

How to Get There From Here: Ecological and Economic Dynamics of Ecosystem Service Provision

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Abstract Using a bioeconomic model of a coral reef-mangrove-seagrass system, we analyze the dynamic path of incentives to achieve an efficient transition to the steady state levels of fish biomass and mangrove habitat conservation. Our model nests different types of species habitat dependency and allows for changes in the extent of habitat to affect the growth rate and the long-run fish level. We solve the two-control, two-state non-linear optimal control problem numerically and compute the input efficiency frontier characterizing the tradeoff between mangrove habitat and fish population. After identifying the optimal locus on the frontier, we determine the optimal transition path to the frontier from a set of initial conditions to illustrate the necessary investments. Finally, we demonstrate how dynamic conservation incentives (payments for ecosystem services) for a particular habitat with multiple services are interdependent, change over time, and can be greater than contemporaneous fishing profits when the ecosystem is degraded.

Keywords Optimal control · Bioeconomic · Rebuilding · Collocation · Habitat

JEL Classification Q22

1 Introduction

In a recent review of the theory and practice of ecosystem service provision, [Daily and Matson \(2008\)](#) argue that despite increasing awareness of ecosystems as natural capital assets,

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several key scientific components, such as ecosystem production functions, are not sufficiently understood and this is a “limiting factor” for incorporating these functions into resource management decisions. In general, these production functions are dynamic process models that map the structure and operation of the biological and physical components of the ecosystems into the provision of services.

In this paper, we develop a structural representation of multiple ecosystem service provision in a production function framework, using fish dynamics in a coupled coral reef-mangrove-seagrass environment as our model system. Our ecological model nests facultative and obligate species-habitat associations, where in the obligate setting the species is entirely dependent on mangroves and in the facultative setting the species is not (Rönnbäck 1999; Sanchirico and Mumby 2009).

We couple the ecological dynamics to a model of a benevolent social planner that determines the optimal path of catches and development of the mangrove habitat over time to maximize the net present value from fishing, conversion, and in situ mangrove values.¹ Although most of the literature has focused either on how mangroves protect from tsunamis and hurricanes (Barbier et al. 2008) or on the role of mangroves in the production of coral reef fish (Nagelkerken et al. 2002), we incorporate both sets of values along with values associated with the development of the habitat (e.g. aquaculture ponds).

Our approach is most similar to Swallow (1990), who develops a model to investigate the optimal development of coastal habitat (a non-renewable, non-restorable resource) that also provides habitat for a biological stock (a renewable resource) that is being optimally harvested. We extend Swallow (1990) by developing an ecological model that nests different species-habitat relationships and by considering the use of restoration (reversible development). Restoration is an important management tool to consider in general² and in our system because worldwide mangroves are being converted at a rate of 1–2% per year (Duke et al. 2007) and approximately 35–50% have been cleared (Valiela et al. 2001).

Using our framework, we calculate the input efficiency frontier or tradeoff curve between steady-state fish population and mangrove conversion, depicted in stylized form in Fig. 1 (obligate association). The curve is similar to the type of tradeoff analysis in Polasky et al. (2008) and Nalle et al. (2004), who consider the tradeoffs between benefits from habitat use and loss of either biodiversity or a single species population. However, since the production function approach supports a single objective function with multiple sources of value, we are able to identify the efficient long-run optimal locus (e.g. either B_1 , B_2 , or B_3) on the frontier.

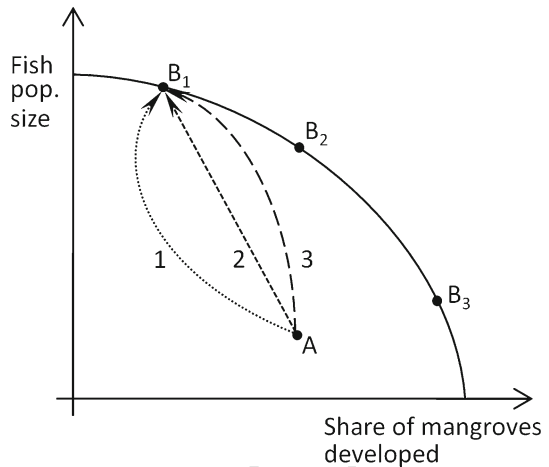
After identifying the trade-off curve and optimal locus, we ask how a coastal planner might optimally go from an interior point to the trade-off curve. That is, we solve numerically for the optimal transition from an interior “status quo” point, for example, from point A to point B_1 in Fig. 1. To our knowledge, this question has not yet been considered in the discussion on ecosystem service provision.

Along the optimal dynamic path, we identify the mix of mangrove and fishing policy and how these optimal policies depend on the nature of the species-habitat relationships. For example, in Fig. 1 where the transition involves restoring mangroves and building the fish population in the long run, we explore whether the path involves a monotonic approach as in curves 1 and 2 or a transitory overshoot of the optimal mangrove steady state as in curve 3. We also investigate how these paths differ when only a subset of the values (nursery habitat

¹ Coastal development and conversion for aquaculture are two primary drivers of mangrove habitat loss (Lal 1990).

² For example, as part of the American Recovery and Reinvestment Act of 2009 (Stimulus Bill), the U.S. National Oceanographic and Atmospheric Administration received \$167 million to restore coastal habitat (see, e.g., <http://www.nmfs.noaa.gov/habitat/restoration/> last accessed March 15, 2010).

Fig. 1 Tradeoff curve for optimal fish population size and share of mangrove habitat removed by development. Points on the curve (B_1 , B_2 , and B_3) represent possible optimal steady-states. Curves from A to B_1 represent alternative transition pathways



and development) is included in the planner's objective as opposed to the case when multiple values are considered (storm protection, nursery habitat, development).

The final contribution of the paper is to use the model to identify the payment for ecosystem service (PES) schedule for mangroves that corresponds to the optimal trajectory. Payments could be either in the form of taxes/subsidies from the government to private coastal landowners or from a fishing sector where the rights to the fish catch have been appropriated, for example, with a territorial use right, cooperative, or some other catch share program. We find that when one habitat (e.g. mangroves) is an input into multiple services (e.g. storm protection and fishery productivity) that the optimal PES schedule for each service is interdependent. These payments depend on the economic and ecological context, especially with a provisioning ecosystem service such as fish catches. For example, in our study system, the optimal schedule of additional incentives for conserving mangroves is a function of the quality of seagrass beds and depends on the relative value of the sectors using the mangroves (fish, development and storm protection). The dependency stems from provision of the fish catches using both mangroves and seagrass as inputs. The latter effect also varies based on the nature of the species-habitat relationship. We also find that when the ecosystem is degraded the PES payment can exceed contemporaneous fishing profits, which raises concerns about when PES can be self-financing and, if not, whether there is access to the necessary capital to fund payments. Furthermore, our results highlight that designing incentive payment programs requires detailed knowledge about the ecological production functions along with the economic conditions of those receiving/demanding the services.

The organization of the paper is as follows. In the next section, we introduce the ecological-economic model by first discussing the ecology. We then derive the optimality conditions and the "golden rule" equations for mangroves and fish populations. The investigation of how to get from an interior point to the optimal point on the frontier is carried out using numerical techniques, which are described after the optimality conditions. The numerical analysis, including a sensitivity analysis precedes the conclusion.

2 Ecological-Economic Model

Our modeling structure fits within the ecological production function approach with mangroves and seagrass as inputs that contribute to the production of fish (as reviewed in Barbier

(2007)). The production function dictates how the fish population changes over time in response to availability and use of mangrove habitats and other ecological processes, such as density-dependence. The ecological model is embedded in an economic framework that maps fish production to fish profits in each time period.

Another approach to valuing mangroves is the market value approach, which calculates fisheries production value of mangroves as the gross revenues of all fish that are observed or thought to be directly or indirectly associated with mangroves (Naylor and Drew 1998; Gren and Soderqvist 1994; Rönnbäck 1999). While this approach allows for a relatively quick and simple estimate of value across a broad set of marine species, the approach does not take into account fishing costs and implicitly assumes that population dependence on mangroves is absolute. Because planning decisions affecting mangroves, and coastal habitat in general, are often incremental choices over restoration, conversion or preservation of habitat, the production methods are advantageous from a policy perspective in their ability to value marginal changes in the extent of mangroves in terms of lost fishery profits or returns from development (Bockstael et al. 2000).

In this section, we describe the ecological model and the social planner's optimization problem where the choice variables are fishing catch and mangrove conversion in each period and the state variables are the fish stock and the proportion of the mangrove habitat conserved.

2.1 Ecological Model

Previous approaches to model mangrove-fishery linkages, and more generally species-habitat associations, make some important ecological assumptions that potentially limit the ability of the methods to be applied in other settings.³ A standard approach is to assume that the population carrying capacity is proportional to the extent of the habitat, usually in a linear fashion (e.g. Barbier and Strand 1998). However, as Freeman (1993) argues, environmental parameters are likely to influence both upper limits on population size and intrinsic growth rates. Mumby et al. (2004), for example, discuss how mangroves function as a nursery habitat and thereby increase "survivorship of young fish".⁴

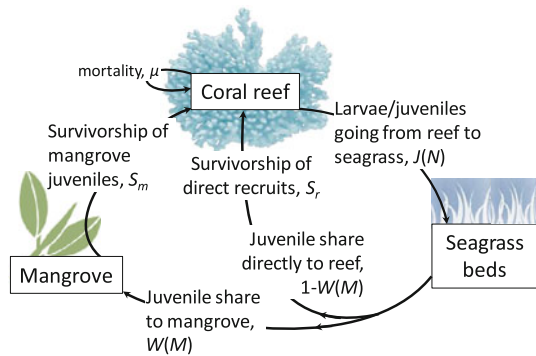
A second typical assumption is that the dependence of the population on the habitat is absolute. Rönnbäck (1999) makes the distinction between obligate use, where mangroves are absolutely necessary for fish survival, and facultative use, where mangroves supplement fisheries production but are not required. Ecologists have shown that species utilize different habitats at different stages in their lives. For example, some fish like the bluestriped grunt (*Haemulon sciurus*) or schoolmaster (*Lutjanus apodus*) take advantage of seagrass beds as juveniles, and then—if the habitat is available—they stop over in mangroves to further develop before finally migrating to their adult stage habitat in coral reefs (Mumby et al. 2004). Other species, however, might recruit directly to their adult coral reef habitat (e.g. *Chromis cyanea*), as examined in Rodwell et al. (2003).

We extend the ecological model of Sanchirico and Mumby (2009) that is based on the empirical findings of Mumby et al. (2004) to incorporate density dependence in the recruitment of juveniles to the adult population. The implication of this extension is that the availability of different habitat along with ontogenic migrations of the species affects both the

³ Barbier (2000, 2007) reviews several techniques for valuing the mangroves as inputs in fisheries production functions, including both static and dynamic modeling approaches.

⁴ In a global survey of the broad dependence of coastal fisheries on mangroves, Rönnbäck (1999) cites food abundance, predation refuge, and larval retention as the primary hypotheses explaining the importance of mangroves as fish habitats.

Fig. 2 Life-cycle schematic for the mangrove, sea grass, and coral-reef fish population model



133 carrying capacity and the growth rate of the population. [Sanchirico and Mumby \(2009\)](#) only
 134 consider the case of growth rates.

135 The model describes a biological (fish) species whose life-cycle spans coral reef, seagrass
 136 bed and mangrove habitats as depicted in Fig. 2. Adults are sedentary and subject to a fixed
 137 rate of natural mortality (μ) and a time-varying rate of fishing pressure on a coral reef (h_t).
 138 New individuals recruit to the reef either directly from seagrass beds or after an intermediate
 139 nursery stage within mangroves.

140 In any period, the share of the juveniles produced from the adult, reef-based population
 141 (N_t) is equal to $J(N_t) = \theta N_t^\gamma$ where γ and θ are non-negative. Egg production is often
 142 thought to follow increasing returns to scale per individual and we can model this with the
 143 assumption that γ is greater than one. The parameter θ could be modeled as a function of the
 144 coverage and quality of the seagrass beds, but for simplicity we assume that it is a constant
 145 parameter.

146 From the total amount of juveniles produced, a fraction goes from the seagrass beds
 147 directly to the reef where they are susceptible to mortality on the reef. The fraction of $J(N_t)$
 148 that migrates directly to the reef is denoted by $(1 - W[M_t])$, where $W[M_t] \in [0, 1]$ is assumed
 149 to be a continuous function of the extent of mangrove habitat that currently exists, M_t . For
 150 simplicity, we measure M_t as a proportion of the mangrove coverage in a pristine and undis-
 151 turbed setting. We define the survivorship rate for juveniles that recruit directly from the
 152 seagrass beds to the reef as S_r .

153 On the other hand, the fraction of $J(N_t)$ that migrates to the mangroves ($W[M_t]$) has a
 154 survivorship rate (S_m) that is greater than for those that go directly to the reef: $S_m > S_r$
 155 ([Chittaro et al. 2005](#)). The increased survivorship for species that utilize the mangroves
 156 occurs, because they are less susceptible to predation than those that go directly to the reef
 157 ([Aburto-Oropeza et al. 2008](#)).

158 The type of functional response captured by $W[M_t]$ to the changes in the coverage of man-
 159 groves is not immediately evident, though it will likely depend on the species, oceanographic
 160 conditions, and spatial distances between the different types of habitats ([Mumby et al. 2004](#);
 161 [Chittaro et al. 2005](#); [Aburto-Oropeza et al. 2009](#)). Following [Sanchirico and Mumby \(2009\)](#),
 162 we impose the following conditions: (1) if there are no mangroves, the fraction of juvenile
 163 fish utilizing them is zero ($W[0] = 0$); (2) even when the mangroves are at their maximum
 164 extent, some of the juveniles might recruit directly from seagrass to reef ($W[1] \leq 1$); and
 165 (3) the fraction utilizing the mangroves increases as the coverage of mangroves increases,
 166 everything else being equal ($dW[M_t]/dM_t > 0$). Support for the last property is found in
 167 [Simpson et al. \(2005\)](#) who showed that larvae of reef fish sense the presence of settlement

168 habitat and swim towards it, using either sound or chemical signatures of different habitats
 169 (see also [Arvedlund and Takemura \(2006\)](#)). By focusing on the fraction of cover, we also put
 170 aside the complexity of distinguishing between depth and perimeter coverage of mangroves.
 171 In the Gulf of California, [Aburto-Oropeza et al. \(2008\)](#) found that the depth of the mangrove
 172 habitat is less important for fisheries production than the coastal perimeter of habitat, because
 173 most species remain within the edge area.

174 Putting the components together, recruitment to the reef at time t is equal to:

$$R(N_t, M_t) = \underbrace{\theta N_t^\gamma}_{\substack{\text{Number of} \\ \text{juveniles} \\ \text{produced} \\ \text{from standing} \\ \text{stock of adults}}} \left(\underbrace{W[M_t]S_m}_{\substack{\text{Share and} \\ \text{survivorship of} \\ \text{juveniles that} \\ \text{utilize the} \\ \text{mangroves}}} + \underbrace{(1 - W[M_t])S_r}_{\substack{\text{Share and survivorship} \\ \text{of juveniles that go} \\ \text{directly to the reef}}} \right). \quad (1)$$

176 Equation 1 allows for a facultative association between mangroves and reproduction that
 177 is dependent on the levels of survivorship in reef and mangrove habitats. In such a setting,
 178 the mangroves provide an enhancement to overall effective survivorship, but the reefs are
 179 still able to supply new recruits even when mangroves are absent. The obligate relationship
 180 occurs when survivorship of direct recruits to the reef, S_r , is equal to zero. In this case, the
 181 reef population is entirely dependent on recruits from the mangroves and if the mangroves
 182 are completely removed, the population will go extinct.

183 Following [Armsworth \(2002\)](#), the density-dependent process is captured by recruits competing
 184 with other recruits for space and resources during settlement. In particular, we assume
 185 that recruits enter the reef according to a Beverton-Holt recruitment function, $g(R_t) =$
 186 $b_1 R_t / (1 + b_2 R_t)$ where b_1 describes the survival rate at low densities, and b_1/b_2 is the
 187 saturation limit with respect to the recruitment.

188 Combining recruitment, fishing and natural mortality, the instantaneous rate of change for
 189 the fish stock on the reef is:

$$\frac{dN_t}{dt} = \frac{b_1 R_t(N_t, M_t)}{1 + b_2 R_t(N_t, M_t)} - \mu N_t - h_t. \quad (2)$$

191 To illustrate how mangroves affect the long-run equilibrium level of the reef population,
 192 we derive the analytical expression for the unexploited steady-state equilibrium of Eq. 2
 193 as a function of the mangrove coverage. Under the assumption that γ is equal to one, the
 194 equilibrium population is:

$$N^{ss}(M) = \frac{b_1}{b_2 \mu} - \frac{1}{b_2 \theta [W(M)S_m + (1 - W(M))S_r]}. \quad (3)$$

196 Inspection of Eq. 3 reveals that if b_1 or θ increases, then the steady-state population will
 197 increase, everything else being equal. The direction of change in N^{ss} from a change in b_2
 198 is ambiguous. We also find that an increase in survivorship of juveniles arriving from either
 199 habitat or a decrease in natural mortality increases the equilibrium population on the reef.
 200 The change in the unexploited steady-state population with a change in M is equal to:

$$\frac{dN^{ss}}{dM} = \frac{(S_m - S_r)}{b_2 \theta [W(M)S_m + (1 - W(M))S_r]^2} \frac{dW(M)}{dM} > 0. \quad (4)$$

202 Equation 4 is positive for all levels of mangrove coverage, given the assumption that man-
 groves increase survivorship ($S_m > S_r$). The magnitude of the change depends on the

203 difference in the survivorship in the two habitats and the how an increase in mangrove coverage affects the share of juveniles that utilize the habitat, everything else being equal.

205 The extent of mangroves connected (within a certain distance) to the reef depends on
 206 whether the planner engages in restoration or clearing. The mechanism by which these activities
 207 translate into changes in mangrove coverage is described by a conversion production
 208 function, $F(D_t)$. The mangrove dynamics are

$$209 \quad \frac{dM_t}{dt} = F(D_t) \tag{5}$$

210 where D_t is effort devoted to mangrove conversion at time t , which can be positive (clearing
 211 for development) or negative (restoration) and $F(D_t)$ is the time rate of change in mangroves.⁵
 212 Equation (5) models a process where mangrove conversion is reversible (though conversion
 213 is costly), which differs from Swallow (1990), who only considers irreversible development.
 214 Of course, since we include restoration or clearing as a control variable in our economic
 215 model, the planner can decide whether reversing development is optimal. Reversible development
 216 is more likely, for example, when the mangroves are cleared for aquaculture, such as
 217 as shrimp farms.⁶

218 We account for asymmetry in the ability to restore mangroves and clearing mangroves
 219 within $F(D_t)$ by assuming that the marginal change $dF(D_t)/dD_t$ depends on whether D_t
 220 is positive or negative. In particular, we assume that the equation of motion for mangroves
 221 has the following properties: $F(0) = 0, F_D < 0, F_{DD} \leq 0$.⁷ This captures the notion that
 222 restoring mangroves may be more difficult than clearing mangroves. Since developed areas
 223 would likely be protected from mangrove encroachment, we do not include a natural growth
 224 process for mangroves that could change the extent of coverage over time.

225 **2.2 Economic Model**

226 Similar to Swallow (1990) and following the long tradition in bioeconomic modeling (Clark
 227 1990), we model a benevolent social planner that can choose the level of mangrove conversion
 228 and fish catch in each period. In our most general formulation, controls are chosen to
 229 maximize the net present value from fishing, development, and mangrove protection.

230 The infinite horizon optimal control problem of the planner is

$$231 \quad V = \max_{h_t, D_t} \int_0^{\infty} e^{-\delta t} [\pi(h_t, N_t) + B(1 - M_t) - C(D_t) + P(M_t)] dt$$

$$232 \quad s.t. \quad \frac{dN_t}{dt} = \frac{b_1 R_t(N_t, M_t)}{1 + b_2 R_t(N_t, M_t)} - \mu N_t - h_t \tag{6}$$

$$233 \quad \frac{dM_t}{dt} = F(D_t)$$

$$234 \quad 0 \leq M_t \leq 1$$

⁵ Given that we rescaled M_t to be a proportion of the maximum extent (pristine area), the rate of mangrove conversion, D_t , is correspondingly scaled to be in the same units.

⁶ We are currently assuming that restored habitat is substitutable for pristine habitat. Most likely, the substitutability is not perfect, at least in the short run. We plan in future work to consider this possibility within the context of a specific place.

⁷ Another approach would be to include two control variables, one for restoration and one for development. While such a model might better capture the on-the-ground realities, it is unlikely to change the qualitative conclusions of our analysis.

235 $0 \leq N_t, 0 \leq h_t$
 236 $N_{t=0}, M_{t=0}$

237 where δ is the discount rate, $\pi(h_t, N_t)$ is fishing profit in time t , $B(1 - M_t)$ is the benefits from
 238 the extent of development given by $1 - M_t$, $C(D_t)$ is the cost of converting mangroves, and
 239 $P(M_t)$ is the in situ value of the mangroves that could be due to providing coastal protection
 240 (Barbier et al. 2008) or from intrinsic value associated with the habitat. For simplicity, we
 241 will refer to $P(M_t)$ as storm protection for the remainder of the paper. Mangroves, therefore,
 242 contribute to the value of the system indirectly through the production of fish and directly in
 243 their protection of the coastal area. Fishing profit is assumed to be increasing at a decreasing
 244 rate in harvest and fish population on the reef ($\pi_h > 0, \pi_{hh} \leq 0, \pi_N > 0, \pi_{NN} \leq 0$).

245 We model the benefits of development, $B(1 - M_t)$, as a function of the amount of man-
 246 groves cleared (e.g. extent of total development which is $1 - M_t$ in any t) rather than from the
 247 flow of conversion (Swallow 1990). Our approach is consistent with the idea that developed
 248 areas will return a flow of rents from some alternative use. We model the total cost of conver-
 249 sion by a quadratic function, which is symmetric with respect to zero and has the following
 250 properties: $C(0) = 0, C_{DD} > 0 \forall D; C_D > 0$ if $D > 0$; and $C_D < 0$ if $D < 0$. Because in our
 251 set-up restoration is simply the negative of development, the appropriate interpretation of
 252 the marginal cost of restoration is $-C_D$ and for the marginal cost of development is C_D . The
 253 increasing cost of conversion takes into account adjustment costs that penalize the planner
 254 for either trying to ramp up restoration or development too quickly.

255 We also include the non-negativity restrictions on the states and control (fishing catch)
 256 along with the restriction that M_t is bounded from above by one (by assumption).

257 **2.3 Necessary Conditions**

258 Because the constraints on the state variables affect the rate of change of N and M with
 259 respect to time when the state variables are at the boundaries, we derive the current value
 260 Lagrangian rather than Hamiltonian (see, e.g., Kamien and Schwartz 1991, p. 237; Chang
 261 1992, pp. 300–303). The current value Lagrangian for our problem is⁸:

262
$$L = \pi(N_t, h_t) + B(1 - M_t) - C(D_t) + P(M_t) + \lambda_t \left(\frac{b_1 R_t(N_t, M_t)}{1 + b_2 R_t(N_t, M_t)} - \mu N_t - h_t \right)$$

 263
$$+ \varphi_t F(D_t) + \underbrace{\Lambda_1 F(D_t)}_{M_t \leq 1} + \underbrace{\Lambda_2 F(D_t)}_{-M_t \leq 0} + \underbrace{\Lambda_3 \left(\frac{b_1 R_t(N_t, M_t)}{1 + b_2 R_t(N_t, M_t)} - \mu N_t - h_t \right)}_{-N_t \leq 0} \quad (7)$$

264 where λ_t is the current value shadow price (or value) of an additional unit of fish stock on
 265 the reef, φ_t is the current value shadow price (or value) of an additional unit of the mangrove
 266 stock, and Λ_i ($i = 1 - 3$) are the Lagrangian multipliers on the state constraints. The shadow
 267 prices are determined jointly with the harvest, conversion, fish population, and mangrove
 268 coverage levels. The first-order necessary conditions are (along with the initial conditions):

⁸ An advantage of this approach is that the shadow prices on the stock variables are continuous while the shadow prices on the state constraints are piecewise continuous (Kamien and Schwartz 1991, p. 237). The derivation of Eq. 7 follows directly from Chang (1992, p. 301). Notice that we also converted the non-negativity constraints from $0 \leq N_t$ to $-N_t \leq 0$. The same holds for the mangrove constraint.

269
$$\frac{\partial L}{\partial h_t} = \pi_{h_t} - \lambda_t - \Lambda_3 \leq 0 \quad h_t \geq 0 \quad h_t \frac{\partial L}{\partial h_t} = 0 \quad (8)$$

270
$$\frac{\partial L}{\partial D_t} = -C_{D_t} + \varphi_t F_{D_t} + \Lambda_1 F_{D_t} + \Lambda_2 F_{D_t} \stackrel{set}{=} 0 \quad (9)$$

271
$$\frac{d\lambda}{dt} = \delta\lambda - \frac{\partial L}{\partial N} = \delta\lambda - \pi_N - (\lambda + \Lambda_3) \left(\frac{b_1 R_N}{(1 + b_2 R)^2} - \mu \right) \quad (10)$$

272
$$\frac{d\varphi}{dt} = \delta\varphi - \frac{\partial L}{\partial M} = \delta\varphi - B_M - P_M - (\lambda + \Lambda_3) \left(\frac{b_1 R_M}{(1 + b_2 R)^2} \right) \quad (11)$$

273
$$\frac{dN_t}{dt} = \frac{b_1 R_t(N_t, M_t)}{1 + b_2 R_t(N_t, M_t)} - \mu N_t - h_t \quad (12)$$

274
$$\frac{dM_t}{dt} = F(D_t) \quad (13)$$

275
$$M_t \leq 1 \quad \Lambda_1[1 - M_t] = 0 \quad d\Lambda_1/dt \leq 0 \quad [= 0 \text{ when } M_t < 1] \quad (14)$$

276
$$-M_t \leq 0 \quad \Lambda_2[-M_t] = 0 \quad d\Lambda_2/dt \leq 0 \quad [= 0 \text{ when } -M_t < 0] \quad (15)$$

277
$$-N_t \leq 0 \quad \Lambda_3[-N_t] = 0 \quad d\Lambda_3/dt \leq 0 \quad [= 0 \text{ when } -N_t < 0] \quad (16)$$

278
$$\frac{dL}{d\Lambda_1} = -F(D_t) \geq 0 \quad \Lambda_1 \geq 0 \quad \Lambda_1 \frac{dL}{d\Lambda_1} = 0 \quad (17)$$

279
$$\frac{dL}{d\Lambda_2} = F(D_t) \geq 0 \quad \Lambda_2 \geq 0 \quad \Lambda_2 \frac{dL}{d\Lambda_2} = 0 \quad (18)$$

280
$$\frac{dL}{d\Lambda_3} = \left[\frac{b_1 R_t(N_t, M_t)}{1 + b_2 R_t(N_t, M_t)} - \mu N_t - h_t \right] \geq 0 \quad \Lambda_3 \geq 0 \quad \Lambda_3 \frac{dL}{d\Lambda_3} = 0 \quad (19)$$

282 where $\pi_h(\pi_N)$ is the derivative of the profit function with respect to $h(N)$, C_D is the deriva-
 283 tive of the cost function with respect to D , F_D is the derivative of the conversion production
 284 function with respect to D , B_M is the derivative of the net benefits of development with
 285 respect to M , P_M is the derivative of the storm protection net benefits with respect to M , and
 286 $R_M(R_N)$ is the derivative of the recruitment function with respect to $M(N)$.

287 Before discussing the economic content of the conditions, it is important to point out that
 288 if all of the state and non-negativity constraints are non-binding, then $\Lambda_i = 0$ for $i = 1, 2, 3$
 289 and the necessary conditions revert back to standard Hamiltonian conditions (Eqs. 8, 9, 10,
 290 11, 12, and 13 would apply).⁹

291 From the harvest optimality condition (Eq. 8), it is evident that when the harvest is positive
 292 the shadow price of the fish stock is equal to the marginal profit from another unit of harvest
 293 ($\pi_h = \lambda_t$). Not surprisingly, the more profitable the fishery, the greater the shadow price of
 294 the fish stock. Equation (8) allows for the possibility that h_t^* is zero over some interval (or for
 295 all t if the fishery is not profitable to operate in). A temporary moratorium is optimal when
 296 $\pi_h \leq \lambda_t$ (assuming $N_t > 0$) or the shadow price is greater than the instantaneous returns
 297 from harvesting a unit of the stock in period t . A temporary moratorium is likely if the initial
 298 fish stock is significantly below its steady-state value, where rebuilding the stock as fast as
 299 possible is potentially economically efficient. A similar condition is found in linear-in-effort
 300 fishery bioeconomic models that are characterized by singular controls (Clark 1990).

301 When D_t is non-zero and the proportion of mangrove coverage is above zero and less
 302 than one, the optimality condition for conversion (Eq. 9) shows that the shadow price on
 303 mangroves is equal to the ratio of the marginal cost to the marginal product of conversion,

⁹ For a discussion of the complimentary slackness condition applied to Eqs. 14, 15, 16, see Chang (1992, p. 302).

where higher marginal costs or lower marginal product lead to a lower shadow price of mangroves. Under these conditions, Eq. 9 also illustrates that the shadow price on mangroves is positive when restoration is occurring ($D_t < 0$) and that the shadow price is negative when development is occurring (recall that development benefits are defined as $B(1 - M_t)$).

Equations (10) and (11) represent the (endogenous) dynamics of the shadow prices over time (called the adjoint or costate equations), which depend on the ecological and economic conditions in the ecosystem.

When the mangrove state constraint changes from nonbinding ($M_t < 1$) to binding ($M_t = 1$), Eqs. 14 and 17 describe how Λ_1 and $d\Lambda_1/dt$ impact the system. In particular, Eq. 17 imposes that dM/dt must either be zero (not changing) or decreasing at the boundary, which corresponds to either zero or positive (development) conversion effort. Similar conditions follow from the other state constraints.

Without putting additional restrictions on the profit function, we cannot gain much traction on the problem. Following our assumptions on the curvature of fishing profits, we assume fishing profits are

$$\pi(h, N) = (\alpha - \beta h)h - \frac{c}{N}h, \tag{20}$$

where α is the choke price, β is the slope of the demand curve, and c is a cost parameter. The per unit cost of harvest in Eq. 20 is a function of the fish stock—it depends inversely on the fish population. Given that these habitats are often found in remote areas of developing countries, we follow Barbier (2007) in specifying the responsiveness of fish prices to catch levels.

2.4 Optimal Interior Steady-State

Following steps outlined in Kamien and Schwartz (1991), we derive the “Golden rule” equations for the optimal fish stock size and mangroves at the steady-state. We put aside for now the possibility of corner solutions in the steady-state (e.g. all development, all mangroves, and no fishing). We explicitly include the possible for corner solutions both in the transition and at the steady-state in the numerical analysis. Specifically, the equations that correspond to an interior steady-state solution are:

$$\underbrace{\delta}_{\text{Discount rate}} = \underbrace{\left(\alpha - 2\beta G(N, M) - \frac{c}{N}\right) G_N}_{\text{Marginal value of catching and selling another fish}} + \underbrace{\frac{c}{N} \frac{G(N, M)}{N}}_{\text{Cost of catching another fish in terms of the reduced average productivity of the stock}} \tag{21}$$

$$\underbrace{B_M}_{\text{Marginal development benefits}} = \underbrace{P_M}_{\text{Marginal benefits from storm protection}} + \underbrace{\left[\alpha - 2\beta G(N, M) - \frac{c}{N}\right] \left[\frac{b_1 R_M}{(1 + b_2 R(N, M))^2}\right]}_{\text{Marginal benefits in the fishery}} \tag{22}$$

where

$$G(N, M) = \frac{b_1 R(N, M)}{1 + b_2 R(N, M)} - \mu N, \tag{23}$$

and the subscripts correspond to the derivatives of the functions with respect to the variables. Recall that setting Eq. 12 to zero implies that the steady-state harvest level is equal to Eq. 23.

338 Beginning with the mangroves, the only feasible steady-state level of conversion D^* is
 339 zero (Eq. 13). Equation 22 illustrates that the optimal extent of mangroves M^* balances
 340 the returns from development (B_M) against the returns from storm protection (P_M) and the
 341 returns from fishing, which depends on the per unit value of catch at the steady-state and how
 342 mangroves affect recruitment. Everything else being equal, in the optimal steady state, higher
 343 development benefits will result in more cleared mangroves while higher fishery returns and
 344 storm protection values will result in less cleared mangroves.

345 Not surprisingly, the optimal fish stock on the reef follows the standard bioeconomic capital-theoretic result (Clark 1990) where the social planner sets the optimal stock level such
 346 that the (instantaneous) returns in perpetuity from harvesting another fish (instantaneously)
 347 at the steady-state less the opportunity cost is equal to the rate of return of selling the fish
 348 and investing the proceeds in capital markets. The opportunity cost is the (instantaneous)
 349 reduction in the (average) productivity of the system weighted by the stock dependent costs
 350 of fishing in perpetuity from taking out an additional unit of the stock forever.

351 Since the recruitment function depends on the nature of how species utilize habitat, the
 352 assumptions regarding facultative and obligate behavior have direct implications for the
 353 optimal steady-state levels of mangroves and fish stocks. If the species has a facultative
 354 relationship—that is, there is some survivorship of recruits that do not depend on the man-
 355 groves—then the value of the mangroves is less than for an obligate relationship, everything
 356 else being equal. Furthermore, we can show that in the limit as the species becomes less and
 357 less dependent on mangroves that the coupling in Eqs. 21 and 22 goes to zero.

358 The interdependent optimality conditions for mangroves and fishing in Eqs. 21 and 22 can
 359 also become effectively decoupled if the planner ignores the value of mangroves in fishery
 360 production when determining how much mangroves to conserve for storm protection. In this
 361 case, the level of mangroves is set such that the marginal gains from clearing for development
 362 are equal to the marginal gains from storm protection, which are the marginal opportunity
 363 costs of clearing the habitat. The decision regarding the optimal fish stock would take the
 364 extent of mangroves as given. The resulting optimal fish stock would be lower than in the
 365 case where the planner takes all values of the mangroves into account, everything else being
 366 equal.¹⁰

368 3 Numerical Analysis

369 In this section, we explore the dynamics of how to get to the optimal steady-state when the
 370 species has a facultative or obligate relationship with mangroves. We also consider the cases
 371 where the planner does and does not take into account the storm protection benefits from
 372 mangroves. In all of the cases, finding the dynamic path in Fig. 1 entails solving the set of
 373 necessary conditions from a set of initial conditions for mangroves.

374 One solution technique available to solve high dimension non-linear optimal control prob-
 375 lems is to solve for the equations that define the two-point boundary value problem (TPBVP)
 376 and use a reverse or forward shooting algorithm (Judd 1998; Bryson 1999). The boundary
 377 conditions are determined by the initial conditions and a salvage value function (defined
 378 for a large and finite time for an infinite horizon problem by, for example, converting the
 379 formulation to the Bolza form of an optimal control problem). A potential issue with the
 380 TPBVP method is that the equations are often derived under the assumption that the controls

¹⁰ Swallow (1990) showed that development will occur too soon or too fast and that a greater cumulative quantity of development will occur when decisions in the fishery and development sectors are made independent of each other.

are interior solutions. In our formulation, we do not want to impose an interior solution, as there are likely many interesting cases where the optimal steady-state for mangroves consists of all development or conservation and includes fishing moratoriums (catch set to zero for some period of time).

Another often more robust method is to use collocation techniques that are based on minimizing a set of residual functions at a set of collocation points/nodes (Judd 1998).¹¹ Collocation techniques can be applied directly to Eq. 6 (Vlassenbroeck and Vandooren 1988; Goto and Kawable 2000) or applied to the TPBVP (Ascher and Petzold 1998). We choose the former, because it converts the optimal control problem into a parameter optimization problem where you are solving for the coefficients of the approximating polynomial function. The transformed optimization problem can then be solved using constrained nonlinear programming algorithms (Vlassenbroeck and Vandooren 1988). An advantage of this method is that it includes corner solutions as part of the optimal dynamic solution for all or part of the path. It also incorporates state and control constraints in a meaningful and rigorous fashion.

Collocation techniques require that the numerical solution satisfies a set of residual conditions at a set of collocation points that span the solution space (Ascher and Petzold 1998; Judd 1998). There are a number of different strategies for picking the location and number of these points and we utilize 60 Gaussian collocation points. Convergence was met at $10e^{-5}$ or higher resolution and took on average 25–50 iterations. The large-scale non-linear constrained parameter optimization problem is solved using the KNITRO solvers within the TOMLAB/PROPT state of the art optimization package for Matlab (release 2009a).

In the numerical analysis we employ functional forms for mangrove conversion ($F(D)$), cost of adjustment for conversion ($C(D)$), share of juveniles that utilize the mangroves ($W(M)$), value of development ($B(1 - M)$) and storm protection ($P(M)$). With a focus on the qualitative results (not quantitative) of the numerical analysis, our strategy in specifying these functions is to utilize the simplest form that is consistent with their properties. We explore the implications of these functional forms along with the values of the some of the key economic and ecological parameters in the sensitivity analysis.

To account for possible asymmetries in the marginal product of conversion to development versus restoration, we employ $F(D_t) = (1 - e^{D_t})$, where $F(0) = 0$, $F_D < 0$ and $F_{DD} < 0$, which captures the notion that restoration ($D < 0$) is more difficult than clearing for development ($D > 0$).¹² The share of juveniles utilizing the mangroves is equal to $W(M) = M^\omega$, where ω specifies the curvature of $W(M)$ with a change in mangroves. The benefits of development are $B(1 - M) = v_1(1 - M)^{v_2}$ and the storm protection benefits follow Barbier et al. (2008) where the specification is $P(M) = \rho_1 M^{\rho_2}$. The costs of development are $C(D) = c_d D^2$.

The ecological and economic parameters for the initial setting and their definition are listed in Table 1. We parameterize the fishing sector such that the open-access equilibrium level corresponds to approximately 10% of the unexploited stock levels (Myers and Worm 2003).¹³ We also parameterize the benefits of development and storm protection such that the social planner chooses an interior level of mangroves when the fishing sector is not considered part of the objective for mangrove management.

¹¹ Another potential solution technique is dynamic programming (DP) where we could use value function iteration to solve for the optimal solution (Judd 1998). DP is an especially useful method when considering the role of stochasticity and decision-making under uncertainty.

¹² We could also include a sluggish (or faster) response between conversion effort and mangrove stock dynamics by specifying $F(D) = \xi(1 - e^D)$, where ξ is a response parameter.

¹³ The steady-state open-access levels are solved for by setting average fishing profits to zero and the dynamics of the fish stock to zero for a given level of mangroves.

Table 1 Ecological and economic parameters

	Parameter	Level	Notes
Ecology	b_1	1	Survival rate of juvenile recruits at low density
	b_1/b_2	10	Saturation rate of recruitment in each t
	Natural mortality rate, μ	.1	10% mortality of the adult standing stock in each t , $\mu \in [0, 1]$
	Seagrass survivorship rate, θ	1	Survivorship of larval and juveniles in the seagrass beds, $\theta \in [0, 1]$
	Mangrove survivorship rate, S_M	.5	Survivorship of juveniles that go to the mangroves after the seagrass beds, $S_M \in [0, 1]$
	Reef survivorship rate, S_r	Facultative: $.5S_M$ Obligate: 0	Survivorship of juveniles that go to the reefs after the seagrass beds, $S_r \in [0, 1]$ and $S_r \leq S_M$
	Larval production per adult, γ	1	If γ is greater than one, then larval production is increasing in the adult standing stock
	Mangrove utilization, ω	.5	Share of juveniles going to the mangroves is $W(M) = M^{-5}$
Economics	Choke price, α	7	Vertical intercept of the demand curve
	Slope of demand curve, β	.75	Slope of the demand curve, when harvest equals to α/β the price is zero
	Harvesting costs, c	20	Cost per unit of harvesting, when holding the stock size constant
	Discount rate, δ	5%	
	Benefit of development	$v_1 = 7, v_2 = 1$	Describes the magnitude and curvature of the benefits of development
	Conversion cost, c_d	15	Costs per unit of conversion
	Benefit of storm protection	$\rho_1 = 7.7$ $\rho_2 = .5$	Describes the magnitude and curvature of the benefits of storm protection

423 We first highlight the results in the base case where the social planner does not take into
 424 account the values from storm protection from the mangroves ($\rho_1 = 0$). The second case
 425 captures the case where storm protection is explicitly part of the objective function. In each
 426 case, we start from two initial conditions to highlight the dynamic paths and stability of the
 427 solution.

428 **Case 1: Storm protection values are omitted from objective function**

429 For the obligate and facultative settings, we derive the input trade-off curve between the
 430 steady-state stock level and the extent of mangroves cleared by solving for the optimal steady-
 431 state of fish stock by varying a fixed (for all periods) level of mangroves. We then illustrate
 432 the optimal steady-state of mangroves and fish stocks when both are chosen by the planner,
 433 the solution of which corresponds to a point on the curve. We find that there are differences
 434 in the trade-off curve (see Fig. 3) between the obligate and facultative setting. In the faculta-
 435 tive case, N^{SS} does not go to zero as the proportion of mangroves developed goes to one. This
 436 result, which also affects the slope of the trade-off curve, is due to the fact that the species
 437 can utilize the reef habitat directly and as such, when there are no mangroves the stock does
 438 not go extinct. Previous research on mangroves has focused on the obligate case.

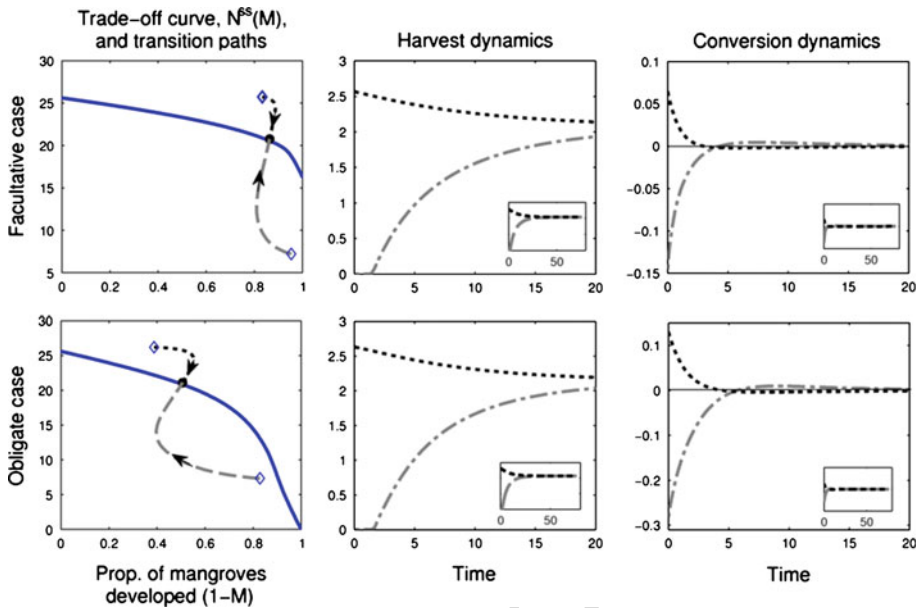


Fig. 3 Optimal dynamic solution of harvest and mangrove conversion without storm protection (Case 1). *Note:* The facultative case corresponds to the top row and the bottom row illustrates the obligate case. The column headings correspond to the vertical axes. In the first column, a dot represents the optimal steady-state levels. The optimal transition path for two initial conditions is presented: one condition corresponds to 125% of the steady-state levels of N and M (dotted line) and the other to 35% of the levels (dashed line). In columns two and three, the first 20 years of the transition paths are highlighted to show the differences across the cases. The insets illustrate the convergence to the steady-state solution that occurs within 50 time steps

439 After having identified the trade-off curve, the question is: how do you go from the
 440 current level (initial conditions) to the frontier and to which point on the frontier? In Fig. 3
 441 we illustrate the optimal path for two initial conditions, where one condition corresponds to
 442 125% of the steady-state levels of N and M and the other corresponds to 35% of the levels.
 443 The latter represents the situation where the planner is engaging in rebuilding the fish and
 444 mangrove habitats and the former is where both are initially above their long-run optimal
 445 equilibrium.

446 Figure 3 illustrates the paths and the locations of the optimal steady-states on the trade-
 447 off curves. For the temporal transitions, in columns two and three, we focus on the first
 448 20 time steps, where most of the interesting dynamics occur but the insets illustrate that con-
 449 vergence to the steady-state occurred in each run (approximately between 50 and 80 time
 450 steps). Although there is little difference in the optimal steady-state fish stock levels between
 451 the facultative and obligate cases, we do find that there is a substantial difference in equi-
 452 librium mangrove levels, where the steady-state in the obligate case corresponds to greater
 453 mangroves.

454 The qualitative nature of the paths is also remarkably similar across the obligate and fac-
 455 ultative settings. For example, when the system needs to be rebuilt (both $N_{t=0}$ and $M_{t=0}$ are
 456 below the steady-state solution), the planner institutes a temporary moratorium on fishing—a
 457 result we would not necessarily have found had we not accounted for the potential $h_t^* \approx 0$

458 solution in the numerical algorithm.¹⁴ Because the dependency on mangroves is greater in
 459 the obligate setting and the long-run equilibrium is further from the initial condition, the
 460 planner forgoes fishing for slightly longer than in the facultative setting to allow the stock
 461 time to rebuild.

462 In addition to the outlay for restoration costs, there is also an opportunity cost to restora-
 463 tion activities in terms of forgone development benefits. In spite of these costs, the planner
 464 finds it profitable to invest in habitat to gain the fishery benefits in the initial periods (recall
 465 storm protection is not considered in this case). Interestingly and unexpected, we find that the
 466 optimal solution is to overshoot the mangrove equilibrium (restore more than what is needed
 467 to reach the steady-state). How could restoring the habitat only to clear it at a later date be
 468 optimal? Essentially, the planner is getting additional benefits earlier from fishing (though
 469 at a decreasing rate) from restoring the habitat via faster recovery rates of the population.
 470 Eventually, however, the planner finds that it pays to divest in habitat and accrue the gains
 471 from development. Overall, the magnitude of restoration is greater in the obligate setting,
 472 which is being driven largely by the differences in the steady-state levels.

473 The optimal paths from a point where the fishery and mangrove are not overexploited are
 474 qualitatively similar across the cases and to the case of rebuilding. Interestingly, overshooting
 475 is still part of the solution.

476 Case 2: Storm protection values are included in the objective function

477 We now ask the question: what are the implications of including non-fishery benefits from
 478 mangroves on the optimal amount of development and fish stock? We maintain the param-
 479 eter assumptions used to generate Fig. 3, except now there is an in situ value to mangroves
 480 from storm protection as specified in Table 1. As we found in case 1, the steady-state fish
 481 stock levels are similar across the two obligate and facultative settings since the steady-states
 482 reside on the upper (flatter) portion of the trade-off curve. We also find that the mangrove
 483 steady-state is greater in the obligate setting (see Fig. 4).

484 Relative to the case with no storm protection, we find that the mangrove steady-state is
 485 larger, which is not surprising since we included an additional value to the standing stock
 486 in the objective function. Given the increase in extent of mangroves when in situ values are
 487 incorporated, the fishery is also more productive. In this case, both the steady-state stock and
 488 harvest levels are greater than when storm protection benefits are not included.

489 Figure 4 illustrates that the overshoot in the mangrove dynamics across the two cases is
 490 still part of the optimal solution. In the obligate setting, a difference between the two cases is
 491 that during the overshoot, the planner completely restores the mangroves (no mangroves are
 492 developed) and maintains this level for a number of periods before redeveloping the habitat.¹⁵
 493 When we increase the adjustment costs of converting mangroves, we still find the overshoot
 494 but whether it pays to restore all mangroves depends on the returns to storm protection and
 495 fishing. We also find that a moratorium on fishing is not part of the optimal solution. The lack
 496 of a moratorium is due both to the economic value in the system being more diverse than just

¹⁴ The temporary moratorium on fishing is dependent on the initial conditions and the economic and ecological characteristics of the fishery. For example, if we increase the initial fish population level (50% of the steady-state level instead of 35%), then the temporary moratorium is no longer part of the optimal solution (catches start low and increase over time but are always positive). Numerically, h_t^* is less than $1e-4$ during the period we are labeling a temporary moratorium.

¹⁵ Recall that we are using storm protection as a mnemonic for potential in situ values. A natural question to ask is whether the value in storm protection is tied to the level of development/infrastructure of mangroves. We abstract away from this level of detail given the nature of the model and focus on qualitative insights. Applying these tools to a particular location would necessitate consideration of these interactions.

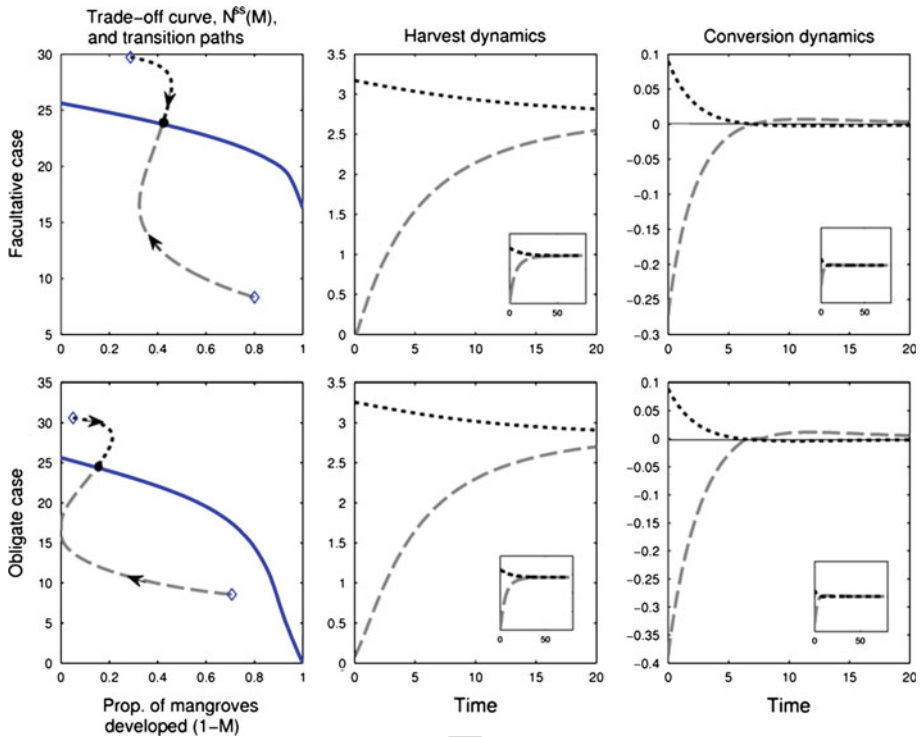


Fig. 4 Optimal dynamic solution of harvest and mangrove conversion with storm protection (Case 2). *Note:* The facultative case corresponds to the top row and the bottom row illustrates the obligate case. The column headings correspond to the vertical axes. In the first column, a dot represents the optimal steady-state levels. The optimal transition path for two initial conditions is presented: one condition corresponds to 125% of the steady-state levels of N and M (dotted line) and the other to 35% of the levels (dashed line). In columns two and three, the first 20 years of the transition paths are highlighted to show the differences across the cases. The insets illustrate the convergence to the steady-state solution that occurs within 50 time steps

497 fishery returns and to the greater initial endowment of mangroves. As such, the planner can
 498 afford to fish at the outset even though it slows rebuilding.

499 3.1 Optimal Payments for Ecosystem Services

500 The dynamic paths and long-run steady states depicted in cases 1 and 2 are consistent with
 501 a benevolent coastal planner. We now use the model to identify the payment for ecosystem
 502 service (PES) schedule for mangroves that corresponds to the optimal trajectory.¹⁶ Assuming
 503 for the moment that there are no values from storm protection, Eqs. 11 and 22 illustrate a
 504 potential optimal payment for ecosystem service (PES) mechanism by which either a coral-
 505 reef fishermen's cooperative (e.g., territorial user right (TURF)) or the government might

¹⁶ In order to focus on the PES for mangroves, we assume that the stock externality in the coral reef fishery has already been addressed either through the creation of a cooperative or some other form of catch share. This assumption allows us to put aside mechanism design issues with respect to PES systems, such as free riding incentives—issues that are important directions for future research.

506 provide via a subsidy to compensate coastal developers for the lost development benefits.¹⁷
 507 In particular, the payment for ecosystem services (per unit) provided by mangroves for the
 508 provisioning of fish catch at time t is given by (assuming $h_t^* > 0$)¹⁸:

$$509 \quad PES_t = \left[\alpha - 2\beta h_t^* - \frac{c}{N_t^*} \right] \left[\frac{b_1 R M_t}{(1 + b_2 R(N_t^*, M_t^*))^2} \right] \quad (24)$$

510 where starred variables represent the dynamically optimal levels. The fishermen's willing-
 511 ness to pay to forgo development, therefore, depends on the marginal value to the fishery
 512 from an additional unit of mangroves at time t . We decompose the marginal value into the
 513 value associated with a change in harvest and the change in the ecological productivity of
 514 the system from an additional unit of mangroves. The former is determined by the demand
 515 for fish and the costs of catching fish, along with the productivity of the fishery (embedded
 516 in h_t^*) and fish stock size. The latter depends explicitly on how species utilize the habitat and
 517 the density-dependent process operating in conjunction with the species-habitat functional
 518 relationships.

519 When values associated with standing stock exist, such as storm protection, we would
 520 expect that insofar as the mangroves occur on private property that the coastal developers
 521 would potentially take these values into account in their decision calculus.¹⁹ On the other
 522 hand, if the mangroves fall on public property and/or if the changes in storm protection are
 523 not appropriated to a particular coastal development project, the full costs of clearing are
 524 not internalized. In this case, a land-use planning agency might ask developers to pay a fee
 525 equal to the marginal value derived from storm protection for clearing in order to induce the
 526 optimal extent of mangroves. In our example, any storm protection values are assumed to be
 527 internalized by landowners.

528 The dynamic path of PES for cases in which storm protection values are positive or zero
 529 and under both facultative and obligate species-habitat relationships is presented in Fig. 5
 530 panel A. To highlight how PES might change over time, we consider the degraded ecosystem
 531 and fish population setting described in the previous section.²⁰ Thus the targeted conversion
 532 path is given by the increasing and concave curve depicted in column three of Figs. 3 and
 533 4. Since the optimal level of restoration starts high and attenuates at a decreasing rate, PES
 534 follow suit. As indicated in Eq. 22 payment varies with respect to whether there exist benefits
 535 from storm protection. When such in situ benefits exist (and are internalized by the private
 536 landowners as assumed here) PES need only make up the difference between marginal bene-
 537 fits from development and storm protection. PES in the case of no storm protection benefits
 538 are greater since the payment must compensate for the entirety of development benefits
 539 forgone.²¹

540 Since PES depend on marginal benefits of M_t to the fishery, which is determined by
 541 the nature of the species-habitat relationship, we find that when the fish population is more

¹⁷ The direction of payments depends on the initial allocation of development rights; for illustrative purposes, we examine the case in which private landowners are endowed with these rights such that payments to forgo mangrove development flow from a fishermen's cooperative or the government to private landowners.

¹⁸ The condition that holds when $0 = h_t^*$ is $PES_t = \lambda_t^* \left[\frac{b_1 R M_t}{(1 + b_2 R(N_t^*, M_t^*))^2} \right]$, where recall $\pi_h \leq \lambda_t$.

¹⁹ A lower insurance payment is one way that these values could be internalized by the developer.

²⁰ The dynamics of the PES are similar for the other initial conditions, except that the PES starts below the long-run level and is increasing.

²¹ This result is sensitive to the assumption over whether private landowners internalize the storm protection benefits. If such in situ benefits are not internalized then the payments from the fishermen would be insufficient to induce the socially optimal solution of mangroves.

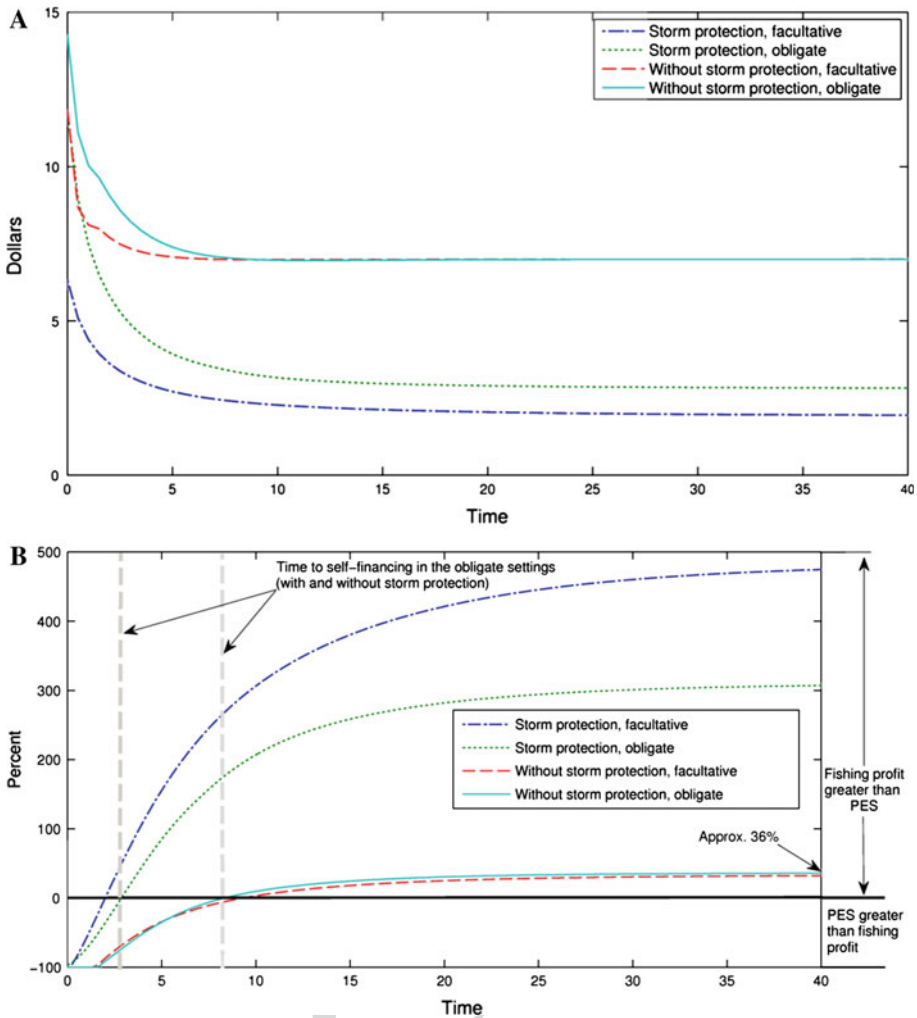


Fig. 5 Optimal PES payment schedule. *Note:* In panels A and B, the analysis is carried out for the case with ($\rho_1 > 0$) and without ($\rho_1 = 0$) storm protection and for the obligate ($S_r = 0$) and facultative ($S_r > 0$) case. Panel A illustrates the levels of the PES in each period and panel B illustrates the percent difference between fishing profits and the PES in each period

542 dependent on the mangrove habitat (the obligate case) more restoration is demanded both in
 543 terms of the immediate rate of conversion and the long-run steady state than in the facultative
 544 case (see Figs. 3 and 4). PES under the obligate case is, therefore, greater in the short run.

545 Finally, we observe that PES under obligate and facultative settings converge when there
 546 are no storm protection benefits while in the alternative case they do not. This result depends
 547 on the linearity (or nonlinearity) of benefits to development and to storm protection with
 548 respect to M_t . Since we have assumed linear benefits to development (see Table 1), marginal
 549 development benefits are constant across M_t . While the steady-state level of M under the
 550 obligate case is greater, under no storm protection benefits the long run PES still converges
 551 since marginal development benefits are independent of M . Storm protection benefits, in

contrast, are assumed to be increasing and concave in M . Therefore, the residual opportunity cost to be covered by PES in this case depends on the steady-state level of M and on whether the setting is obligate or facultative.

To put the magnitude of these payments in perspective, Fig. 5 panel B illustrates the difference between fishing profits and the PES payment in each period t as a percentage of the PES payment.²² During the initial moratorium when the fish stock is rebuilding, fishing profits are zero, but the PES payment is still positive (corresponds to a negative percentage in Fig. 5 panel B). The threshold time where fishing profits become greater than PES payments for the obligate cases is less than two periods with storm protection and less than 10 periods without storm protection. In general, the relative magnitudes of fishing profits and PES payments depend on the ecological relationships and whether storm protection benefits are included. Consistent with the actual payment amounts, we find that the fishing profits are significantly greater than the PES payment when storm protection benefits are included (on the order of 300–400%).

PES payments greater than fishing profits during the rebuilding period highlights a potential issue regarding self-financing that can arise when setting up PES mechanisms in degraded ecosystems. That is, without access to capital either from government loans, subsidies, or private sources, the ability of the fishing cooperative or group to pay the land developer to restore mangroves is potentially in jeopardy. To our knowledge, this potential issue has not been raised yet in the discussion of PES mechanisms.

3.2 Sensitivity Analysis

The optimal ecosystem service payment depends on the ecological and economic parameters of the system and it is not always clear how changes in one parameter will affect the PES schedule. For example, a decrease in the survivorship rate of the juveniles on the seagrass beds affects the productivity of a unit of mangroves, which in turn potentially reduces the profitability of the fishery (similar to a decrease in the intrinsic growth rate in a logistic population model). On the one hand, a less profitable fishery would be willing to pay less, everything else being equal. This effect is compounded by the potential strategy of harvesting less and increasing the standing stock of the fish population, everything else being equal. On the other hand, investing in more mangroves is another strategy to offset the decline in seagrass survivorship, implying that fisherman might be willing to pay more to have a greater amount of mangroves conserved in the long-run and to pay more sooner to speed up the process of restoration.

In this section, we undertake a sensitivity analysis on some of the key parameters and functional forms assumed in the base case to get a better picture of how the optimal PES schedule depends on the ecological and economic context within which the services are delivered. We continue to start from the initial conditions used to derive Fig. 5, but the optimal paths and steady-states will differ from the base case.²³ We alter both the baseline ecological model and economic model in two ways. For the ecological model, we investigate the effect of two adjustments that both significantly decrease the juvenile survivorship: a 20% decrease in the survivorship rate on seagrass beds, and a linear (rather than concave) specification of mangrove utilization ($W[M]$). For the economic model we examine a 50% increase in the cost of conversion, and a 50% decrease in the slope of the demand curve.

²² Specifically, we are computing $100 * (\pi_t - PES_t) / PES_t$.

²³ Qualitatively, the optimal path of harvest, conversion, and PES payment dynamics are similar to those illustrated in the base case and are therefore not presented.

Table 2 Sensitivity analysis summary

	<i>Model alteration</i>	<i>Storm protection benefits</i>	<i>Species-habitat relationship</i>	<i>Initial change in rate of mangrove restoration</i>	<i>Change in length of catch moratorium</i>	<i>Change in steady state extent of M</i>	<i>Change in steady state of N</i>	<i>Change in time to self-financing PES</i>	
Ecological model	Seagrass survivorship rate, θ , decreased by 20%	Yes	Obligate	Positive	Longer	Greater	Lower	Longer	
		No	Facultative						
	Yes		Obligate	Negative					
		No	Facultative						
	Mangrove utilization, γ , shifted from 0.5 to 1 (concave to linear)		Yes	Obligate	Positive	No change (none)	Greater	Greater	Longer
		No		Facultative					
Yes			Obligate	Negative	Shorter	Lower	Lower	Shorter	
		No	Facultative						
Economic model	Conversion cost increased by 50%		Yes	Obligate	Negative	No change (none)	No change	No change	Longer
		No		Facultative					
			Yes	Obligate		Positive			
		No		Facultative					
	Slope of demand curve, β , decreased by 50%		Yes	Obligate	Positive	Longer	Greater	Lower	Shorter
		No		Facultative					
Yes			Obligate	Negative	No change				
		No	Facultative						

595 A number of key effects for each case are summarized in Table 2, including: the initial
 596 change in the rate of mangrove restoration, the change in the length of a fishing moratorium,
 597 the change in the steady-state extent of mangroves, the change in the steady state fish stock,
 598 and the change in the time-span before PES payments can be self-financed through fishing
 599 profits.

600 *3.2.1 Seagrass Survivorship*

601 Because we have found that there are potentially important interactions between services
 602 in terms of the amount and timing of the optimal PES schedule, we hypothesize that there
 603 must also be interdependencies across different habitats. This is especially likely when the
 604 production chain of ecosystem services entails multiple habitats.

605 We find that indeed there is an effect on the relative sizes of fishing profits and PES pay-
 606 ments when we decrease the seagrass survivorship rate. We also find that the magnitude and
 607 qualitative pattern of the effects depend on the other ecosystem services. In the case of no
 608 storm protection, for example, the PES payment is greater than fishing profits for a longer
 609 period of time and the PES is a larger share of fishing profits than in the base case. Without
 610 storm protection, we find that there is a slower rate of restoration and a longer fishing mor-
 611 atorium relative to the base case. The optimal steady-state of mangroves in both the facultative
 612 and obligate setting is on the order of 15–20% larger and the steady-state fish stock is on the
 613 order of 9–13% lower than in the base case. In the long-run in the obligate setting, fishing
 614 profits are less than 4% of the PES payment implying that in this setting at least the PES
 615 payments are a significant outlay relative to the economic values from fishing.

616 With storm protection, PES payments quickly become significantly less than fishing prof-
 617 its though it takes slightly longer than in the base case. Restoration occurs at a faster rate,
 618 as there are additional benefits from mangroves. Interestingly, the fishing moratorium is still
 619 longer than in the base case and this is because even though the level of mangroves is increas-
 620 ing at a faster rate, the increase is not enough to offset the lower survivorship of juveniles
 621 in the seagrass beds. As with the case of no storm protection benefits, the drop in seagrass
 622 survivorship leads to an increase in the steady-state extent of mangroves and a decrease in
 623 the steady-state fish stock level.

624 3.2.2 Mangrove Utilization

625 The assumption that the share of juveniles utilizing mangroves is linear ($\omega = 1$) over M
 626 rather than concave ($\omega = .5$) results in a decrease in the proportion of juveniles utilizing
 627 mangroves (and thus fewer juveniles benefiting from the bump in survivorship from utilizing
 628 this rearing habitat), everything else being equal.²⁴ Overall, this adjustment to the form of
 629 $W[M]$ reduces the number of juveniles eventually making it back to the reefs, particularly
 630 in the obligate setting, which is entirely dependent on the mangroves for recruits.

631 Beginning with the case of no storm protection, we find a divergence between the facul-
 632 tative and obligate setting across a number of dimensions. The facultative setting has lower
 633 rates of restoration, a 9% lower steady-state level of mangroves, a 11% lower steady-state
 634 level of fish stock, and a longer fishing moratorium than the base case. With the substitu-
 635 tion possibilities across the habitats (under a facultative setting) and the current assumptions
 636 regarding the differences in survivorship, mangroves are not as important. The opposite is
 637 true for the obligate setting. Here we find that optimal steady-state of mangroves is over
 638 60% larger than in the base case (9% larger steady-state fishing stock) and level of the PES
 639 payments are greater than in the base case to both speed up the recovery of the fish population
 640 and to pay for the additional conservation of mangroves.

641 With storm protection, the optimal steady-state level of mangroves in the both the fac-
 642 ultative and obligate setting is larger than in the base case (on the order of 20–40%). The
 643 resulting payment schedule is greater than in the base case and consistent with our earlier
 644 results; the payment in the obligate setting is greater than in the facultative setting and both
 645 are much smaller share of fishing profits.

646 3.2.3 Cost of Conversion

647 What is the impact on the relative values of fishing profits and PES payments when the cost
 648 of conversion of mangroves is greater? In the steady-state, the incremental cost of conversion
 649 does not affect the level of mangroves or fish stocks (since the marginal cost approaches zero
 650 as D approaches zero) and therefore, any differences from the base case should be transitory.
 651 When we increase the cost of conversion by 50%, we indeed find only a transitory effect
 652 where the payment is larger to compensate developers for restoration activities (recall we are
 653 starting at an initial condition with M_t below its long-run steady-state). Not surprisingly then,
 654 increasing the cost of conversion increases the time span over which profits are not sufficient
 655 to self finance the PES. Across the board, the steady state level of M and N are unchanged,
 656 but it is approached at a slower rate of restoration. The length of fishing moratorium differs
 657 by the species habitat association but just as in the base case, there is no moratorium in the
 658 obligate setting with storm protection.

²⁴ Note that $W[M] = M$ is everywhere below $W[M] = M^5$ on the unit interval, except for the case of all mangroves ($M = 1$) or no mangroves ($M = 0$) where there is no difference.

659

3.2.4 Slope of the Demand Curve

660 When we decrease the slope of the demand curve (holding the vertical intercept constant)
661 the fishery is more profitable for a given level of harvest, everything else being equal. The
662 time to self-financed PES is shorter than in the base case for all settings (with or without
663 storm protection benefits; obligate or facultative species-habitat relationship). We also find
664 that in the obligate case without storm protection, the ratio of fishing profits to PES is about
665 1.59 in the steady-state. Because the PES is a smaller share of fishing profits, this ratio might
666 be more politically acceptable than those found in the previous analysis. We also find that
667 the initial length of the fishing moratorium is longer in all cases while the initial investment
668 in restoration is dependent on whether storm protection benefits are included. We also find
669 that the optimal steady-state level of mangroves is larger and the steady-state fish stock is
670 smaller in each of the cases. The planner, therefore, is trading-off investing in greater levels
671 of mangroves during the transition, which lead to a faster growth rate of the fish populations,
672 against a lower steady-state -stock of fish due to greater fishing pressure (and fishing profits).

673

4 Conclusion

674 Building on recent advances in ecology on the understanding of fishery-habitat linkages
675 (Mumby et al. 2004; Harborne et al. 2006; Mumby 2006), we advance the economic-eco-
676 logical science for valuing multiple types of fish habitats as natural capital. In particular,
677 our modeling framework better illuminates the mechanisms through which multiple types
678 of habitats impact the population dynamics of fish and how key ecological and economic
679 variables inform decisions on how to value and conserve habitats, using mangroves, seagrass,
680 and coral reefs as our model system.

681 Our paper also contributes to the broader goal that calls for the further development and
682 refinement of production methods to measure and value ecosystem services (Heal et al. 2005;
683 Daily and Matson 2008). With more realistic depictions of ecological production functions,
684 the possibilities to develop payment systems for ecosystem services and other conservation
685 tools that take into account their total economic value are enhanced. Such values will better
686 inform how to get the greatest return per conservation dollar spent. Incorporating a more
687 accurate value of mangroves into resource management is arguably a crucial step in moving
688 towards sustainable use of coastal environments (Barbier 1993; Rönnbäck 1999; Lugo 2002).

689 We illustrate in our model system that the qualitative nature of the path to the long-run
690 steady state is similar for the obligate and facultative settings, while the steady state level of
691 mangroves is (intuitively) greater in an obligate relationship. We show that the optimal path
692 can involve temporarily overshooting the long run mangrove stock. In the case of rebuilding,
693 for example, the overshoot is optimal, because additional mangroves speed up the rebuild-
694 ing of fish stocks. The robustness of the optimal overshoot is an interesting area for future
695 research, especially when the assumption that restored habitat is immediately and equally
696 ecologically productive for the fishery is relaxed. Other interesting research questions include
697 measuring the costs of going to other (not optimal) points on the frontier and the economic-
698 ecological differences in the transition to these non-optimal points.

699 Ultimately, we find that efficient PES incentives for habitat conservation depend critically
700 on the nature of the ecological and economic conditions where the services are provided and
701 demanded. Generally, the additional dynamic incentives will need to be equal to the marginal
702 benefit to the fishery, which includes current as well as future values. When private marginal
703 in situ values (e.g. storm protection) exist and are internalized, the necessary additional PES

704 payment to account for the value of mangroves in the fishing sector is reduced. The political-
 705 economy implication of this finding is that by including multiple ecosystem services, each
 706 stakeholder group that benefits from an ecosystem function with multiple services will likely
 707 have lower outlays relative to the situation where fewer services are considered, everything
 708 else being equal (at least in the case of synergistic ecosystem service provision).

709 We also find that for degraded systems that the PES payments can exceed contemporane-
 710 ous fishing profits. This result highlights a potential difficulty in instituting PES schemes in
 711 the very places (degraded ecosystems) that likely need them the most. In particular, the PES
 712 program would need to be coupled with access to capital to help finance the payments until
 713 the value of the ecosystem services derived from the ecosystem function can pay for itself.
 714 We also find that in some cases the PES payments comprise a significant share of the fishing
 715 profits. Our analysis also shows that details that will likely affect the political adoption of
 716 these schemes, such as how long until fishing profits are greater than PES payments and the
 717 relative size of the payment, are dependent on the local ecological and economic conditions.

718 To illustrate the dynamic and interrelated nature of ecosystem service payments, we
 719 abstract away from important mechanism design and governance issues, such as informa-
 720 tion asymmetries, free-riding incentives, transaction type (public-private, private-private),
 721 property rights, etc., that are associated with market or incentive schemes. Our analysis
 722 also demonstrates that the level of knowledge of the ecological-economic system required
 723 to develop efficient PES programs is quite extensive (see, e.g., [Heal et al. 2005](#) and [Bar-
 724 bier et al. 2008](#)). Critical parameters—for example the survivorship of juveniles utilizing
 725 the mangroves—may be highly uncertain. Optimal learning over whether the species-hab-
 726 itat relationship is obligate or facultative could be embedded into the planner's investment
 727 problem. Challenging questions for future research revolve around how fishing policies or
 728 mangrove policies (e.g. payments for ecosystem services) can be used efficiently to manage
 729 the resources while simultaneously learning about the ecological-economic system.

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Revised Proof