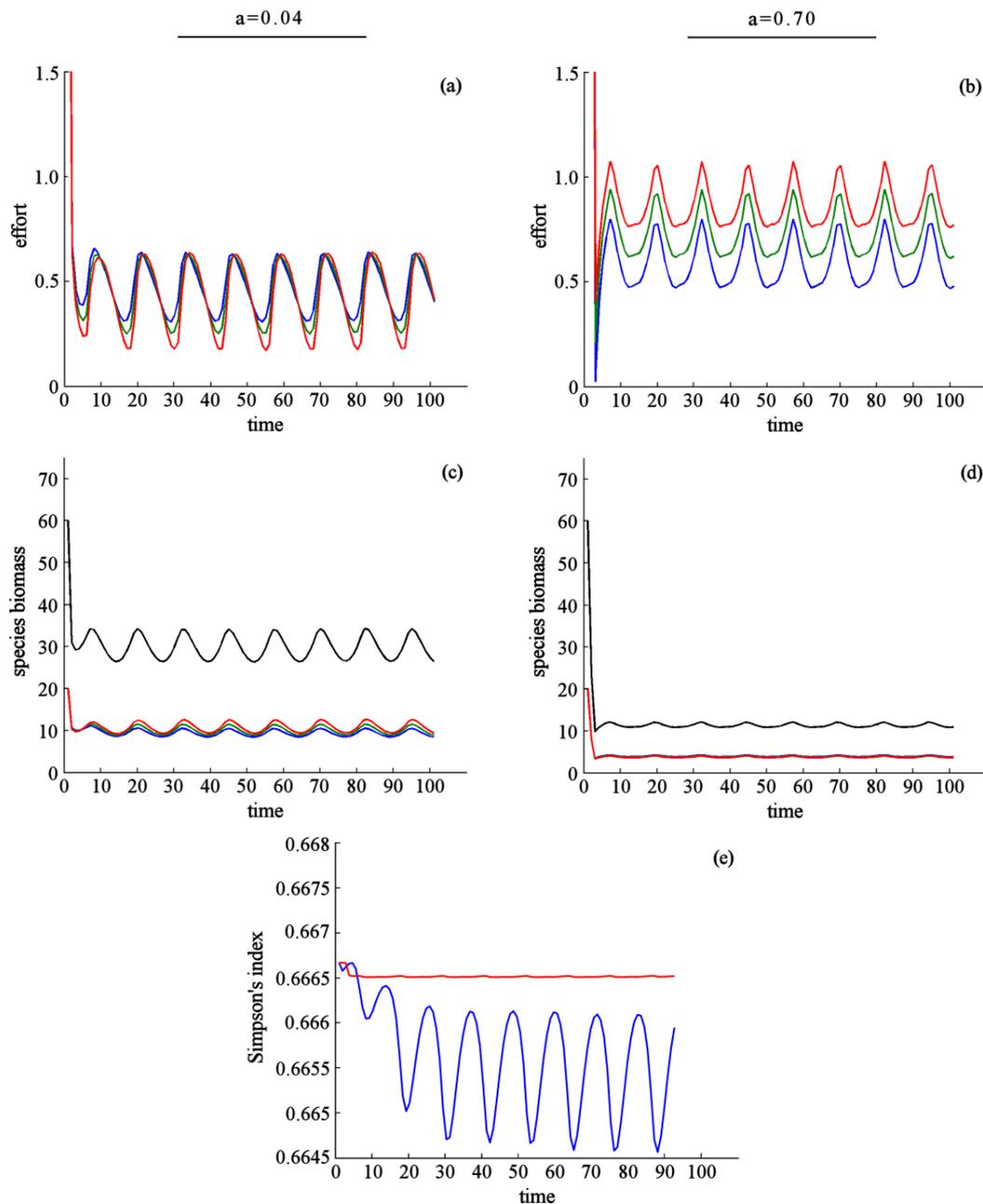
248
 249 Figure 3. Effect of dispersal when species have *identical* ecological parameters, benefits are
 250 obtained through harvest only, and preferences for species are *identical* across patches.
 251 Environmental conditions *differ* between patches. Harvest effort (a, b), species biomass (c, d),
 252 and biodiversity (e). In (a-d) dispersal rate is indicated by column: $a=0.07$ (a, c), and $a=0.40$
 253 (b, d). Color indicates harvest effort and species biomass for species 1 (red, highest harvest
 254 price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows aggregate
 255 species biomass. In (e) color indicates the dispersal rate: intermediate (blue, $a=0.07$), high (red,
 256 $a=0.40$).

257 conserving species falls with the inflow of species - which is taken as exogenous in the harvest
 258 regime. Since managers fail to internalize the effects that their harvest decisions have on other
 259 communities, harvest drives down the size of breeding stocks retained in each community
 260 limiting local growth in each community.

261 If preferences are not uniform, species are valued differently in each community. That is,
 262 the set of relative prices for each unit of species harvested varied between communities
 263 ($p_{i,1} \neq p_{i,2} \neq p_{i,3}$ for all i). The most highly valued species in one community was taken to be the
 264 least valued in another. Harvest regimes, and by extension the abundance of species, differed
 265 between communities. At low and intermediate dispersal rates, we found the same harvest
 266 strategies as when preferences for species were the same between patches (Figure 4a, c).
 267 However, at high dispersal rates, we found a strong effect on harvest. The greater the rate of
 268 dispersal between communities, the stronger the source-sink effect —the rate at which depleted
 269 populations were replenished. This additional biomass was harvested depending on its relative
 270 value: the highest valued species being harvested the most, the lowest valued being harvested the
 271 least (Figure 4b, d). The Simpson's index was maximized at an intermediate dispersal rate,
 272 although the difference in the index "over the hump" was found to be negligible (Figure 4e).

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 274
 275 *4.4. Dispersal - Harvest of functionally **different** species for consumptive benefits*

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 277 In our second scenario we assumed all species within each community to be functionally unique
 278 and to respond to environmental conditions differently ($H_1 = 1; H_2 = 1/2; H_3 = 0$, Figure 1). We
 279 further assumed all species to be positively valued ($p_{ij} > 0$) for their consumptive benefits only,



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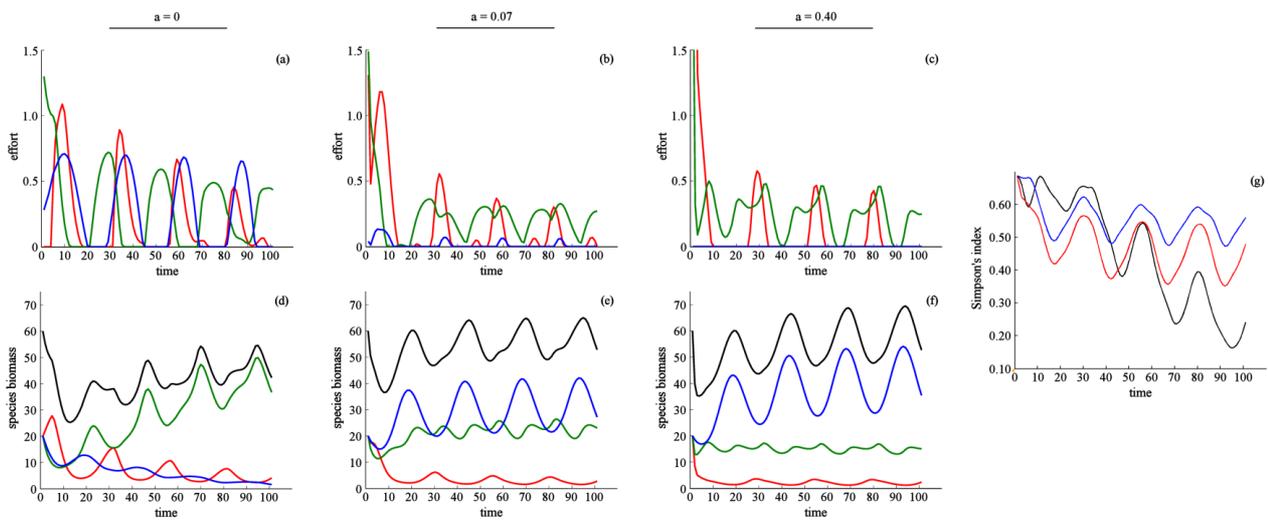
281 Figure 4. Effect of dispersal when species have *identical* ecological parameters, benefits are
 282 obtained through harvest only, and preferences for species *differ* across patches. Environmental
 283 conditions *differ* between patches. Harvest effort (a, b), species biomass (c, d), and biodiversity
 284 (e). In (a-d) dispersal rate is indicated by column: $a=0.04$ (a, c), and $a=0.70$ (b, d). Color
 285 indicates harvest effort and species biomass for species 1 (red, highest harvest price), species 2
 286 (green), and species 3 (blue, lowest harvest price). Black shows aggregate species biomass. In (e)
 287 color indicates the dispersal rate: intermediate (blue, $a=0.04$), high (red, $a=0.70$). Results are
 288 presented for patch 1. Other patches are symmetric with respect to the preferences for each
 289 species.

290 and again explored the implications of uniform and non-uniform preferences over species. Recall
291 that in the *absence of harvest* the generalist species, or the species with the highest average
292 consumption rate, dominates the system. At low rates of dispersal, we found that the
293 combination of harvest and competition allowed the generalist species to dominate the system
294 even if it was the least valued (Figures 5d, 6d).

295 As before, we first considered the case where preferences for species were the same
296 across communities ($p_{i,1} = p_{i,2} = p_{i,3}$ for all i). In this case, increasing dispersal rates caused
297 harvest to decline, particularly for the least valued species (Figure 5a-c). The most valued species
298 were heavily harvested, while the generalist species were partially suppressed. What is
299 particularly interesting is that at intermediate dispersal rates harvest relieved competitive
300 pressure on the least valued species, allowing for a more even distribution of species abundances.
301 However, at high dispersal rates the least valuable species was able to dominate the system
302 (Figure 5d-f).

303 Harvest and abundance were jointly determined by harvest price and species growth.
304 These in turn depended on resource consumption, harvest and dispersal (mortality is held
305 constant). When multiple species are considered, competitive pressure from the generalist
306 species plays a large role in determining abundances. The effect of harvest is twofold. Harvest
307 can suppress highly competitive species but can also place additional pressure on species
308 biomass. In our case, the least valuable species was not valuable enough to be harvested, nor are
309 the benefits great enough to justify suppression. In contrast, the generalist species was harvested
310 for its benefits and, particularly at high dispersal rates, suppression.

311 Biodiversity measured by a Simpson's index first rose and then fell due to two shifts in
312 the ratio of species abundances (Figure 5g). At low dispersal rates generalist species dominated.



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Figure 5. Effect of dispersal when species have *different* ecological parameters, benefits are obtained through harvest only, and preferences for species are *identical* between patches. Environmental conditions are the *same* across patches. Harvest effort (a-c), species biomass (d-f), and biodiversity (g). In (a-f) dispersal rate is indicated by column: $a = 0$ (a, d), $a = 0.07$ (b, e), and $a = 0.40$ (c, f). Color indicates harvest effort and species biomass for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows aggregate species biomass. In (g) color indicates the dispersal rate: low (black, $a = 0$), intermediate (blue, $a = 0.07$), high (red, $a = 0.40$). For visualization we present results with a 100 step time horizon. At longer timescales the dynamics follow the same trends and trajectories (Appendix G).

322 At intermediate dispersal rates the least valuable species and the generalist species coexisted. At
323 high dispersal rates the least valuable species dominated.

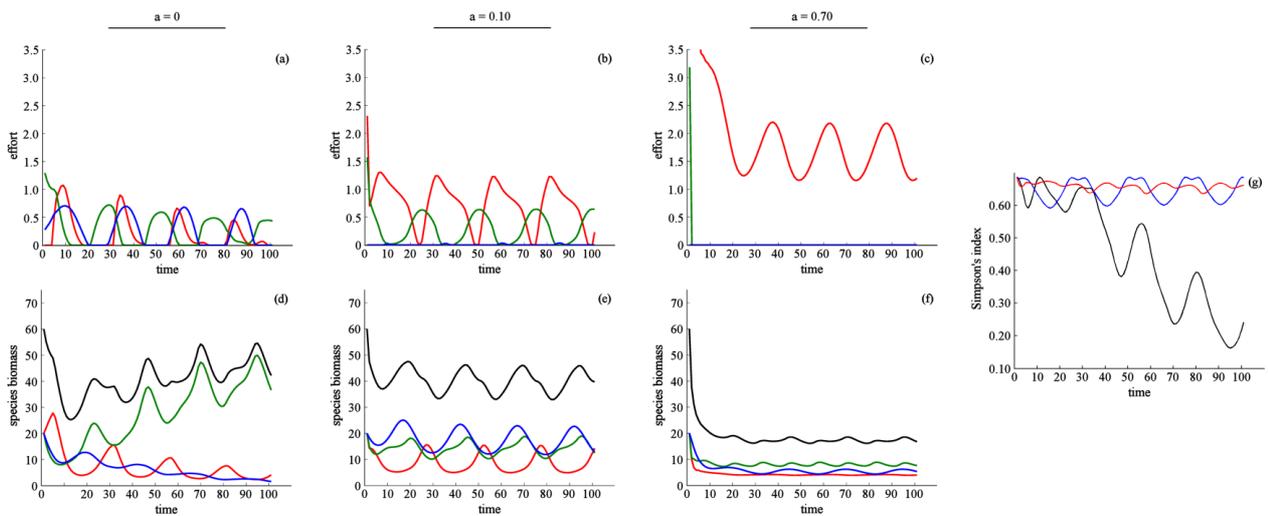
324 We finally considered the case where preferences for species were different between
325 patches. In particular, species 1 was assumed to be the highest valued species in patch 1, species
326 2 the highest valued species in patch 2, and species 3 the highest valued species in patch 3. We
327 found that as dispersal rates increased, harvest increased in the most valuable species. For the
328 less valuable species, we observed two simultaneous shifts in harvest. Specifically, we observed
329 declining rates of pulsed (on-off) harvest, and increasing rates of initial suppression. After the
330 initial suppression, competition and dispersal maintained a more even ratio of species
331 abundances (Figure 6a-f), implying that biodiversity, as measured by the Simpson's index,
332 increased with dispersal (Figure 6g). However, aggregate species biomass declined as the
333 metacommunity became more connected (Figures 6d-f).

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336 5. DISCUSSION

337 In ecological systems without people, the spatial insurance hypothesis predicts a non-monotonic
338 relationship between biodiversity and dispersal (Gonzalez et al., 2009; Loreau et al., 2003;
339 Mouquet and Loreau, 2003). However, in a social-ecological system the effect of dispersal on
340 biodiversity depends only partly on the competitive interactions between species. Just as
341 important is the structure of human preferences for species within and across locations. Since
342 the structure of preferences determines the rate at which each species is harvested, it also
343 determines relative abundances. The consequence is that background species dispersal plays a
344 different role than it does in a pure ecological model. Specifically, we found that biodiversity



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Figure 6. Effect of dispersal when species have *different* ecological parameters, benefits are obtained through harvest only, and preferences for species *differ* between patches. Environmental conditions *differ* across patches. Harvest effort (a-c), species biomass (d-f), and biodiversity (g). In (a-f) dispersal rate is indicated by column: $a = 0$ (a, d), $a = 0.10$ (b, e), and $a = 0.70$ (c, f). Color indicates harvest effort and species biomass for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows aggregate species biomass. In (g) color indicates the dispersal rate: low (black, $a = 0$), intermediate (blue, $a = 0.10$), high (red, $a = 0.70$). Results are presented for patch 1. Other patches are symmetric with respect to the preferences for each species. For visualization we present results with a 100 step time horizon. At longer timescales the dynamics follow the same trends and trajectories (Appendix G).

354 increased monotonically with dispersal *either* if species possessed the same ecological
355 competition parameters *and* preferences were identical across communities, *or* if species
356 possessed different ecological competition parameters *and* preferences were different across
357 communities. Biodiversity was maximized at intermediate dispersal rates only if ecological
358 competition parameters and preferences were different between communities.

359 The difference between our findings and those that bound the system in a way that
360 excludes humans is due to the non-random pressure harvest places on particular species. Indeed,
361 what determines the relative abundances of species in a social-ecological system are the
362 interactions between competition, dispersal, and harvest. If people elect to specialize in the
363 consumption of a single highly-valued species, then dispersal of competitors is undesirable.
364 Indeed, this is often the case in agriculture where people select for particular crops in
365 monocultures and competitors (weeds) are controlled. The rate at which any one species is
366 harvested depends on the relative value of the benefits it offers. If only the direct benefits from
367 consumption are considered, we frequently observe the suppression of less valuable species—a
368 specialization effect of the sort identified by Brock and Xepapadeus (2002). Other joint-harvest
369 models have found that extirpation of the least valuable species may be privately optimal (Clark,
370 1973; Hilborn, 1976; Mesterton-Gibbons, 1996), particularly if the manager can sufficiently target
371 the low or negatively valued species (Fenichel and Horan, 2007b; Fenichel and Horan, 2016). In
372 contrast, considering benefits other than direct consumption leads to the preservation of species
373 (Bertram and Quaas, 2016).

374 If people's preferences are for services supported by aggregate biomass, such as carbon
375 sequestration, or for services supported by the diversity of species in the system (e.g. the
376 regulation of soil erosion or water quality), then the degree of connectivity that leads to the

377 greatest biodiversity is less clear. In practice, species deliver a mix of benefits depending of their
378 traits and abundances. These characteristics determine the degree to which different species are
379 complements or substitutes in the provision of ecosystem services. System management in such
380 cases reflects the ecological interactions between species, and species dispersal from other
381 locations can either be beneficial or harmful. In cases where a species might not naturally persist,
382 dispersal can either accelerate or slow the process. Whether dispersal is beneficial or not then
383 depends on the value attached to the various services that such a species provides.

384 One of the stylized facts reflected in this paper is that resource managers in each
385 community do not consider the effects of dispersal to other communities. The impacts of their
386 decisions on other communities are 'external effects' of those decisions (Bird, 1987; Brock and
387 Xepapadeus, 2010; Fenichel et al., 2014; Shogren and Crocker, 1991; Smith et al., 2009). By
388 changing the abundance of species in each community, resource managers determine the rate at
389 which those species disperse to other communities, but ignore the consequences of this. This
390 allows us to explore the unanticipated effects of dispersal. These effects may be positive or
391 negative. Mass and rescue effects (Brown and Kodric-Brown, 1977; Shmida and Wilson, 1985)
392 can prevent extinction of at-risk species, and source-sink effects can maintain spatially distinct
393 populations of species (Holt, 1985; Pulliam, 1988), but these effects are only a benefit if the
394 target populations are positively valued. There are certainly empirical examples of dispersal
395 replenishing depleted but valuable stocks (Brown and Roughgarden, 1997; Sanchirico and
396 Wilen, 1999), and the relation between harvest and the dispersal of harvested species is one of
397 the main motivations for establishing marine protected areas (Gell and Roberts, 2003;
398 Lubchenco et al., 2003) or wildlife management areas (Johannesen and Skonhøft, 2005; Schulz
399 and Skonhøft, 1996). There are also empirical examples of dispersal causing changes in species

400 composition and/or ecosystem dynamics (Chisholm, 2012; Ehrenfeld, 2010; McKinney and
401 Lockwood, 1999; Rhymer and Simberloff, 1996b). The dispersal of non-native species, for
402 example, is argued to be among the greatest threats to local biodiversity (Gurevitch and Padilla,
403 2004; Sax and Gaines, 2008). From an economic perspective it could be a form of "biological
404 pollution" with potentially harmful species damaging valued species through either predation or
405 competition (Horan et al., 2002). Whether dispersal has positive or negative effects for the social
406 system therefore depends on the social value attaching to the species impacted by it.

407 If resource managers in each community take no account of the effects of their decisions
408 on others, their actions may harm the metacommunity as a whole. In such cases there notionally
409 exists an aggregate social-planner problem in which an overarching decision-maker, possessing
410 perfect information about the states of the world, coordinates local decision-makers and selects
411 harvest rates of species across all communities to maximize aggregate system-level social
412 welfare (Clark, 2010; Conrad and Clark, 1987). The role of the ecological analysis is then to
413 identify the cross-community consequences of dispersal, and hence provide the scientific basis
414 for developing corrective measures to protect the public interest.

415 There are many possible extensions to the model including solving the aggregate social-
416 planner problem or allowing decision-makers to take account of the states of other patches.
417 Decision-makers could also form coalitions, cooperating to jointly maximize the benefits of their
418 group. By eliminating the externality of species dispersal a social planner will provide the
419 highest social welfare. Increasing coordination between decision-makers or information on the
420 states of other patches will increase welfare compared to our baseline case, though it will be
421 second best to the social planner. Further, while we only considered benefits from harvest with

422 species dispersal, there are many extensions regarding the types and distribution of preferences
423 across the metacommunity.

424 The relationship between dispersal and the pattern of species diversity in a social-
425 ecological system depends both on the competitive interactions between species, and the
426 preferences that determine human interventions in the system. In many real systems, the central
427 driver of anthropogenic biodiversity change is the production of foods, fuels, and fibers from a
428 limited set of plants and domesticated animals. This has led to a reduction in species diversity,
429 and with it the capacity of the system to accommodate changing environmental conditions. In the
430 language of the Millennium Ecosystem Assessment, it has led to a reduction in the buffering or
431 regulating services (Millennium Ecosystem Assessment, 2005; Perrings, 2014). In this paper, we
432 see the same effect when the resource-manager values only the consumptive benefits of
433 individual species. As in real systems, the effect is the result of feedbacks between the values
434 that determine harvest, and the dynamic interactions between harvested species. The scientific
435 challenge is to bring feedbacks of this kind into the analysis of ecosystem dynamics in a routine
436 way. We have focused on dispersal as one of the main drivers of ecological change, but the point
437 applies to all anthropogenic stressors equally. Our results, for example, imply that accounting for
438 only ecological and environmental conditions is insufficient to accurately predict community
439 assemblages in response to climate change. Modeling ecological dynamics in the Anthropocene
440 requires that human behavior be integrated into the analysis of species interactions more
441 generally.

442

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CAPTIONS AND TITLES FOR TABLES AND FIGURES

Table 1. Ecological and economic model parameters. Note that " ij " indicate species i on patch j where $i = 1, 2, 3$ and $j = 1, 2, 3$.

Table 2. Summary of results.

Figure 1. Community environmental variation (a) and species consumption (b) curves over time. In (a), color denotes community number: black (community 1, $x_1 = \pi/2$), blue (community 2, $x_2 = 0$), red (community 3, $x_3 = -\pi/2$). The phase parameter, x_j , shifts environmental variation along its x-axis. In (b), species consumption rates are for community 1 and species is indicated by color: black ($H_1 = 1$), charcoal ($H_2 = 1/2$), and light gray ($H_3 = 0$). Consumption rate is determined by the interaction by the species competition parameter and environmental variation. Reproduced from Shanafelt et al. (2015).

Figure 2. Effect of harvest price when benefits are obtained from harvest only (a, d), harvest and abundance (b, e), and harvest and the mix of species (c, f). Harvest effort (a-c), species biomass (d-f), and biodiversity (g, h). In (a-f) color indicates harvest effort and species biomass for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows aggregate species biomass. In (g, h) color indicates the types of benefits: harvest only (black), harvest and abundance (blue), harvest and the mix of species (red). Note the difference in the y-axes in (g) and (h). The dynamics when benefits are derived solely from harvest take longer to reach equilibrium than when benefits are also derived from abundance and the mix of species, or when the system is coupled via dispersal. For the sake of comparison we present results for a 100 step time horizon here (a, d, g). We present results for a longer timescale in Appendix G. The dynamics follow the same trajectory as here, saturating and settling into a persistent, fluctuating equilibrium.

Figure 3. Effect of dispersal when species have *identical* ecological parameters, benefits are obtained through harvest only, and preferences for species are *identical* across patches. Environmental conditions *differ* between patches. Harvest effort (a, b), species biomass (c, d), and biodiversity (e). In (a-d) dispersal rate is indicated by column: $a = 0.07$ (a, c), and $a = 0.40$ (b, d). Color indicates harvest effort and species biomass for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows aggregate species biomass. In (e) color indicates the dispersal rate: intermediate (blue, $a = 0.07$), high (red, $a = 0.40$).

Figure 4. Effect of dispersal when species have *identical* ecological parameters, benefits are obtained through harvest only, and preferences for species *differ* across patches. Environmental conditions *differ* between patches. Harvest effort (a, b), species biomass (c, d), and biodiversity (e). In (a-d) dispersal rate is indicated by column: $a = 0.04$ (a, c), and $a = 0.70$ (b, d). Color indicates harvest effort and species biomass for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows aggregate species biomass. In (e) color indicates the dispersal rate: intermediate (blue, $a = 0.04$), high (red, $a = 0.70$). Results are

726 presented for patch 1. Other patches are symmetric with respect to the preferences for each
727 species.

728

729 Figure 5. Effect of dispersal when species have *different* ecological parameters, benefits are
730 obtained through harvest only, and preferences for species are *identical* between patches.
731 Environmental conditions are the *same* across patches. Harvest effort (a-c), species biomass (d-
732 f), and biodiversity (g). In (a-f) dispersal rate is indicated by column: $a = 0$ (a, d), $a = 0.07$ (b, e),
733 and $a = 0.40$ (c, f). Color indicates harvest effort and species biomass for species 1 (red, highest
734 harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows
735 aggregate species biomass. In (g) color indicates the dispersal rate: low (black, $a = 0$),
736 intermediate (blue, $a = 0.07$), high (red, $a = 0.40$). For visualization we present results with a
737 100 step time horizon. At longer timescales the dynamics follow the same trends and trajectories
738 (Appendix G).

739

740 Figure 6. Effect of dispersal when species have *different* ecological parameters, benefits are
741 obtained through harvest only, and preferences for species *differ* between patches.
742 Environmental conditions *differ* across patches. Harvest effort (a-c), species biomass (d-f), and
743 biodiversity (g). In (a-f) dispersal rate is indicated by column: $a = 0$ (a, d), $a = 0.10$ (b, e), and
744 $a = 0.70$ (c, f). Color indicates harvest effort and species biomass for species 1 (red, highest
745 harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows
746 aggregate species biomass. In (g) color indicates the dispersal rate: low (black, $a = 0$),
747 intermediate (blue, $a = 0.10$), high (red, $a = 0.70$). Results are presented for patch 1. Other
748 patches are symmetric with respect to the preferences for each species. For visualization we
749 present results with a 100 step time horizon. At longer timescales the dynamics follow the same
750 trends and trajectories (Appendix G).