

THE BIODIVERSITY AND PRODUCTIVITY EFFECTS OF PREFERENCES OVER THE STOCK AND FLOW BENEFITS OF SPECIES

David Shanafelt, William Brock, Charles Perrings, Ingela Alger, Jean Clobert, Michael Hochberg, Ann Kinzig, Michel De Lara, Michel Loreau, Pablo Marquet, Francois Salanie, Claire de Mazancourt, Ann-Sophie Lafuite

ABSTRACT

Accelerating rates of biodiversity loss have led ecologists to explore the effect of changes in species richness on ecosystem functioning, and the resulting flow of ecosystem services. In this paper we consider the relation between biodiversity, productivity and ecosystem services within a single system. In human dominated systems, the competitive processes between species are the result of both competitive processes of the ecological system and human decisions to promote or suppress species. Moreover, at least some valuable services arise from non-consumptive benefits, such as flows of services generated from ecosystem services and function. In this study, we consider the impact of resource use decisions on biodiversity and productivity, where resource use depends on the preferences people have for the direct consumption (harvest) of biomass of different species, the non-consumptive benefits of biomass, and the non-consumptive benefits of biodiversity. We find that the inclusion of two different kinds of non-consumptive benefit significantly affects harvest rates, biodiversity and productivity.

JEL Codes: Q57

Keywords: bioeconomics, biodiversity, productivity, non-consumptive benefits

INTRODUCTION

Accelerating rates of biodiversity loss have led ecologists to explore the effect of changes in species richness on ecosystem functioning, and the resulting flow of ecosystem services (Assessment 2005; Cardinale et al. 2012). While some studies have evaluated the effect of species richness on mean levels of ecosystem functioning, most have focused on the impact of biodiversity on the variability of ecosystem functioning (Loreau 2010; Loreau and Hector 2001; Loreau et al. 2012). One of the primary mechanisms proposed is the spatial insurance hypothesis, which centers on the idea that the functional complementarity of species across space and time insures the system against environmental variability, including spatially distributed anthropogenic shocks (Loreau et al. 2003). Specifically, the stability of primary production in the meta-community resides on the number of functionally redundant species within each spatially distributed sub-community, which is a function of the rate at which species disperse between sub-communities. The hypothesis addresses one of the main challenges posed by the closer integration of ecological systems, e.g. the consequences of community integration on the stability of those systems.

While we are ultimately interested in the implications of the closer integration of coupled ecological-economic systems, in this paper we consider the relation between biodiversity, productivity and ecosystem services within a single system. In human dominated systems, the competitive processes within communities play out alongside the effects of human decisions. The relative abundance of species is a result both of competitive processes in the ecological system and of the choices people make to promote or suppress species. Species are selected for or against depending on whether they positively or negatively affect the production of valuable ecosystem services. Crops may be promoted while crop competitors, predators, and pathogens are suppressed. Charismatic mega fauna may be protected while undistinguished plants or insects are ignored. The resulting mix of species reflects the joint effect of human control and natural ecological dynamics.

Peoples' preferences over the range of species depend on the traits that make individual species useful sources of foods, fuels, fibers, pharmaceuticals, inspiration, information and amenity. But they also

depend on the role that combinations of species play in the production of different ecosystem services. People derive both stock and flow benefits from species. In some cases the benefits depend on the harvest and consumption of species. In others the benefits are non-consumptive, and depend on the role of multiple stocks in the provision of ecosystem services. For services such as carbon sequestration or storage the traits of individual species are less important than the biomass of all species. For services such as pollination, or soil stabilization, what matters is the capacity of the members of functional groups of species to operate in different environmental conditions. The benefits of species in such cases are a function of the stocks of all members of the functional group, and the variability of environmental conditions (Assessment 2005).

In this study, we consider the impact of resource use decisions on biodiversity and productivity, where resource use depends on the preferences people have for the direct consumption (harvest) of biomass of different species, the non-consumptive benefits of biomass, and the non-consumptive benefits of biodiversity. The importance of the distinction between consumptive and non-consumptive benefits of species for their optimal management has already been recognized in the literature (Brock and Xepapadeas 2002; Horan and Shortle 1999). For instance, the International Whaling Commission's 1985/86 moratorium on Minke whales was shown to be optimal only if stock values were considered (Horan and Shortle 1999). However, less attention has been paid to the joint effect of multiple uses on the stability and productivity of the ecosystem. In a model with fluctuating growth that considers the joint management of multiple species, we find that the inclusion of two different kinds of non-consumptive benefit—one more sensitive to the composition of species than the other—significantly affects harvest rates, biodiversity and productivity.

THE ECOLOGICAL MODEL

We assume the same ecological dynamics of Loreau et al. (2003) and Gonzalez et al. (2009). Consider a metacommunity with M communities and S species. Within each community, each species competes for

a single limiting resource of which the quantity consumed varies by species, environmental conditions, and time. Communities are coupled together by the natural dispersal of species. When dispersal rates are low, each community functions as a separate closed system; when dispersal rates are high, the metacommunity functions as a single patch.

Formally the change in species biomass N and resource biomass R in the j th community are governed by the set of 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 $i = 1, 2, \dots, S$ and communities $j = 1, 2, \dots, M$ at time t . Species are assumed to consume resource at the normalized 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 . Species are assumed to disperse between communities at a constant rate a . Species consumption of natural resource is a non-linear function of species-specific traits and environmental variation fluctuating over time for each species in each community such that:

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

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

H_i is a dimensionless, species and community-dependent competition parameter such that $H_i = 1$ and $H_i = H_{i-1} - 1/M$ for $i=1,2,\dots,S$. It is assumed that environmental conditions, E_j , vary temporally fluctuating over time as a sinusoidal function. x_j , a phase parameter, is a random variable drawn from a uniform distribution $[-2\pi, 2\pi]$ which shifts the environmental variation along its horizontal axis (Figure 1). T determines the period of the environmental variation and the subsequent periodicity of species consumption rates. The length of the period was chosen so that in the absence of dispersal ($a = 0$) a single species quickly drives all other species to extinction. Too large a period with respect to the total simulation time causes consumption to be functionally linear. It is known that in such cases local species coexistence is impossible (Armstrong and McGehee 1980).

By construction, this setup ensures that, in the absence of human intervention or dispersal, a single species will completely exclude all others in a given community. This will be the species that possesses the highest initial consumption rate as designated by the interaction between the species competition parameter H_i and the initial level of environmental variation. A "generalist" species may be defined as a species whose consumption rates are closest to the average over the course of the simulation period. In a tightly coupled, high dispersal system the most "generalist" species will exclude all others across the metacommunity.

Productivity, or "ecological utility," is measured as the average increment in species biomass per unit of time given by:

$$\varphi(t) = \frac{\sum_{i=1}^S \sum_{j=1}^M e c_{ij}(t) N_{ij}(t) R_j(t)}{M}$$

[5]

System stability is then measured by the inverse of the coefficient of variation over time in productivity, a commonly used metric in ecology (Tilman et al. 1998).

The ecological model depends on several assumptions that should be noted. First, it is assumed that communities initially contain the same set of species and differ only in their environmental variation over time as defined by the phase parameter x_j . Ecologically, the set of species may be different between natural systems (though they may be functionally similar). However, as humans introduce species into non-native ranges, we have begun to see a homogenization of species worldwide. Similarly, in urban areas, people often choose which species are present, such as which plants to include in a landscape or crops in a field. Second, species differ only in consumption rates that vary by community and time as a function of H_i , x_j , and t . This implies that species are more or less similar in their ecological function, such as of different subspecies or phenotypes, and exist within a single trophic level. Third, species compete for a single limiting resource whose natural influx and loss rates are constant across time and communities. This could be thought of as water in a desert ecosystem or nitrogen in a forest ecosystem, or by extension fertilizer or irrigation in an agricultural system. Fourth, species competition arises solely from resource consumption; there is no direct interaction between species within and across patches (e.g. competition for light or nutrients in plant systems). These assumptions simplify the analysis while providing a structure for species competition across environmental conditions, and may prove more valid in coupled socio-economic systems. For a detailed analysis and extension of the model, see Loreau et al. (2003), Gonzalez et al. (2009), Urban (2006), and Shanafelt et al. (*In Review*).

THE BIOECONOMIC MODEL

Consider a single patch, which now can be thought of as a country, with S functionally similar species in which humans exist. People gain utility ("well-being") from the direct consumption of species and from non-consumptive benefits arising from species abundance and biodiversity. The latter may include, for example, the value of biomass for carbon sequestration, the recreational, aesthetic, totemic or spiritual

values of biodiversity, or the benefits from stabilizing effects of biodiversity on ecosystem functioning and the subsequent flow of ecosystem services.¹

We may rewrite [1] and [2] to account for species extraction as:

$$[6] \quad \frac{dN_i}{dt} = N_i(t)(ec_i(t)R(t) - m) - qL_i(t)$$

$$[7] \quad \frac{dR}{dt} = I - lR(t) - R(t) \sum_{i=1}^S c_i(t)N_i(t)$$

where L_i is the quantity of labor invested in species i ($0 \leq L_i \leq 100$) and q is the harvest efficiency or proportion of species harvested that is available for consumption.

We assume that a single institution or manager determines the quantities of species harvest that maximizes social utility, or the aggregate utility of all individuals in the community. Formally, we define the utility maximization problem as:

$$[8] \quad \max_{L_i} \int_0^T \left[\sum_{i=1}^S \left(p_i q L_i(t) - \frac{w L_i(t)}{N_i(t)} + A_i N_i(t) \right) + B \left(1 - \sum_{i=1}^S \left(\frac{N_i(t)}{N(t)} \right)^2 \right) \right] e^{-\delta t} dt$$

subject to:

[6] and [7]

$N_i(0), R(0), \lambda_i(T), \mu(T)$

$N_i(t) \geq 0, R \geq 0$

¹ It is generally accepted in ecology that biodiversity is linked to ecosystem functioning and the subsequent flow of ecosystem services (Assessment 2005, Cardinale et al. 2012).

where p_i is the price per unit species harvested (a measure of the marginal social benefit of species i), w the per unit cost of labor, A_i the benefit per unit of the abundance of species i , and B the total non-consumptive benefits of biodiversity. Non-consumptive benefits from species biomass is a non-saturating function and may be thought of as benefits from, for example, carbon sequestration. Note that B is a scalar index of biodiversity, in our case a Simpson's index (Simpson 1949). 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.² $N(t)$ indicates the sum of all species in the community. δ is the discount rate. λ_i and μ represent the value of an extra unit of species and resource biomass respectively, termed the "shadow value" or "shadow price."

The cost function (C) exhibits two important properties. First, marginal costs of labor are always positive ($\partial C_i / \partial L_i > 0, \forall i$). Second, $N_i(t)$ in the denominator reflects the fact that costs are inversely related to species biomass. As species abundances fall, individuals are more difficult to locate and more costly to harvest.

Suppressing time arguments, we may define the current-value Hamiltonian as:

$$\begin{aligned}
 H^{CV} = & \sum_{i=1}^S \left(p_i q L_i - \frac{w L_i}{N_i} + A_i N_i \right) + B \left(1 - \sum_{i=1}^S \frac{N_i}{N} \right) \\
 [9] \quad & + \sum_{i=1}^S (\lambda_i N_i e c_i R - \lambda_i N_i m - \lambda_i q L_i) + \mu \left(I - lR - R \sum_{i=1}^S c_i N_i \right)
 \end{aligned}$$

The first order necessary conditions for L_i to maximize social utility include:

$$\frac{\partial H}{\partial L_i} = p_i q - \frac{w}{N_i} - \lambda_i q = 0$$

[10]

² Many indices exist to measure biodiversity, many of which are strongly correlated (Bandeira et al. 2013).

$$[11] \quad \dot{\lambda}_i = -\frac{\partial H}{\partial N_i} = \mu R c_i + \lambda_i (m - e c_i R + \delta) - \frac{w L_i}{N_i^2} - A_i - \frac{2 \left(\sum_{k \neq i} N_k^2 - N_i \sum_{k \neq i} N_k \right)}{\left(\sum_{k=1}^S N_k \right)^3}$$

$$[12] \quad \dot{\mu} = -\frac{\partial H}{\partial R} = \mu \left(l + \sum_{i=1}^S c_i N_i + \delta \right) - \sum_{i=1}^S \lambda_i N_i e c_i$$

From [10], we can see that the shadow value of an extra unit of species biomass increases with the marginal net benefit of labor - the difference between the price of a unit of harvested species and the cost per unit harvested species.

$$[13] \quad \lambda_i = p_i - \frac{w}{N_i q}$$

Differentiating [13] with respect to time yields:

$$[14] \quad \dot{\lambda}_i = \frac{w e c_i R}{N_i q} - \frac{w m}{N_i q} - \frac{w L_i}{N_i^2}$$

By substituting [13] and [14] into [11], it can be shown that:

$$[15] \quad \mu = \frac{w \delta}{N_i q R c_i} + \frac{p_i (e c_i R - m - \delta)}{R c_i} + \frac{A_i}{R c_i} + 2B \left[\frac{\sum_{k \neq i} N_k^2 - N_i \sum_{k \neq i} N_k}{\left(\sum_{i=1}^S N_i \right)^3} \right]$$

Differentiating [15] with respect to time yields an expression for $\dot{\mu}$, which by substituting into [12] along with [13] and [14] allows us to solve for the optimal value of labor as a function of our state variables and model parameters. The derivation of $\dot{\mu}$ and L_i^* in this manner is found in the Appendix.

Alternatively, evaluating [11] and [12] at the steady state, we can see that:

$$[16] \quad \mu = \frac{\sum_{i=1}^S \lambda_i N_i e c_i}{l + \sum_{i=1}^S c_i N_i + \delta}$$

The value of an extra unit of resource changes according to the ratio between the value of new growth of all species and marginal losses of the resource. By substituting λ_i and μ into [11], we may solve for the optimal labor (harvest) of species i in terms of the model parameters:

$$[17] \quad L_i^* = \frac{N_i^2}{w} \left[\frac{e c_i R \sum_{j=1}^S \left(p_j N_j c_j - \frac{w c_j}{q} \right)}{l + \sum_{j=1}^S (c_j N_j) + \delta} + \left(p_i - \frac{w}{N_i q} \right) (m - e c_i R + \delta) - A_i - B \left(\frac{2 \left(\sum_{k \neq i} N_k^2 - N_i \sum_{k \neq i} N_k \right)}{\left(\sum_{k=1}^S N_k \right)^3} \right) \right]$$

The first term in [15] captures the value of the resource made available for species consumption. It is price of an extra unit of resource multiplied by the proportion of resources that are actually used to generate new species biomass. The second term represents the cost of a loss of species biomass due to extraction. The final two terms are the marginal losses of species abundance and biodiversity due to the loss of species by harvest.

For our analysis, we consider three cases: 1) people gain benefits solely from the direct consumption of species biomass (species harvest), 2) people gain benefits from the direct consumption of species biomass and the non-consumptive benefits of species biomass (species abundance), and 3) people gain benefits from the direct consumption of species biomass and the non-consumptive benefits of species biodiversity.

We solve the maximization problem [8] using the forward-backward sweep method of Lenhart and Workman (2007).³ For each iteration of the numerical analysis, we solve [6] and [7] forwards in time, given initial conditions of species and resource biomass and labor. Then, with the updated species biomass and resource vectors, we solve [11] and [12] backwards in time to generate the optimal path of the costate variables.⁴ The resulting optimal values of N_i and R are substituted into [15] to solve for the optimal labor values for each species per moment in time. Vectors for state, costate, and labor are compared with values from the previous iteration to determine convergence to a single solution. If the solutions do not differ by ε percent, the solution is said to have converged; otherwise the labor vector is re-fed into [6] and [7] and the forward-backward sweep is repeated. In order to reflect human time scales, simulations were run for a time horizon of 100 time steps or years. For a full list of parameter values, see Table 1.

RESULTS - BENEFITS FROM HARVEST

Because the manager considers the effect of current harvest on future stock populations, it follows that species are harvested according to their growth rates with the most valuable species experiencing the greatest rate of extraction (Figure 2a). At the same time, given forward looking behavior, it is in the best interest of the manager to maintain the population of the most valuable stock for future harvest. In choosing their level of harvest, managers balance the current net profits of harvest and implicitly the future benefit of greater growth in the most profitable species. In the community, species compete for resources - the manager may suppress less valuable species in order to relieve competitive pressure on the

³ Alternatively, we solved the maximization problem using the method of dynamic programming (Conrad and Clark 1987). By maximizing the Bellman equation, we obtain qualitatively similar results.

⁴ [6]-[7] and [11]-[12] are solved numerically using a 4th order Runge-Kutta ODE estimator with an adjustable step size.

most profitable. We observe this by a high initial pulse of harvest at the beginning of the simulation which drives down species biomass. Specifically, the lesser profitable species populations driven down the most, and are then maintained at monotonically decreasing population levels. Populations of the most profitable species utilize the extra resources and grow at a faster rate despite increasing levels of harvest (Figure 2a, d).

Productivity (net growth) and resource biomass reach a cyclic equilibrium - although the lesser valued species populations are in decline, the system experiences greater ecological growth in the most profitable species that maintains productivity (Figure 2c, e). Suppression relieves competitive pressure for the limiting resource, increasing the growth rate of the most profitable species. However, this comes at the expense of biodiversity (Figure 2f), whose variance increases over time.

RESULTS - BENEFITS FROM HARVEST AND ABUNDANCE

Allowing people to gain utility from species harvest and species abundance causes harvest rates of species to converge to similar levels. When the non-use abundance value of species are equal, harvest rates approach the same value regardless of the market price. However, as the benefits of abundance increase, harvest may decrease until minimal or no species are harvested - species are more valuable in the "wild" than for consumption (Figure 3a, d, g).

The minimal harvest scenario is equivalent to a no-catch zone or wildlife protected area. (Any harvest in this scenario may be viewed as wildlife management such as culling in deer populations or harvest and replanting of the timber industry.) The dominant or most abundant species in the community shifts from the most profitable species to the least profitable, although eventually species populations are maintained at equivalent levels (Figure 3b, e, h). Since benefits are still gained from harvest and the non-consumptive benefits of species biomass are equivalent for all species, then managers maximize the net benefits of each species by balancing benefits from harvest and abundance - for the most profitable species, more benefits are gained through harvest, while benefits from less profitable species are gained

more through abundance. This behavior is reflected in a shift to a low level bang-bang harvest policy (Figure 3d, g).

As harvest decreases, aggregate species biomass increases leading to lower resource biomass (Figure 3c, f, i). Productivity and biodiversity are higher than the harvest-only case, although we observe a diminishing returns of scale. As the non-consumptive benefits of species biomass increases, we see a smaller effects on productivity, biodiversity, and utility (Figure 4). In fact, productivity is maintained regardless of the decreases in harvest.

RESULTS - BENEFITS FROM HARVEST AND BIODIVERSITY

Assume that people gain utility from species harvest and biodiversity ($p_i, B > 0, A_i = 0$). As we increase the benefits gained from biodiversity, labor and aggregate species biomass are maintained at the same level as the harvest only case, but labor is more evenly distributed across species (Figures 5a, b, d, e). This causes the proportion of species biomass to be more even and the Simpson's biodiversity index to increase to a maximum (Figure 6c). Although the biomass of the most profitable species is maintained at higher levels than other species, the benefits from biodiversity cause managers to sustain the populations of other species. We do not observe the suppression of less profitable species.

However, despite increases in biodiversity, productivity remains constant (Figure 6b). This is contrary to other studies of our ecological model, which associated biodiversity with greater rates of productivity (Gonzalez et al. 2009; Loreau et al. 2003). Contrarily, Shanafelt et al. (*In Review*), found that with the same ecological model, productivity was robust to a broad spectrum of biodiversity.

DISCUSSION

In all cases managers harvest species in a manner that fluctuates with species growth rates. Managers implicitly take into account species growth rates by considering the effects of harvest on current utility

but also future stocks in their management decisions. This result confirms several economic analyses that consider fluctuating growth rates in species stocks (Carson et al. 2009; Costello et al. 1998; Costello et al. 2001; Hannesson and Steinshamn 1991; Parma 1990).

When only benefits from the direct consumption of species are considered, we observe the suppression of less valuable species within a given patch. Initially the lesser (most) profitable species populations are heavily (lightly) harvested, then harvested at a lower (higher) rates that maintain negative (positive) growth of those species. This removes competitive pressure on the most preferred species and allows its populations to grow despite increased harvest rates later in time. This effect is driven by the preferences between species. In a similar bioeconomic model with constant species growth rates, Brock and Xepapadeus also find specialization of species, which is driven by the proportion of price per unit species harvest and the rate of resources consumed per species (Brock and Xepapadeus 2002)

We find that decreased or zero harvest may be optimal when managers consider stock benefits—the non-consumptive benefits from biomass and biodiversity—in their decision to harvest species. This result has been a common theme in resource economics - if a stock possesses value other than as a strict consumptive resource, it is harvested at a lower rate (Hartman 1976). Several other studies have found that the incorporation of non-consumptive benefits alters the optimality conditions of harvest (Brock and Xepapadeus 2002; Horan et al. 2002). If existence value was incorporated into the evaluation of Minke whale harvest, moratorium (cessation) may be optimal (Horan and Shortle 1999). Similarly, inclusion of benefits from species biomass shifts the specialization of species within a given patch to be dependent on the price per unit resource consumption and the value assigned to the flow of benefits arising from species biomass (Brock and Xepapadeus 2002).

We find differential effects of preferences for services that depend on biodiversity and species biomass. As the benefits of abundance increase, harvest rates switch from high rates of specialized harvest to low rates of pulse harvest. In the case of flows of benefits from biodiversity, managers harvest at much the same harvest rates but do not specialize between species. It is possible for a country with low species abundances and a country with high species abundances to possess the same Simpson's diversity

index, given the ratio of species abundances are equal. A key finding is that when non-consumptive benefits are considered in management decisions, the impact on the stability and productivity of the ecological system reflects the relative value of the various services involved. A tradeoff exists between the direct economic consumption of species biomass and the non-consumptive benefits of abundance and biodiversity.

REFERENCES

- Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. *The American Naturalist* 115:151-170.
- Assessment, M. E. 2005. *Ecosystems and human well-being: Biodiversity synthesis*. Washington, DC, World Resources Institute.
- Bandeira, B., J. L. Jamet, D. Jamet, and J. M. Ginoux. 2013. Mathematical converges of biodiversity indices. *Ecological Indicators* 29:522-528.
- Brock, W., and A. Xepapadeus. 2002. Optimal ecosystem management when species compete for limiting resources. *Journal of Environmental Economics and Management* 44:189-220.
- Cardinale, B. J., E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani et al. 2012. Biodiversity loss and its impact on humanity. *Nature* 486:59-67.
- Carson, R. T., C. W. J. Granger, J. B. C. Jackson, and W. Schlenker. 2009. Fisheries management under cyclical population dynamics. *Environmental Resource Economics* 42:379-410.
- Conrad, J. M., and C. W. Clark. 1987, *Natural resource economics: Notes and problems*, Cambridge University Press.
- Costello, C., R. M. Adams, and S. Polasky. 1998. The value of El Nino forecasts in the management of salmon: A stochastic dynamic assessment. *American Journal of Agricultural Economics* 80:765-777.

- Costello, C., S. Polasky, and A. Solow. 2001. Renewable resource management with environmental prediction. *The Canadian Journal of Economics* 1.
- Gonzalez, A., N. Mouquet, and M. Loreau. 2009. Biodiversity as spatial insurance: The effects of habitat fragmentation and dispersal on ecosystem functioning *in* S. Naeem, D. E. Bunker, A. Hector, M. Loreau, and C. Perrings, eds. *Biodiversity, Ecosystem Functioning, and Human Wellbeing*, Oxford University Press.
- Hannesson, R., and S. I. Steinshamn. 1991. How to set catch quotas: Constant effort or constant catch? *Journal of Environmental Economics and Management* 20:71-91.
- Hartman, R. 1976. The harvest decision when a standing forest has value. *Economic Inquiry* 14:52-58.
- Horan, R., and J. S. Shortle. 1999. Optimal management of renewable resource stocks: An application to Minke whales. *Environmental Resource Economics* 13:435-458.
- Horan, R. D., C. Perrings, F. Lupi, and E. H. Bulte. 2002. Biological pollution prevention strategies under ignorance: The case of invasive species. *American Journal of Agricultural Economics* 84:1303-1310.
- Lehman, C. L., and D. Tilman. 2000. Biodiversity, stability, and productivity in competitive communities. *The American Naturalist* 156:534-552.
- Lenhart, S., and J. T. Workman. 2007, *Optimal Control Applied to Biological Models*, Chapman and Hall.
- Loreau, M. 2010, *From populations to ecosystems: Theoretical foundations for a new ecological synthesis*. Princeton, New Jersey, Princeton University Press.
- Loreau, M., and C. de Mazancourt. 2013. Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters* 16:106-115.
- Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72-76.
- Loreau, M., N. Mouquet, and A. Gonzalez. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *PNAS* 100:12765-12770.

- Loreau, M., J. Sapijanskas, F. Isbell, and A. Hector. 2012. Niche and fitness differences relate the maintenance of diversity to ecosystem function: Comment. *Ecology* 93:1482-1487.
- Parma, A. M. 1990. Optimal harvesting in fish populations with non-stationary stock-recruitment relationships. *Natural Resource Modeling* 4:39-76.
- Simpson, E. H. 1949. Measurement of diversity. *Nature* 163:688.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: A search for general principles. *Ecology* 80:1455-1474.
- Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity-stability relationships: Statistical inevitability or ecological consequence? *The American Naturalist* 151:277-282.
- Urban, M. C. 2006. Maladaptation and mass effects in a metacommunity: Consequences for species coexistence. *The American Naturalist* 168:28-40.

Table 1. Model parameters.

Variable	Value	Interpretation	Units
H_i	1/2, 1/2, 1/2	Species competition parameter	-
$c_i(t)$	variable [0, 0.15]	Species consumption rate of resource biomass	$\frac{1}{\text{species biomass} * \text{time}}$
e	0.2	Resource to species biomass conversion efficiency	$\frac{\text{species biomass}}{\text{resource biomass}}$
m	0.2	Natural mortality rate	time^{-1}
I	165	Patch resource influx	$\frac{\text{resource biomass}}{\text{time}}$
l	10	Rate of resource loss	time^{-1}
T	25	Environmental periodicity	time
p_i	14,15,16	Price per unit species harvested	dollars
w	25	Cost per unit labor	$\frac{\text{dollars} * \text{species biomass}}{\text{labor}}$
q	0.2	Harvest efficiency	$\frac{\text{labor}}{\text{species biomass}}$
δ	0.01	Discount rate	-
A	variable [0, 1.4]	Non-consumptive benefit per unit species biomass	$\frac{\text{dollars}}{\text{species biomass}}$
B	variable [0, 50]	Non-consumptive benefit on biodiversity	dollars
$N_i(0)$	20	Initial species biomass	species biomass
$R(0)$	15	Initial resource biomass	resource biomass
$\lambda_i(T)$	unbounded	Value of an extra unit of species biomass at end of time horizon	dollars
$\mu(T)$	unbounded	Value of an extra unit of resource biomass at end of time horizon	dollars

Note that a value of "-" indicates a dimensionless parameter.

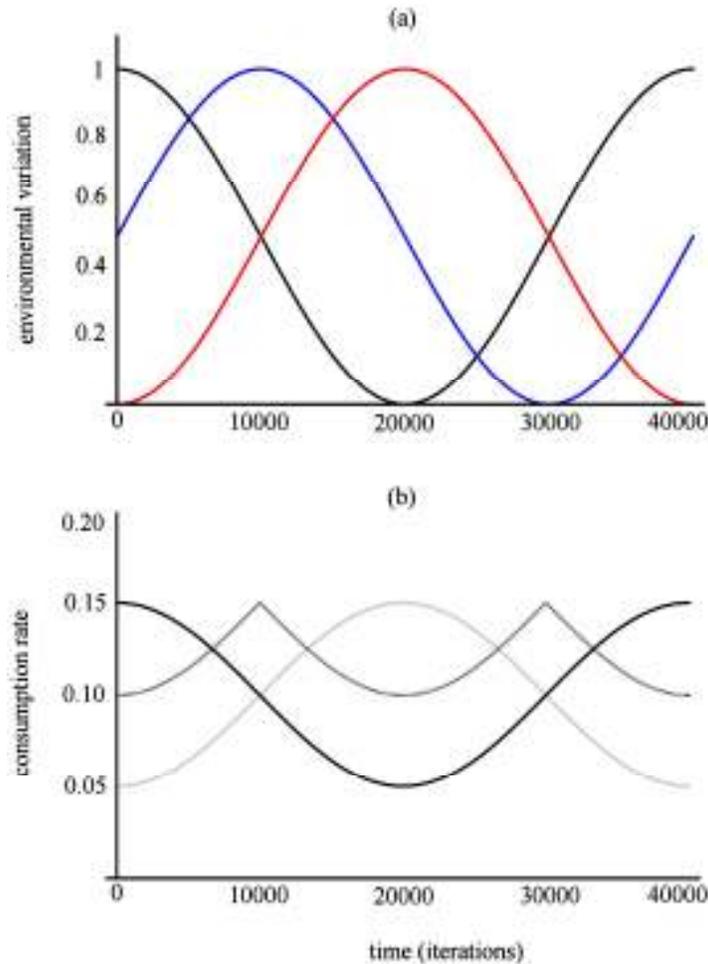


Figure 1. Community environmental variation (a) and species consumption (b) over time. (a) color denotes community number: black (community 1, $x_1 = \pi/2$), blue (community 2, $x_2 = 0$), red (community 3, $x_3 = -\pi/2$). The phase parameter, x_j , $H_1 = 1$, shifts the environmental variation along the x-axis. (b) species consumption rates for community 1 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 times environmental variation. Values of x_j and H_i were chosen to illustrate the full spectrum of potential environmental variation and consumption rate curves.

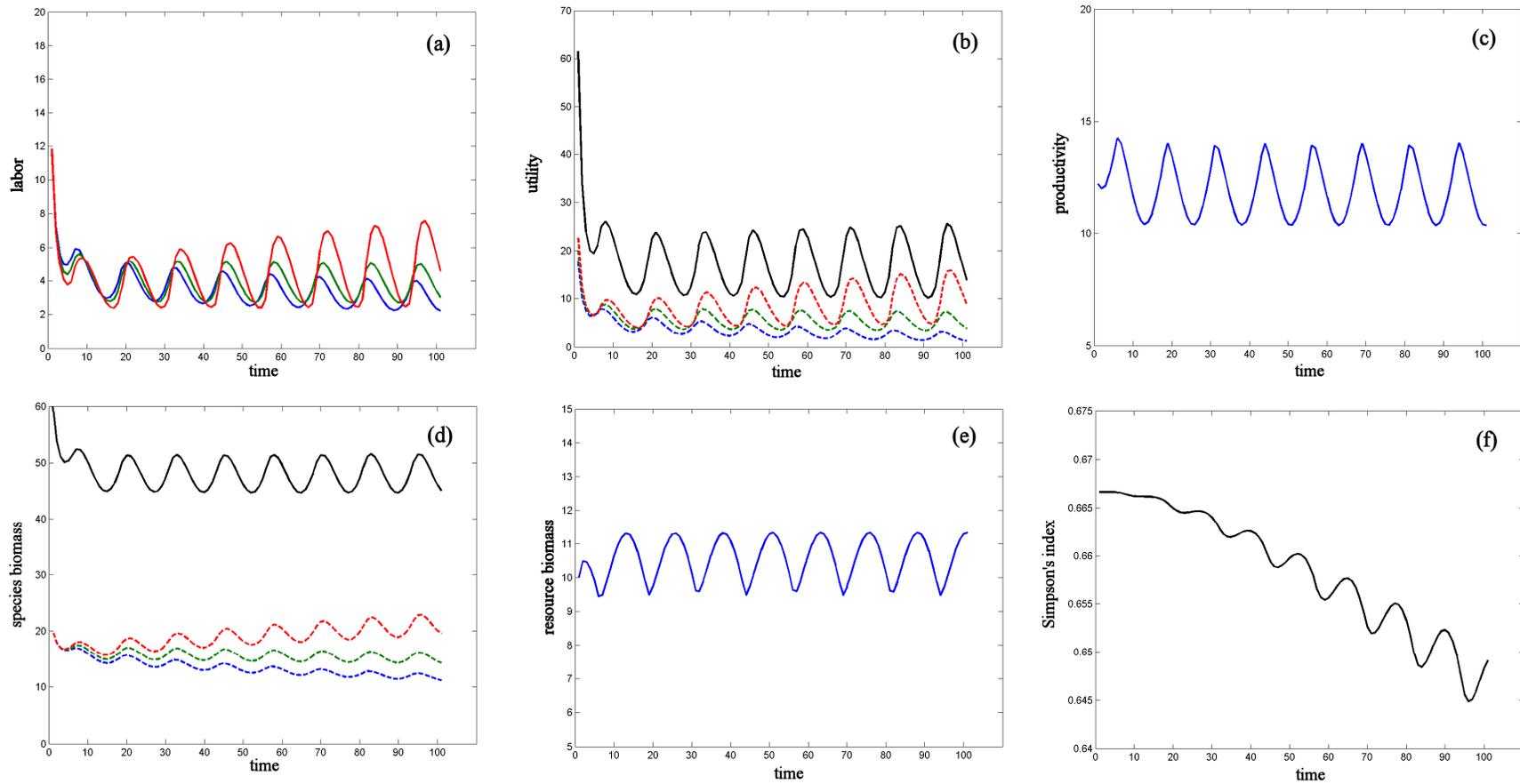


Figure 2. Effect of heterogeneous prices when benefits are obtained solely through the direct consumption of species. Labor (a); utility (b); productivity (c); species biomass (d); resource biomass (e); biodiversity (Simpson's index). Color indicates species: species 1 (blue, lowest harvest price), species 2 (green), species 3 (red, greatest harvest price). In (b) and (d), dashed lines denote values of individual species biomass utility and biomass respectively; the solid, black line is the aggregate level of utility or biomass across all species.

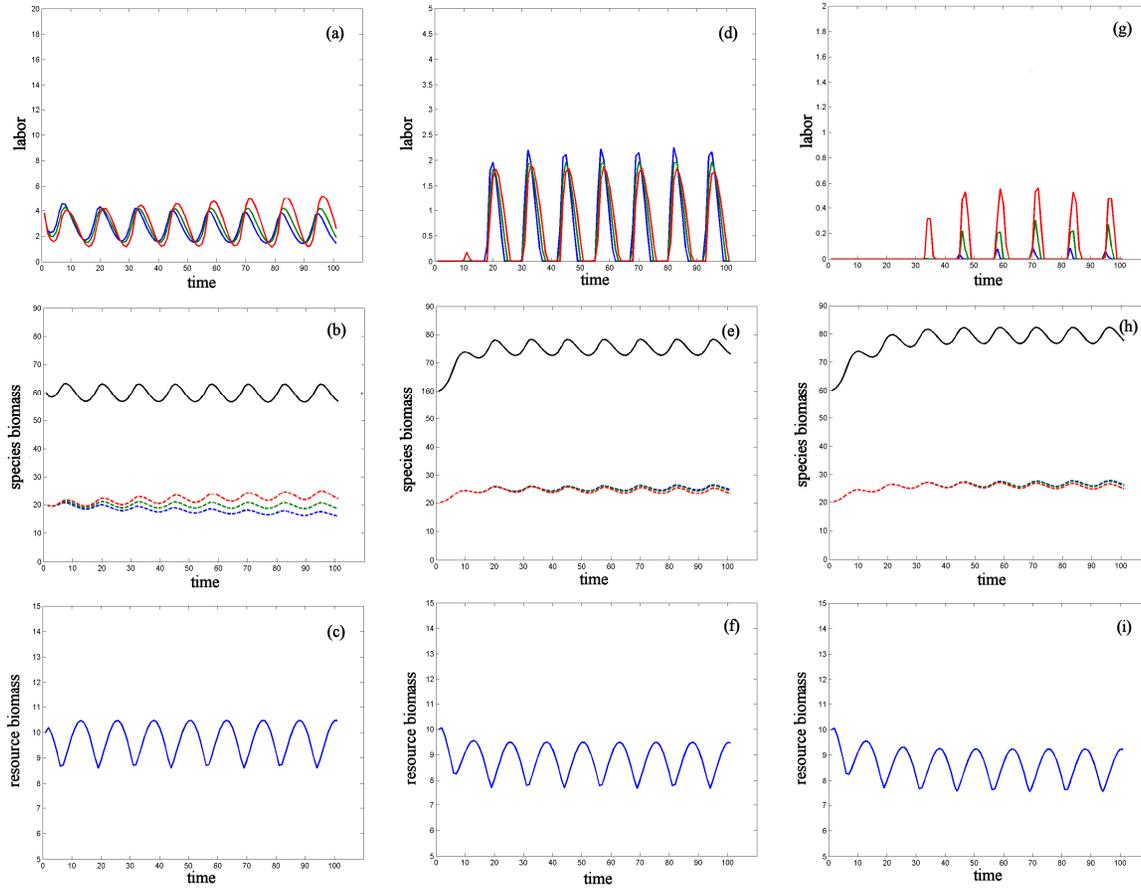


Figure 3. Effect of heterogeneous prices when benefits are obtained through the direct consumption of species and non-consumptive benefits of species biomass. The non-consumptive benefits, A , are equivalent for all species: $A = 0.5$ (a-c), $A = 1$ (d-f), and $A = 1.14$ (g-i). Labor (a, d, g); species biomass (b, e, h); resource biomass (c, f, i). Color indicates species: species 1 (blue, lowest harvest price), species 2 (green), species 3 (red, greatest harvest price). In (b, e, h), dashed lines denote values of individual species biomass; the solid, black line is the aggregate level of biomass across all species. When $A > 1.14$, the optimal labor value is zero for all species.

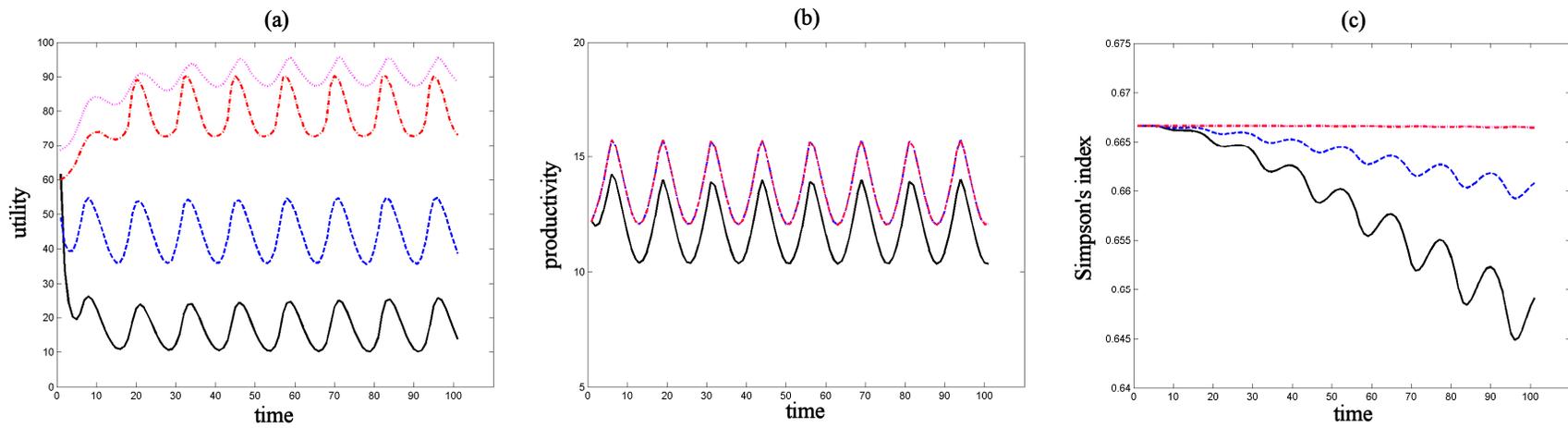


Figure 4. Effect of heterogeneous prices when benefits are obtained through the direct consumption of species and non-consumptive benefits of species biomass. (a) Utility; (b) productivity; (c) biodiversity (Simpson's index). Color and style indicate the level of non-consumptive benefits from species abundance: solid, black ($A = 0$), dashed, blue ($A = 0.5$), dot-dashed, red ($A = 1$), and dotted, magenta ($A = 1.14$).

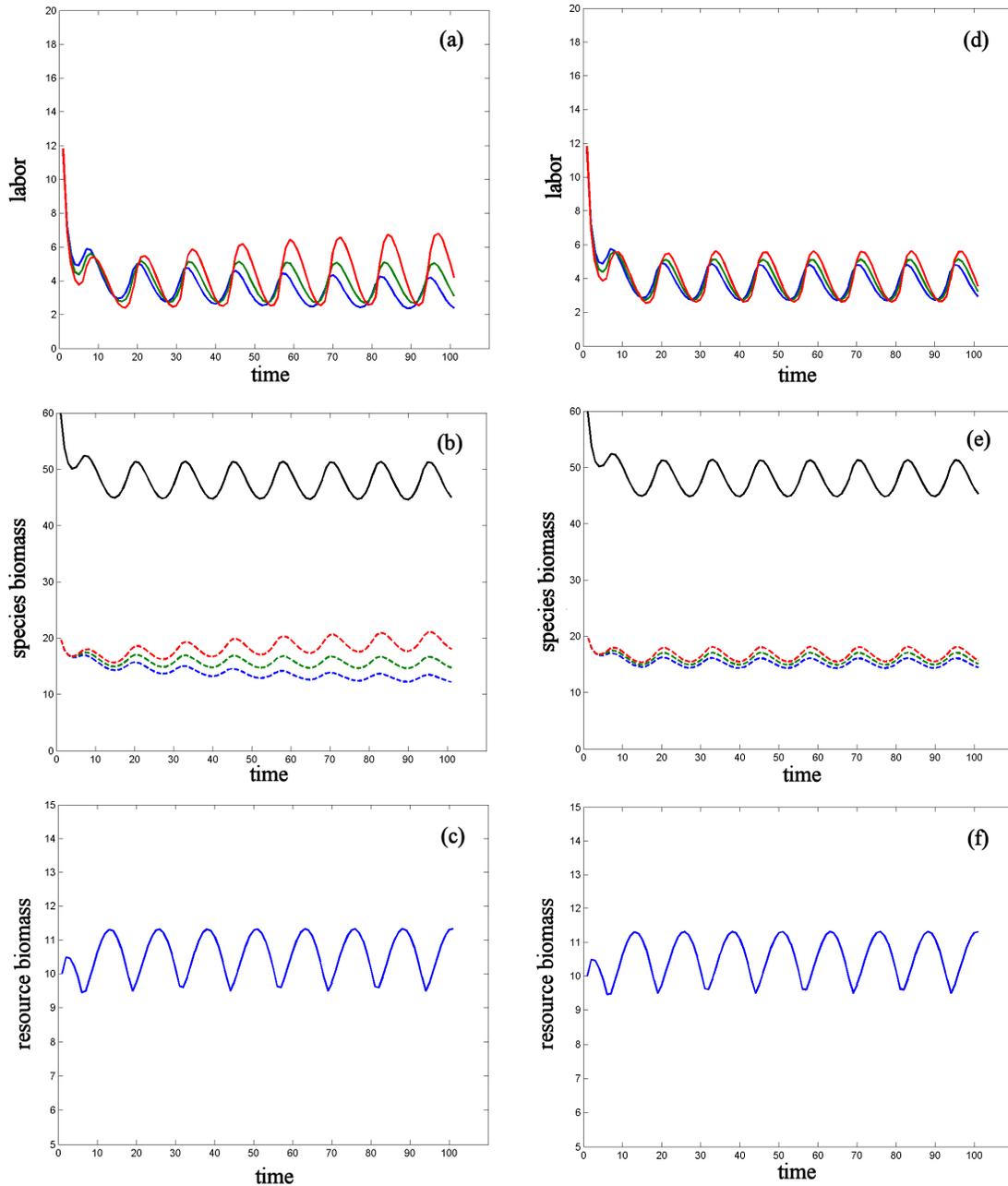


Figure 5. Effect of heterogeneous prices when benefits are obtained through the direct consumption of species and non-consumptive benefits of species biodiversity, B : $B = 10$ (a-c); $B = 50$ (d-f). Labor (a, d); species biomass (b, e); resource biomass (c, f). Color indicates species: species 1 (blue, lowest harvest price), species 2 (green), species 3 (red, greatest harvest price). In (b, e), dashed lines denote values of individual species biomass; the solid, black line is the aggregate level of biomass across all species.

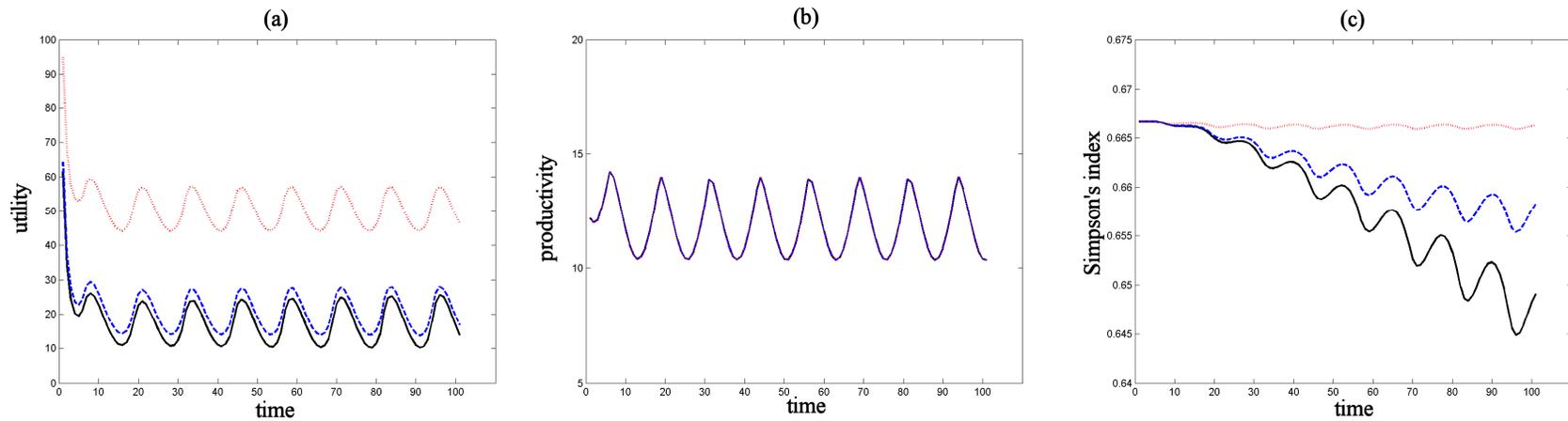


Figure 6. Effect of heterogeneous prices when benefits are obtained through the direct consumption of species and non-consumptive benefits of species biodiversity. (a) Utility; (b) productivity; (c) biodiversity (Simpson's index). Color and style indicate the level of non-consumptive benefits from species biodiversity: solid, black ($B = 0$), dashed, blue ($B = 10$), and dotted, red ($B = 50$).

APPENDIX

Derivation of $\dot{\mu}$ and L_i^ .*

Given the current-value Hamiltonian and first order conditions for L_i to maximize social utility:

$$\begin{aligned}
 H^{CV} = & \sum_{i=1}^S \left(p_i q L_i - \frac{w L_i}{N_i} + A_i N_i \right) + B \left(1 - \sum_{i=1}^S \frac{N_i}{N} \right) \\
 & + \sum_{i=1}^S \left(\lambda_i N_i e c_i R - \lambda_i N_i m - \lambda_i q L_i \right) + \mu \left(I - lR - R \sum_{i=1}^S c_i N_i \right)
 \end{aligned}$$

[A1]

$$\frac{\partial H}{\partial L_i} = p_i q - \frac{w}{N_i} - \lambda_i q = 0$$

[A2]

$$\dot{\lambda}_i = -\frac{\partial H}{\partial N_i} = \mu R c_i + \lambda_i (m - e c_i R + \delta) - \frac{w L_i}{N_i^2} - A_i - \frac{2 \left(\sum_{k \neq i} N_k^2 - N_i \sum_{k \neq i} N_k \right)}{\left(\sum_{k=1}^S N_k \right)^3}$$

[A3]

$$\dot{\mu} = -\frac{\partial H}{\partial R} = \mu \left(l + \sum_{i=1}^S c_i N_i + \delta \right) - \sum_{i=1}^S \lambda_i N_i e c_i$$

[A4]

From [A2] it can be shown that:

$$\lambda_i = p_i - \frac{w}{N_i q}$$

[A5]

$$\dot{\lambda}_i = \frac{w e c_i R}{N_i q} - \frac{w m}{N_i q} - \frac{w L_i}{N_i^2}$$

[A6]

Then, by substituting [A5] and [A6] into [A3] and differentiating with respect to time, one can solve for:

$$[A7] \quad \mu = \frac{w\delta}{N_i q R c_i} + \frac{p_i (e c_i R - m - \delta)}{R c_i} + \frac{A_i}{R c_i} + 2B \left[\frac{\sum_{k \neq i} N_k^2 - N_i \sum_{k \neq i} N_k}{\left(\sum_{i=1}^S N_i \right)^3} \right]$$

$$[A8] \quad \dot{\mu} = \frac{w\delta(m + \sum_{i=1}^S c_i N_i + l)}{N_i R c_i q} + \frac{w\delta L_i}{N_i^2 R c_i} - \frac{w\delta I}{N_i R^2 c_i q} - \frac{w\delta e}{N_i q} \\ - \frac{p_i}{R c_i} \left((m + \delta) \left(\frac{I}{R} - l - \sum_{i=1}^S c_i N_i \right) \right) + \frac{A_i}{R c_i} \left(-\frac{I}{R} + l + \sum_{i=1}^S c_i N_i \right) \\ + \frac{2B}{R c_i} \left[\left(\frac{\sum_{k \neq i} 2N_k \dot{N}_k - N_i \sum_{k \neq i} \dot{N}_k - \dot{N}_i \sum_{k \neq i} N_k}{\left(\sum_{i=1}^S N_i \right)^3} - 3S \frac{\left(\sum_{k \neq i} N_k^2 - N_i \sum_{k \neq i} N_k \right) \sum_{i=1}^S \dot{N}_i}{\left(\sum_{i=1}^S N_i \right)^4} \right) - \frac{\dot{R}}{R} \frac{\left(\sum_{k \neq i} N_k^2 - N_i \sum_{k \neq i} N_k \right)}{\left(\sum_{i=1}^S N_i \right)^3} \right]$$

Finally, substituting [A7] and [A8] into [A4] allows one to solve for the optimal path of the harvest per species:

[A9]

$$\begin{aligned}
& \frac{2B \left(\sum_{k \neq i} N_k^2 - N_i \sum_{k \neq i} N_k \right)}{\left(\sum_{i=1}^S N_i \right)^3} \left(l + \sum_{i=1}^S c_i N_i \right) - p_i (m - ec_i R + \delta) - \sum_{i=1}^S p_i N_i ec_i - \frac{wec_i}{q} + \frac{w\delta}{N_i} \left(\frac{e}{q} - \frac{m}{Rc_i q} + \frac{I}{R^2 c_i q} \right) + A_i \left(\frac{I}{R} + \delta \right) \\
& - \frac{2B}{c_i} \left[\frac{(N_i ec_i R - N_i m) \sum_{k \neq i} N_k}{\left(\sum_{i=1}^S N_i \right)^3 R} + \frac{3 \left(N_i \sum_{k \neq i} N_k \right) \left(N_i ec_i R - N_i m + \sum_{k \neq i} N_k \right)}{\left(\sum_{i=1}^S N_i \right)^4 R} - \frac{3 \left(\sum_{k \neq i} N_k^2 \right) \left(N_i ec_i R - N_i m + \sum_{k \neq i} N_k \right)}{\left(\sum_{i=1}^S N_i \right)^4 R} \right] \\
& - \delta \left(p_i (m - ec_i R + \delta) + \frac{w\delta}{N_i Rc_i q} + 2B \frac{\left(\sum_{k \neq i} N_k^2 - N_i \sum_{k \neq i} N_k \right)}{\left(\sum_{i=1}^S N_i \right)^3} \right) \\
L_i^* = & \frac{\frac{w\delta}{N_i^2 Rc_i} + 2Bq \frac{\sum_{k \neq i} N_k}{\left(\sum_{i=1}^S N_i \right)^3 Rc_i} + 6Bq \frac{\sum_{k \neq i} N_k}{\left(\sum_{i=1}^S N_i \right)^4 Rc_i} - 6Bq \frac{N_i \sum_{k \neq i} N_k}{\left(\sum_{i=1}^S N_i \right)^4 Rc_i}}{\left(\sum_{i=1}^S N_i \right)^3}
\end{aligned}$$