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# The Bioeconomics of Spatial-Dynamic Systems in Natural Resource Management

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## **Abstract**

We synthesize literature on the spatial aspects of coupled natural-human systems across a variety of natural resource contexts and introduce a framework that can be used to compare modeling approaches and findings across applications. The important components of these systems include spatial heterogeneity in benefits and costs and connectivity of the network. One or more of these components is necessary for spatial policies to be the efficient solution. We highlight the importance of these components by identifying their role in previous work that shows that spatial differentiation in policy implementation is optimal. We pay particular attention to research highlighting the difference between spatial and aspatial policies and the presence of optimal boundary solutions. Finally, we develop a stylized metapopulation model to relate findings in the spatial bioeconomic literature to the theory of second best in public economics and suggest areas for future analysis.

**Key Words:** bioeconomics, spatial dynamics, metapopulation, connectivity, optimal control

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# The Bioeconomics of Spatial-Dynamic Systems in Natural Resource Management

Kailin Kroetz and James N. Sanchirico\*

## Introduction

Over the last 30 years, the technology to discover, understand, and visual spatial patterns in animal or pollution levels, pest or disease outbreaks, habitat quality and quantity, and watershed connectivity has improved dramatically. These tools include geographical information systems (GIS), computer memory and storage, remote sensing platforms, ocean-observing systems, and autonomous vehicles for data collection. During this same period, scientists have been actively researching the potential structural mechanisms that could lead to such patterns. A fundamental conclusion of this research is that spatial patterns of natural resource abundance are not static. Rather, the patterns result from the dynamic evolution of coupled natural-human systems operating over a hierarchy of spatial and temporal scales.

Given the scientific advances, a number of public policy questions arise. Many involve how best to design policy instruments that address the suite of market failures associated with common pool resources. Sample questions include: What is the potential magnitude of efficiency gains from implementing spatially differentiated policies over a spatially uniform policy? What are likely conditions under which a spatially differentiated policy is optimal, i.e., where these gains outweigh any increased administrative or monitoring costs from the spatial policy? How do these conclusions depend on the nature of the hierarchy of scales and the interactions among them in the coupled system?

A classic example of a market failure is an open-access fishery in which rational fishermen overharvest the resource over time due to the negative (stock) externality associated

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with incomplete property rights to the resource. The spatial analog is that the distribution of the overharvesting will not necessarily be uniform across the range of the species, with some areas being hot spots of fishing efforts (Sanchirico & Wilen 1999). A first-best policy instrument in this setting might therefore consist of differential entry charges or harvest levies or the implementation of separate cap-and-trade programs (that could be linked with trading ratios) (Sanchirico & Wilen 2008).

Bioeconomics has already contributed to our understanding of how ecological, economic, and policy characteristics can lead to patterns in both unmanaged and managed systems. Given the nature of the questions asked and applications (including diseases, invasive species, commercial fisheries, biodiversity conservation, and water), it will continue to play an important role in understanding the benefits and costs of potential solutions to market failures that occur across space and time.

In this review, we synthesize spatial bioeconomic literature across a variety of natural resource contexts and introduce a framework that can be used to compare modeling approaches and findings across applications. Specifically, we identify the mechanisms, one or more of which is necessary for spatial-dynamic policies to be the efficient (first-best) solution under the assumption of a single decision-making entity for the coupled natural-human system.<sup>1</sup> We examine past work on spatial-dynamic systems, with a focus on papers that (a) compare a spatially differentiated policy with an aspatial policy and/or (b) find an optimal boundary solution whereby the first-best solution includes a control value of zero somewhere in space.

For the purposes of illuminating the role that aligning the biological and economic gradients plays in optimal spatial-dynamic systems, we develop a stylized discrete space model that allows for spatial heterogeneity in costs and benefits, as well as for connectivity controls.

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<sup>1</sup> There are, however, many other ways to organize a review of the spatial and dynamic bioeconomic literature. For example, we could focus on modeling efforts and divide the literature into papers that focus on few locations versus large-scale spatial models, as there are a number of interesting numerical challenges associated with the latter (see, e.g., Aadland et al. 2014). Another division could be with respect to models that use continuous versus discrete spatial representation (see, e.g., Smith et al. 2009) or deterministic (Sanchirico & Wilen 2008) versus stochastic (Costello & Polasky 2008) systems. Still other ways could be based on application; for example, the control or eradication of invasive species (Epanchin-Niell & Hastings 2010) and the large body of work on fisheries (see, e.g., Conrad & Smith 2012 and Wilen 2004) could warrant review articles. Additionally, due to space limitations, we do not consider the nature of spatial-dynamic issues associated with the presence and stability of cooperative solutions to the commons problem.

This modeling framework highlights potential differences between settings in which the management controls, directly (e.g., invasive species dispersal controls) and/or indirectly (e.g., harvest levels in each location), the connectivity flows among the locations. Beyond providing a unifying framework to use in the organization of the current literature and results, the model also provides insights into factors that can lead to economically optimal spatial specialization in systems in which such a result would be unexpected. We conclude with a set of research questions and areas of inquiry that can further push the frontier of spatial bioeconomics.

### **Spatial Heterogeneity in Natural Resources**

Designing policies to address market failures requires understanding the mechanisms that lead to the failure. We know, for example, that a fundamental result of public economics is that the spatial resolution of the policy instrument should be the smallest scale that encompasses all the benefits and costs, assuming zero transaction costs (Oates 1999). Furthermore, to achieve the first-best outcome, the level of the policy instrument needs to be tailored to the spatial heterogeneity (see, e.g., Montgomery 1972 and Tietenberg 2006), which is likely changing over time. There also needs to be one policy instrument for each market failure (Lipsey & Lancaster 1956). In this section, we describe the general drivers of spatial heterogeneity, including differences in area-specific benefits and costs and the linkages across the network of locations that would form the basis of spatially explicit first-best policies.

### ***Spatial Heterogeneity in Benefits and Costs***

Heterogeneity across locations can be due to the underlying economics, environment, geography, topography, ecology, or some combination. Economic heterogeneity might stem from the costs of fishing differing across locations due to travel costs (Smith & Wilen 2003). Another example is provided by Hofer et al. (2000), who estimate the spatial distribution of expected benefits and costs with respect to illegal hunting in the Serengeti and find the distributions are driven by travel costs and by the differential risks of being caught in each location.

The environment, geography, and topography can also lead to heterogeneity in benefits and costs. For example, there are cases that stem from differential benefits (e.g., damages averted) associated with improvements in water quality upstream of various land uses. Location-specific benefits and costs are also possible in situations in which the potential damages from an invasive species could be greater in some invaded locations, for example, if an invasive species moves into an area where it competes with an endangered species (Aadland et al. 2012, Lampert

et al. 2014). Muller & Mendelsohn (2009) show that the benefits of a pollution abatement policy (damages averted) differ across the United States.

There are also examples in which heterogeneity in benefits and costs is driven by the underlying ecology of a system (see Figure 1a). Terrestrial habitats, such as forests, plains, and grasslands, create heterogeneity in habitat suitability for a particular species and therefore in species composition. The same holds for ocean habitats, such as coral reefs, sea grass beds, and sandy bottoms.<sup>2</sup> Figure 1a illustrates the spatial heterogeneity for the Great Barrier Reef Marine Park (GBRMP) in Queensland, Australia (Ellis et al. 2011). The variation across the GBRMP summarizes many factors, such as benthic habitat types (sand, mud, gravel, reef), bathymetry, ocean color and chemistry, and oceanographic forcing (Ellis et al. 2011). Even within a single habitat type there is heterogeneity between interior and boundary regions (edges) that may lead to differential ecological production across the land- or seascape (Epanchin-Niell & Wilen 2012).

### **Connectivity**

The presence, strength, and type of connectivity between nodes in a network influence the design of efficient policies. For example, along river corridors, the connectivity is unidirectional, with some economic activities upstream and some downstream of each other. Groundwater pools have multidirectional flows based on relative concentration differentials (see, e.g., Kuwayama & Brozović 2013 and Pfeiffer & Lin 2012). Migration and remittances, along with trade (imports and exports), are examples of economic sources of connectivity (see, e.g., Fujita et al. 1999) for which the flows can be in multiple directions. Connectivity is an important factor in human (Rowthorn et al. 2009) and animal (Horan & Wolf 2005) disease transmission, for which the frequency of migration of susceptible and infected individuals will affect the ability to manage the disease. Optimal pest management also depends on the migration rates and patterns across parcels of land (see, e.g., Bhat & Huffaker 2007 and Zhang et al. 2010). Furthermore, there is a long history of modeling the migration of species that are the focus of extractive activities, such as wildlife hunting (Ling & Milner-Gulland 2008, Sirén et al. 2013)

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<sup>2</sup> Habitat heterogeneity and quality are not simply two dimensional. In coral reefs, for example, rugosity of the reef is a critical factor in the ecological dynamics on the reefs (see, e.g., Harborne et al. 2012).

and commercial fisheries (see, e.g., Armstrong & Skonhøft 2006 and Bjørndal et al. 2004).<sup>3</sup> We use the latter application to illustrate some of the key features of connectivity in the remainder of the section.

One parsimonious conceptual framework for understanding the nature of connectivity is the concept of a metapopulation, which is a system consisting of local populations occupying discrete habitat patches with significant demographic connectivity between patches (Sale et al. 2006). The metapopulation concept is attributed to Levins (1969, 1970), who focused on terrestrial species and considered only whether a patch was occupied. Over time, the concept has been expanded to consider within-patch population dynamics and local abundances and has been adapted for and applied to the marine environment (Sale et al. 2006).<sup>4</sup> The metapopulation concept has the advantage of capturing, in a simple yet insightful method, the interactions between two scales: the local or patch level and the metapopulation (system-wide) scale.

In a marine metapopulation, the dispersal process might pertain to either adult or larval dispersal processes or both. For many marine species, adults and juveniles are likely to have different rates of movement and dispersal processes because currents largely transport juveniles, whereas adults may have more directed and purposeful movement. For example, a benthic population might have a common pool larval dispersal process in which larvae collect in gyres off a coastline, as well as an adult dispersal process linking up patches that are essentially linearly distributed along the same coast.

Figure 1*b,c* illustrates the dispersal component of a metapopulation model for coral trout in the GBRMP on the basis of oceanographic currents, coral reef locations, and species characteristics (Bode et al. 2014). This metapopulation has more than 1,000 patches (each reef in the GBRMP is a patch). Figure 1*b* shows a simulation of output predicting larval flows for coral trout. Figure 1*c* represents the larval connectivity matrix for coral trout on the basis of the average connectivity over a large number of simulations, like those illustrated in Figure 1*b*. In general, larvae are not necessarily passive dispersers, and the degree to which individuals are essentially retained by active biological mechanisms (like changing buoyancy) and/or by

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<sup>3</sup>Other contexts in which spatial heterogeneity in location (of extraction or pollution) is important to consider include water quality and air pollution (see, e.g., Farrow et al. 2005, Lankoski et al. 2008, and Muller & Mendelsohn 2009).

<sup>4</sup>For a recent application to terrestrial management, see Groeneveld & Weikard (2006).

external drivers in their natal or local habitat is becoming better understood (e.g., Cowen et al. 2000, 2006; Warner & Cowen 2002).<sup>5</sup>

For expositional purposes, we discuss a metapopulation model that combines the features of implicit larval dispersal processes (Brown & Roughgarden 1997, Polacheck 1990, Tuck & Possingham 1994) with (adult) movements (Sanchirico & Wilen 1999, 2001).<sup>6</sup> In each patch  $i$  of the system that consists of  $n$  patches, assume that the instantaneous rates of change of biomass are

$$\begin{aligned}\frac{dx_i}{dt} &= f_i(x_1, x_2, \dots, x_n) + ND_i(x_1, x_2, \dots, x_n) & \forall i=1, \dots, n \\ \frac{dx_i}{dt} &= f_i(x_1, x_2, \dots, x_n) + ND_i(x_1, x_2, \dots, x_n), \forall i = 1, \dots, n.\end{aligned}\quad (0)$$

Growth in each patch depends upon the own-growth function in patch  $i$ ,  $f_i(x_i, \dots, x_n)$ , generally assumed to be a density-dependent process, and upon net dispersal,  $ND_i$ , of adult biomass into and out of patch  $i$ , which may depend upon own biomass as well as upon biomass in any or all of the other patches. In this formulation, the “adult” dispersal process can be flexibly modeled via appropriate choice of the net dispersal function, and the juvenile or larval dispersal stages can be modeled via interactions that occur in the growth function. For the most part, the literature has used a linear net dispersal function of the general form

$$\begin{aligned}ND_i(x_1, x_2, \dots, x_n) &= d_{ii}x_i + \sum_{\substack{j=1 \\ i \neq j}}^N d_{ij}x_j & \forall i=1, \dots, n \\ ND_i(x_1, x_2, \dots, x_n) &= d_{ii}x_i + \sum_{\substack{j=1 \\ i \neq j}}^N d_{ij}x_j, \forall i = 1, \dots, n,\end{aligned}\quad (1)$$

where  $d_{ii}$  is the rate of emigration out of patch  $i$  ( $d_{ii} < 0$ ) and  $d_{ij}$  is the dispersal rate from patch  $j$  to patch  $i$ . Modelers often employ an adding-up assumption that whatever leaves patch  $i$  for

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<sup>5</sup> The rates and nature of dispersal of different age classes within a species are difficult to measure (e.g., Shanks et al. 2003), and movement rates appear to be highly variable among even closely related species.

<sup>6</sup> Other approaches to including space into models of biological populations include continuous time-spatial models formulated as partial differential equations (Brock & Xepapadeas 2002, Neubert 2003, Skellam 1951) and integrodifference equations that are continuous in space and discrete in time (Gerber et al. 2003). Our approach follows that of Levin (1974), Levin (1976), and Hastings (1982).

patch  $j$  arrives in patch  $j$  from patch  $i$  (Sanchirico & Wilen 1999). This approach assumes no mortality in the adult dispersal process and no deviations in movement along the dispersal route.

Typically, dispersal is generated by a random process whereby species redistribute themselves between the patches on the basis of relative densities of the patch populations.<sup>7</sup> The simplest representation of such a process depicts the dispersal mechanism between patch one and patch two as  $d_{11}x_1 + d_{12}x_2 \equiv b[(x_2/k_2) - (x_1/k_1)]$  and the dispersal mechanism between patch two and patch one as  $d_{22}x_2 + d_{21}x_1 \equiv b[(x_1/k_1) - (x_2/k_2)]$ , where  $b$  is a common dispersal rate. In this formulation, the adult dispersal cancels out in the aggregate (system wide) in each  $t$  (Sanchirico 2005). In a bioeconomic equilibrium, the patch density levels are likely to differ, and dispersal will therefore be a feature of the solution (flux equilibrium).

To depict own growth and the role played by larval dispersal processes, we use a model from Sanchirico (2005). In this model, the growth function in each patch is

$$f_i(x_1, x_2, \dots, x_n) = r_i(\alpha_i x_i + \beta_i \sum_{j=1}^N (1 - \alpha_j) x_j) (1 - \frac{x_i}{k_i}), \quad (2)$$

where  $r_i$  is the intrinsic growth rate in patch  $i$ ,  $k_i$  is the carrying capacity in patch  $i$ ,  $\alpha_i$  is the probability that larvae in patch  $i$  remain and successfully settle in patch  $i$ ,  $1 - \alpha_i$  is the probability that larvae leave patch  $i$  and enter a larval pool, and  $\beta_i$  is the probability that larvae survive the journey to and from the larval pool to resettle in patch  $i$ . If one assumes that  $\beta_i = m/N$ , where  $m$  is the survival probability, all larvae that do not settle in their local area  $[(1 - \alpha_i)x_i]$  are perfectly mixed in a larval pool and are evenly redistributed among all patches (e.g., Gerber et al. 2003, Hastings & Botsford 1999). The implication is that the distribution of larvae is so widespread that they cover the entire range of patches in the fishery (Hastings & Botsford 1999) (Figure 2a). Equation 2, however, permits other formulations and asymmetries in larval settlement rates that might be due to ocean and wind circulation patterns, such as gyres (Figure 2b).

Equation 2 depicts a process whereby regional larval production is density independent but whereby larval settlement is subject to local density-dependent mechanisms (Sanchirico 2005). The model predicts higher marginal and total biological growth than if the patches were not connected via larval dispersal, and it predicts that the effect of the population in patch  $j$  on

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<sup>7</sup> Rather than a random process, another possibility is that there is directed dispersal where species migrate to certain areas for spawning every year.

patch  $i$ 's production is greatest when patch  $i$ 's population is low. At the other extreme, if patch  $i$  is close to its carrying capacity, the effect of other patches' population levels is dampened because of competition for limited space and food in patch  $i$ . In the limit when each patch is at its carrying capacity (e.g., unexploited equilibrium), the net effects of larval dispersal on biological production are equal to zero. These characteristics are commonly referred to in the biological literature as postdispersal density dependence (Gerber et al. 2003).<sup>8</sup>

The model is capable of depicting a variety of behavioral characteristics of a metapopulation as well as a general set of connectivity patterns. Figure 2 nests many possibilities from fully integrated in panel *a* to source–sink in both adult and larval dispersal in panel *b*. We focus on these extreme cases because their characteristics are valuable in interpreting the literature. Specifically, we define symmetrical dispersal models as capturing a process in which, in an unexploited equilibrium, the dispersal process cancels out and there is no movement. This is the case, for example, in a system in which you can get from every patch to every other patch and in which dispersal is based on relative density levels (e.g.,  $b[(x_1/k_1) - (x_2/k_2)]$ ). Symmetric dispersal processes still influence the transient dynamics of the system, in which such processes operate so as to reduce density differentials over space and time (see, e.g., discussion in Janmaat 2005 and in Sanchirico & Wilen 1999).

The other case is asymmetrical dispersal, which in an unexploited equilibrium dispersal is nonzero (it does not go to zero). Sanchirico & Wilen (1999) describe this case as a flux equilibrium, and in population dynamics such a system is often termed a sink–source. The asymmetry in the connectivity can stem from many sources, including topography and upwellings. In one example of topography, the system being studied is a canyon and dispersal is blocked by the mountains, and oceanographic currents, such as gyres, dominate currents (e.g., California Current on the West Coast of North America). Furthermore, for these systems dispersal impacts both the transient dynamics and equilibrium characteristics.

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<sup>8</sup> When all larvae are retained locally ( $\alpha_i = 1$  for all  $i$ ), the growth function in each patch reduces to the standard logistic growth function, which is the model used in Sanchirico & Wilen (1999).

Although the literature typically analyzes these dispersal processes as present or not, both symmetric and asymmetric dispersal processes are almost certain to be simultaneously present in a seascape (see, e.g., Figure 1c). However, this distinction is valuable in understanding how connectivity affects the design of efficient policies.

### Spatial-Dynamic Policies

In this section, we review a subset of the literature to illustrate how the fundamental spatial characteristics of the natural resource and connectivity processes alone and together influence the first-best design of optimal spatial-dynamic policies. Although the design of the policies will depend on the particular characteristics of the system, Figure 3 presents a stylized representation of a number of cases by using a discrete space representation with three patches, each based on the existence of at least one externality and of a single decision-making entity. These different cases are for expositional purposes and to develop intuition; they are not meant to represent an exhaustive coverage of the universe of possible cases. Furthermore, the cases are motivated by ecology, but the intuition applies more generally to other contexts such as watershed management (often characterized by asymmetric connectivity). We discuss each case in turn.

First, if there is no economic, social, or biological connectivity but there is spatial heterogeneity (Figure 3a), then the optimal policy is independent and tailored to the characteristics of the patches. The policy is independent in the sense that you could break up the problem into separate optimization problems and arrive at the same solution as you would have had you jointly solved the system. Figure 3a depicts the case in which all the policies are interior (e.g., nonzero), but whether that holds in practice will depend on the characteristics of the patches. For example, a patch may be so high cost that engaging in economic activity there may not pay. The corollary is that when there is no spatial heterogeneity and no connectivity, the optimal policy is homogeneous across the system (with the same policy in each location).

Spatial policies leading to efficient solutions, however, are not necessarily dependent on benefits and costs varying. That is, policy heterogeneity may result, even if all the locations are the same and connectivity is symmetric. This outcome can happen when, for instance, the initial conditions on the state of the system differ; for example, one area has lower initial population levels than another area does (Costello & Kaffine 2010, Sanchirico et al. 2010). Figure 3b shows this situation. The optimal dynamic policy is to manage the extraction in the locations in each

period differently until the equilibrium is reached in which the lack of structural heterogeneity combined with symmetric dispersal results in a spatially uniform policy (see Figure 2*b*).

A corollary to the case shown in Figure 3*b* is that system connectivity is not a guarantee that a spatially differentiated policy is first best. For example, with symmetric biological dispersal and no heterogeneity in benefits and costs, the optimal solution is to do the same thing in every location in every period (a uniform policy) (see, e.g., Costello & Polasky 2008 and Sanchirico & Wilen 2005). Another corollary is that the presence of both spatial heterogeneity and symmetric connectivity will result in spatially differentiated policies over time; dispersal will be a feature in the long-run equilibrium due to the location-specific heterogeneity creating a wedge between the relative densities of the populations. In a structurally homogeneous system, asymmetrical connectivity can create policy heterogeneity across space (Sanchirico & Wilen 2005).<sup>9</sup>

Figure 3*c* illustrates that, even though the initial conditions might be the same, the asymmetry in the connectivity leads to differences over time and at the optimal equilibrium. Not surprisingly, the combination of structural heterogeneity and asymmetrical dispersal can lead to nonintuitive policies. Sanchirico & Wilen (2005) and Sanchirico et al. (2006), for example, show that under certain conditions asymmetries in the dispersal process can lead to boundary solutions for which fishing in the source is optimally set to zero. The gain by following such a process is the increase in the flow of dispersal to the sink patches. The likelihood of this outcome depends on whether the economic gradient (e.g., high- to low-cost patches) can be aligned with the biological dispersal gradient, which occurs when the sink is the more valuable area in which to harvest the fish.

Although a spatially differentiated policy is the first-best solution when any spatial heterogeneity is present, in practice the decision to implement spatially explicit policies will depend on the benefits derived from the spatial differentiation relative to the costs of implementing these policies (see, e.g., Kolstad 1987 and Tietenberg 1995 for a general

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<sup>9</sup> In continuous space models, the nature of the boundary conditions that describe how the biomass does or does not cross the boundary of the space can lead to heterogeneity in the optimal solution (see, e.g., Neubert 2003). If the assumption is that biomass units reflect back into the space when they try to cross the boundary, then the optimal solution is to maintain the same harvest level at each point in the space. In contrast, if biomass crosses the boundary and dies, then the optimal solution is to impose spatial heterogeneity on the harvest to account for the loss associated with species leaving the system and dying.

discussion; see, e.g., Kuwayama & Brozović 2013 and O’Ryan 1996 for examples in which the gains from spatial differentiation are found to be low). In many contexts, monitoring, enforcement, and other management costs can be large and can increase with spatial differentiation.

### ***Spatial versus Aspatial Policies***

In many systems, identifying that the optimal policy has a spatial-dynamic component is not surprising given the characteristics of the system. A natural question to ask, however, is how the spatial policies differ from an aspatial policy in terms of both their application and their performance. This question has formed the basis of many bioeconomic papers. For example, Robinson et al. (2008) model community use of nontimber forest product extraction. In their application, villagers must travel from the village to gather forest products, and therefore the cost of harvesting increases with the distance from the extraction site. The authors assume homogeneous forest plots and no connectivity between plots. With heterogeneity only in terms of the location of the economic agents relative to the plots, the authors find the optimal extraction path is cyclical, with optimal quantities to harvest varying year to year and often being zero. Their optimal solution differs from the aspatial counterfactual case in which the optimal extraction is a smooth path.

Sanchirico & Wilen (2005) explore the impacts of spatial heterogeneity and connectivity on the first-best spatially differentiated landings and effort taxes in a regulated open-access system. They examine a connected system of patches and explore the impact of different types of connectivity on their results (specifically, the authors explore dispersal based on density dependence, source–sink dynamics, and no connectivity). Fishermen are modeled as responding to profit, and therefore effort can be spatially heterogeneous. The authors show that economic and biological heterogeneity results in spatial differentiation of the first-best landings and effort taxes. However, the degree to which second-best non–spatially differentiated policies approximate the first-best solution depends greatly on the type and degree of spatial connectivity.

Patch models of wildlife disease spread and management have shown that when spatial connectivity is present, spatially explicit management can perform better than management that treats the patches as a single population. For example, Horan & Wolf (2005) examine optimal management strategies when the number of infected versus susceptible animals can vary by patch, the disease mortality rate can be patch specific, and the migration direction and rate can be patch specific. Aspatial management of a diseased population is often based on a threshold population level below which the proportion of the population that is infected goes to zero and

above which that proportion goes to one. This threshold effect has led to reducing wildlife densities as a means of managing disease. In the spatial case, in which migration occurs, the optimal management may change. For example, when migration flows one way from a healthy patch to an unhealthy patch, it may be optimal to harvest all the animals in the unhealthy patch and to allow the patch to repopulate with animals from the other patch where the animals are not infected.

Another example is Newbold & Eadie (2004), who develop a bioeconomic model with the objective of maximizing total breeding mallard abundance by choosing wetland area to restore around each site, subject to a limit on the total hectares restored. In the model, mallards have strong spatial preferences over breeding sites on the basis of site attributes, including connectivity and configuration of sites. The authors find that, when the spatial preferences are accounted for, there can be more than a proportional increase in the population relative to the percentage increase in land conserved.

Hard boundaries or biophysical forcing mechanisms stemming from, for example, topography or oceanographic currents can result in spatially explicit optimal management strategies. Epanchin-Niell & Wilen (2012) show that optimal management of an invasive species can depend on where in the landscape (e.g., interior or boundary cell) the invasion occurs as well as on the shape of the invasion. The authors model the landscape as a grid with cells linked via dispersal, with heterogeneity in dispersal and management costs in the cells related to differences in interior versus exterior (boundary) edges. Costello and coauthors, in a number of papers, look at the management implications of larval dispersal processes that are driven by oceanographic currents in Southern California (see, e.g., Costello et al. 2010 and White et al. 2008).

### ***Boundary Solutions***

A substantive literature highlights how the presence of connectivity results in spatial specialization (e.g., boundary solutions) whereas the case without connectivity does not. The literature on the economics of marine reserves (which entails no fishing in one or more areas) is one example. For instance, Sanchirico et al. (2006) explore optimal management of a metapopulation, whereby a marine reserve is a corner solution associated with an optimal patch fishing level equaling zero in equilibrium. The authors find that reserves are potentially part of

the economically optimal solution, depending on the nature of the settlement process, on dispersal rates, and on relative costs of fishing.

Costello & Polasky (2008) model stochastic growth within each patch and dispersal between patches.<sup>10</sup> The authors conclude that in most cases the optimal management plan depends on connectivity (dispersal) patterns. Furthermore, they find instances in which extreme forms of spatial heterogeneity in management across patches, including reserves in some patches and not in others, is optimal. Finally, the authors find that stochasticity tends to lead to temporary closures over permanent reserves under optimal management. Other papers that look at the optimality of marine reserves include Pezzey et al. (2000), Neubert (2003), Sanchirico & Wilen (2006), and White et al. (2008).

In discerning what factors might lead to a boundary solution, Helfand & Rubin (1994) show that the optimal management of negative externalities may be to concentrate the externality (e.g., through pollution generation) at one of the sites, even if the sites are homogeneous to start with. Their model explores the relationship between the cost required to spread the externality between sites, the relationship between production of the externality and the stock of the externality, and the social welfare associated with various amounts of the externality at each site. The authors find that increasing returns to scale (nonconvexities) can lead to instances in which the optimal approach is to concentrate the externality spatially.<sup>11</sup>

In a spatial fisheries model, Brown & Roughgarden (1997) show that specialization—that is, harvesting the adults in only one of the possible locations—is the efficient solution when the connectivity is due to larval dispersal. They argue that this extreme result is due to the nonconvexity introduced into the optimization model by the unique dispersal process of larvae that mix in common pools. Sanchirico (2005) further explores how the properties of different dispersal processes can lead to spatial specialization in the context of marine reserves.

Although nonconvexities are one potential source of optimal boundary solutions in the presence of spatial externalities, another dimension that leads to boundary solutions is when a single decision-making entity is trying to balance multiobjectives. Sanchirico (2011), for

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<sup>10</sup> See also Grafton et al. (2005).

<sup>11</sup> See Lewis & Schmalensee (1977) for a more general discussion of the role of nonconvexities in optimal resource extraction.

example, illustrates how in a metapopulation a decision maker trying to balance the returns to fishing and the returns from nonconsumptive values might, under certain heterogeneity and dispersal conditions, specialize the production of fishing in certain patches and the production of nonconsumptive values in other locations. Skonhofs & Solstad (1996) investigate spatial management of a terrestrial resource that has multiple values and management objectives.

Boundary solutions may also stem from multiple externalities simultaneously operating in these systems (Smith 2012). For example, in a fisheries context, there is the well-known stock externality, and there is the spatial externality due to the dispersal of the fish stock in the system. The presence of constraints on the ability to apply one policy instrument for each market failure due to being either nature dictated or policy induced will result in a second-best setting (Lipsey & Lancaster 1956). The spatial processes are often dictated by nature and are often uncontrollable. That is, in spatial bioeconomic models, the controls available to managers are often the harvest, development, or restoration of species or habitat in a particular location, whereas the processes unfolding across space are due to the activities at each location and the dispersal or diffusion of species (e.g., fish, birds, pests, and bees).<sup>12</sup> Therefore, the use of second-best policies like location-specific controls that are meant to address a local market failure are very likely to create distortions in the spatial domain relative to the situation in which you can address market failures occurring both locally and due to spatial processes. As a result, a boundary solution in a spatial system is likely to be associated with the optimal solution trying to “control” dispersal (connectivity) and with the economic returns from the production in each patch. That is, align the biological gradient with the economic gradient.

In a spatial bioeconomic analysis that considers the implications of multiple externalities for the spatial management of a nine-patch metapopulation, Sanchirico (2004) finds that multiple marine reserves are part of the optimal solution in the presence of stock, space, and habitat externalities. In the model, the habitat externalities are derived from the direct impact of fishing effort (bottom trawling) on the growth of the fish population (Morgan & Chuenpagdee 2003).

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<sup>12</sup> There are, however, exceptions in which the regulator is explicitly considering spatial controls to influence the dispersal between patches. Contexts include the management of invasive species, disease, or pests, and controls include import/export bans and barrier controls that break the spatial linkage or process. In the invasive species literature, controls include barriers, habitat quality change, monitoring/search, enforcement, and eradication (Albers et al. 2010, Brown et al. 2002, Epanchin-Niell & Hastings 2010, Epanchin-Niell et al. 2012, Kaiser & Burnett 2010, Sharov 2004).

However, Sanchirico (2004) finds that if a habitat externality is not present, marine reserves are not part of the optimal solution.

### Spatial Bioeconomic Model

We develop a simple two-patch discrete space nonlinear optimal control model to illustrate how the two features of spatial-dynamic problems combine to determine optimal policies (see the Supplemental Text for a more in-depth description of the model). Specifically, we introduce controls on the dispersal process (e.g., fish ladders and terrestrial connectivity corridors) in addition to the harvest controls. With this addition, the choice not to control dispersal becomes a corner solution and will not be the optimal solution if controls are available at costs low enough to profitably employ. The purpose of the model is to demonstrate the potential efficiency gains from addressing the spatial externality through dispersal controls (or, conversely, the second-best optimal results of fisheries models that only indirectly control dispersal through harvest controls).

We frame the problem from the manager (sole owner) perspective, where the objective is to maximize the net present value of rent from harvesting in the two patches less the cost associated with implementing the dispersal controls. There are four possible controls available to the manager: harvest levels in each patch and dispersal control in each direction (i.e., from patch 1 to 2 and from patch 2 to 1). We assume a Schaefer production function commonly used in fisheries, that fishing cost is quadratic in effort, and the cost of dispersal control is convex (increasing at an increasing rate) as dispersal is pushed further away from the natural dispersal conditions. The net dispersal functions are modified (Equation 2) to include controls on the dispersal process ( $ND_i = b[u_j(x_j / k_j) - u_i(x_i / k_i)]$ , where  $u_i$  refers to control of dispersal of biomass from patch  $i$  and  $u_j$  refers to control of dispersal of biomass from patch  $j$  to patch  $i$ ).

Figure 4 illustrates the increase in optimal steady-state profitability when dual dispersal controls are available relative to no dispersal controls, as we vary the fishing costs in patch 1 (high-cost patch) and the dispersal cost (see Supplemental Figure 1 for all the cases). We find significant gains relative to the no-control case—more than a 40% increase in profitability in some cases. The optimal solution is to increase the net dispersal to patch 2 (the low-cost patch) by increasing dispersal from patch 1 to patch 2 and decreasing dispersal from patch 2 to patch 1 (see Supplemental Figure 2). Not unexpectedly, the increase in profitability associated with dispersal controls decreases as dispersal control costs increase. More interestingly, the gain relative to the no-dispersal case is highest when the difference in fishing costs between the two patches is greatest. The greater difference in harvesting costs between patches makes the transfer

of biomass to patch 2 (the low-cost patch) a more attractive option. This scenario suggests that low or no dispersal control (and therefore the cost associated with ignoring potential dispersal control) is optimal when there is little difference in harvest costs between patches and when the cost of dispersal is high relative to price and harvest costs. We do not find significant steady-state gains when there is only one dispersal control relative to the no-control case, unless the degree of the cost heterogeneity is significant and the dispersal cost is low. In the limit, we find that as the dispersal costs decrease, the optimal equilibrium solution is to harvest exclusively from patch 2 (the low-cost patch), creating a boundary solution in which there is no fishing (marine reserve).

We also illustrate the optimal dynamics under the assumption that the manager is rebuilding the metapopulation from open-access conditions (Figure 5). We find that the optimal solution without dispersal controls consists of more biomass in patch 1 relative to patch 2. We also find that biomass in patch 1 disperses to patch 2. The dispersed biomass can then be harvested from patch 2. In this case, harvest in patch 2 is higher than in patch 1. This is similar to the finding of Sanchirico & Wilen (2005). The single control cases are very similar, but with slightly lower patch 1 stock and slightly higher patch 2 stock (see Supplemental Figure 3 for the optimal stock path).

With dual controls and relatively low control costs relative to fishing costs, the situation changes. The higher the biomass, the lower are the marginal fishing costs, and therefore there is the incentive to maintain a high biomass in patch 2. Dispersal controls allow for the higher biomass while still allowing biomass to disperse into patch 2. We observe a higher patch 2 biomass (relative to patch 1) but also a higher patch 2 harvest. This result is due to high levels of net dispersal (see Figure 5) that are maintained by increasing the flow to patch 2 while decreasing the flow to patch 1. In our numerical example, the optimal solution is a boundary solution (no fishing) for all  $t$ . Regardless of whether dispersal controls are feasible (and/or realistic), our findings support the conjecture that boundary solutions that align the biological and economic gradients represent second-best solutions dictated by nature.

## Discussion

The visualization and processing of spatial information and patterns of natural resource abundance will continue to increase in the future, as will our understanding of the implications of the different interactions occurring across local, regional, national, and global scales. Bioeconomic analysis can provide a framework within which to organize these new data and,

thereby, develop a deeper understanding of the nuances and trade-offs related to the political, economic, social, and ecological aspects of natural resources and their users.

One important question is the feasibility of implementing spatial policies (see also Sanchirico & Wilen 2008). The GBRMP example we discuss above, for instance, has more than 1,000 coral reef habitats, all of which have a self-sustaining population of coral trout and which are connected to varying degrees. How do we reconcile the scale of GBRMP with the findings of public economics, which requires that the level of the policy instrument be tailored to the spatial heterogeneity and that there be one policy instrument for each market failure? It would not be surprising to find that as the spatial resolution of the policy increases, the overall returns to the system are increasing at a decreasing rate. Therefore, there might be a point at which the gains of achieving the first-best solution no longer outweigh the costs of implementation (although these costs are likely decreasing over time, e.g., with the increasing use of tracking software). Where and under what conditions this point is reached are empirical questions that are challenging to solve due to the scale of the system and the potential for many confounding factors (Smith 2008).

Nested within the spatial resolution issue is the additional factor that there are many margins for which common pool resource extraction and conservation are distorted (Smith et al. 2010, Wilen 2005). In this respect, the current situation for many natural resources is that we are already operating in a second- or third-best setting stemming from nature and policies. As Lipsey & Lancaster (1956) discuss, when you begin to unravel such a system partially (e.g., one issue at a time), overall welfare is very likely to decrease. Understanding where the transition from an aspatial policy instrument to a spatial policy instrument falls in that spectrum is critical in assessing both *ex ante* and *ex post* the policy impact of such a change.

The challenges of managing natural resources across both space and time will likely increase with climate change as species ranges and dispersal patterns shift. For some resources, these shifts will occur within a single jurisdiction, but for many resources, these shifts will cross political jurisdictions. The implication is that these resources are likely to be subject to different management objectives and management entities.

Finally, in this review, we confine ourselves to consideration of a single management entity with control over the entire metapopulation. Growing areas of research explore potential solutions and issues in the presence of multiple decision makers. The focus of this literature is generally on smaller numbers of stakeholders, often two or three, and interactions are modeled using game theoretic frameworks (see, e.g., Bailey et al. 2010, Clark 1980, Kaitala and Pohjola

1988, and Munro 1990). Further exploration of the cooperative and noncooperative outcomes in spatial-dynamic systems is a fruitful area of policy-relevant research that will help policy makers predict the need for collaboration among countries as ranges of different metapopulations shift with the changing climate.

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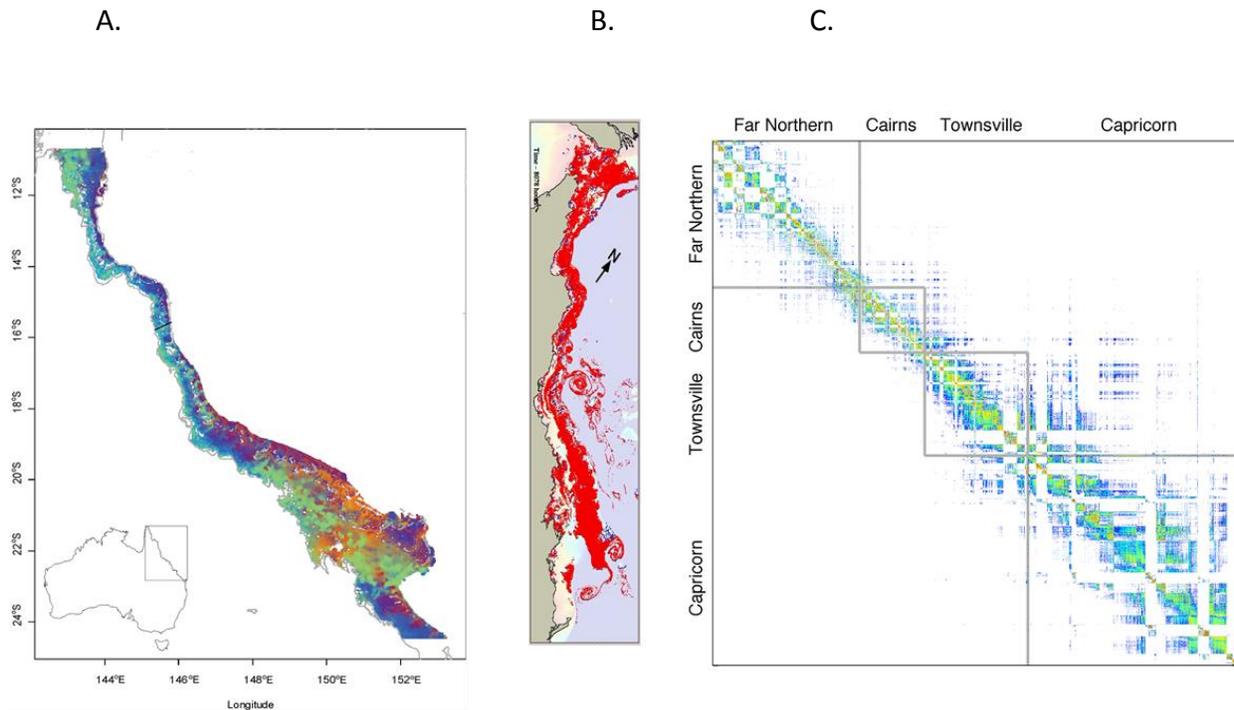
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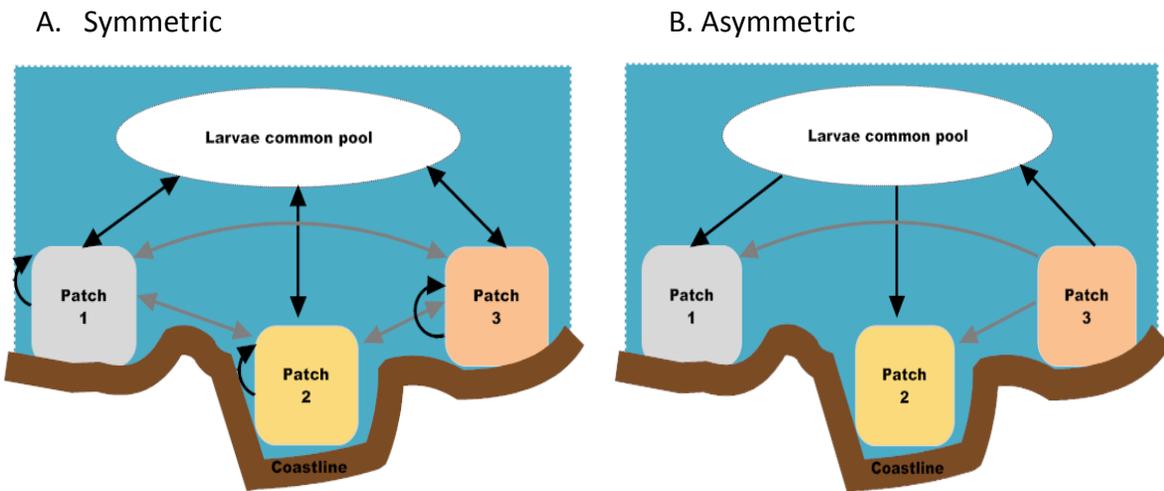
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## Figures



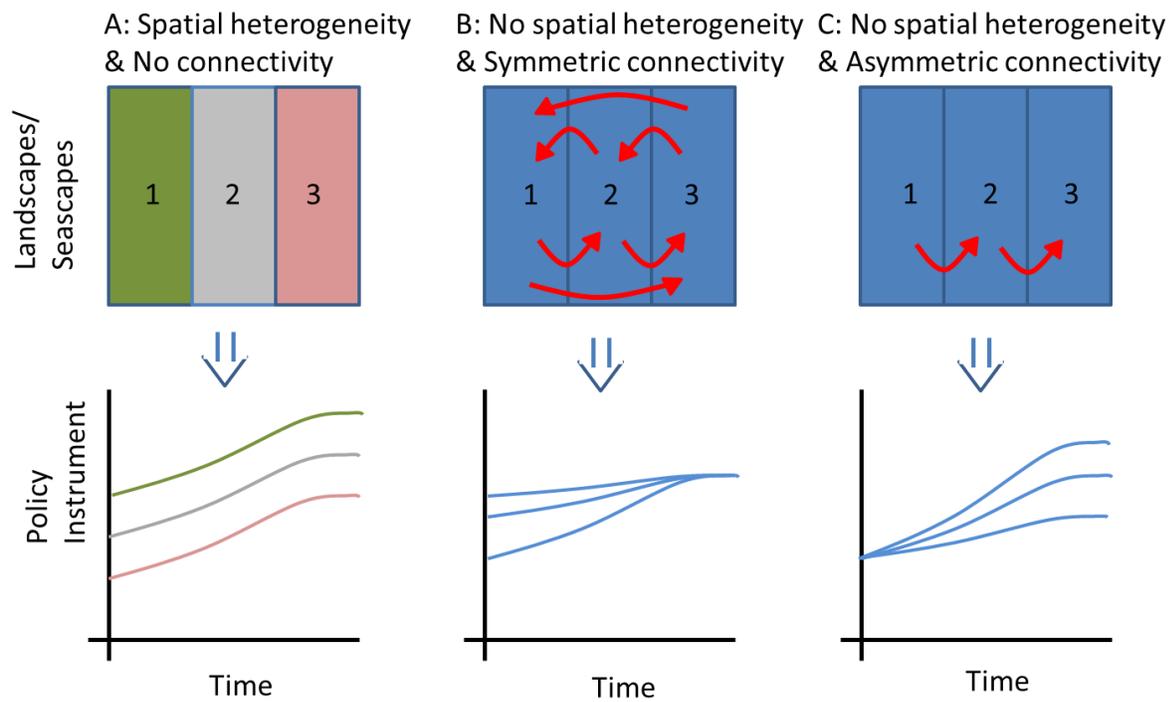
**Figure 1. Example of spatial heterogeneity, larval dispersal flows, and larval connectivity in the Great Barrier Reef Marine Park (GBRMP) in Queensland, Australia.**

(a) A biophysical map of the Great Barrier Reef continental shelf. The different colors represent predicted patterns of biodiversity composition. Panel *a* modified from figure 5 in Ellis et al. (2011). (b) An example of a simulation output predicting larval flows for commercially fished coral trout on the basis of oceanographic currents, coral reef locations, and species characteristics. (c) The average larval connectivity matrix for coral trout based on a large number of the simulations illustrated in panel *b*. The y-axis is the source patch, and the x-axis is the receptor patch. The colors indicate the strength of the connectivity between a source patch and a receptor patch (*red* denotes a higher probability of connectivity). The 45-degree line represents local retention of the larvae. Asymmetry in the off-diagonals stems from the main oceanographic current in this region from the north to the south. Panels *b* and *c* are from Bode et al. (2012) and Bode et al. (2014).



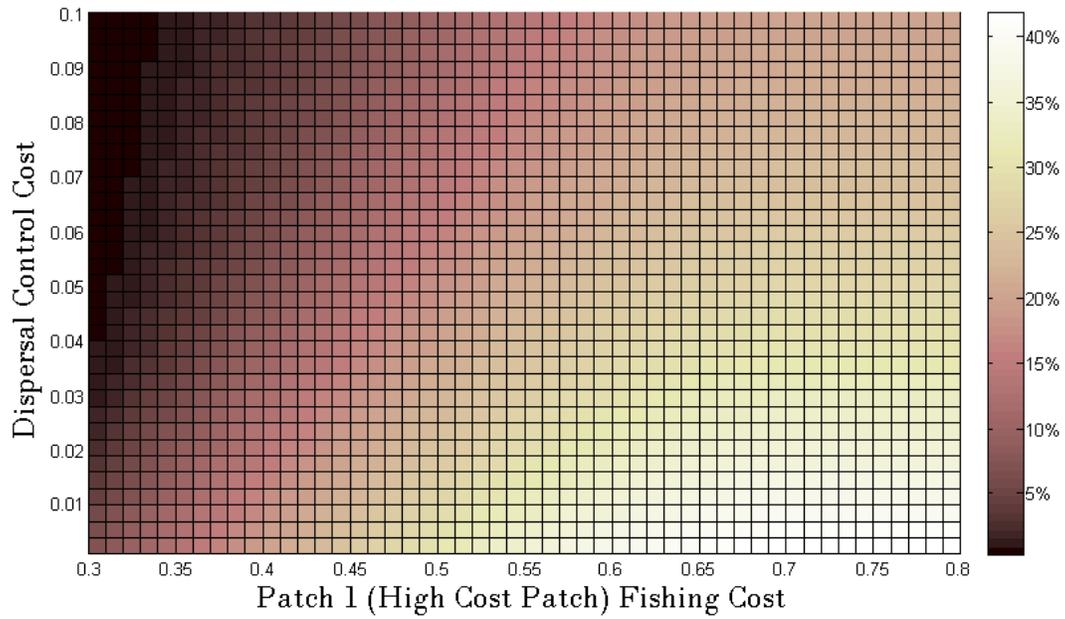
**Figure 2. Examples of (a) symmetric and (b) asymmetric connectivity structures.**

The black arrows represent larval dispersal, and the gray arrows represent adult dispersal. The black arrows that feed back directly into the patch represent local retention of larvae. The asymmetric case depicts a source–sink system in which patch 3 is a source of larvae and adult dispersal.



**Figure 3. A schematic of optimal spatial-dynamic policy instruments in the presence of a single decision-making entity.**

(*Top*) The different colors in the landscapes in panel *a* represent structural heterogeneity. The red arrows represent dispersal flows. (*Bottom*) The *y*-axis represents the level of a policy instrument for each patch, and the *x*-axis is time. The paths of the optimal policies converge toward the optimal steady state.



**Figure 4. Percentage increase in optimal steady-state profitability.**

This figure compares the percentage increase in equilibrium profitability achieved when dual controls are available relative to no controls. See the Supplemental Text for information on the numerical parameters used to derive this figure.

Figure 5.

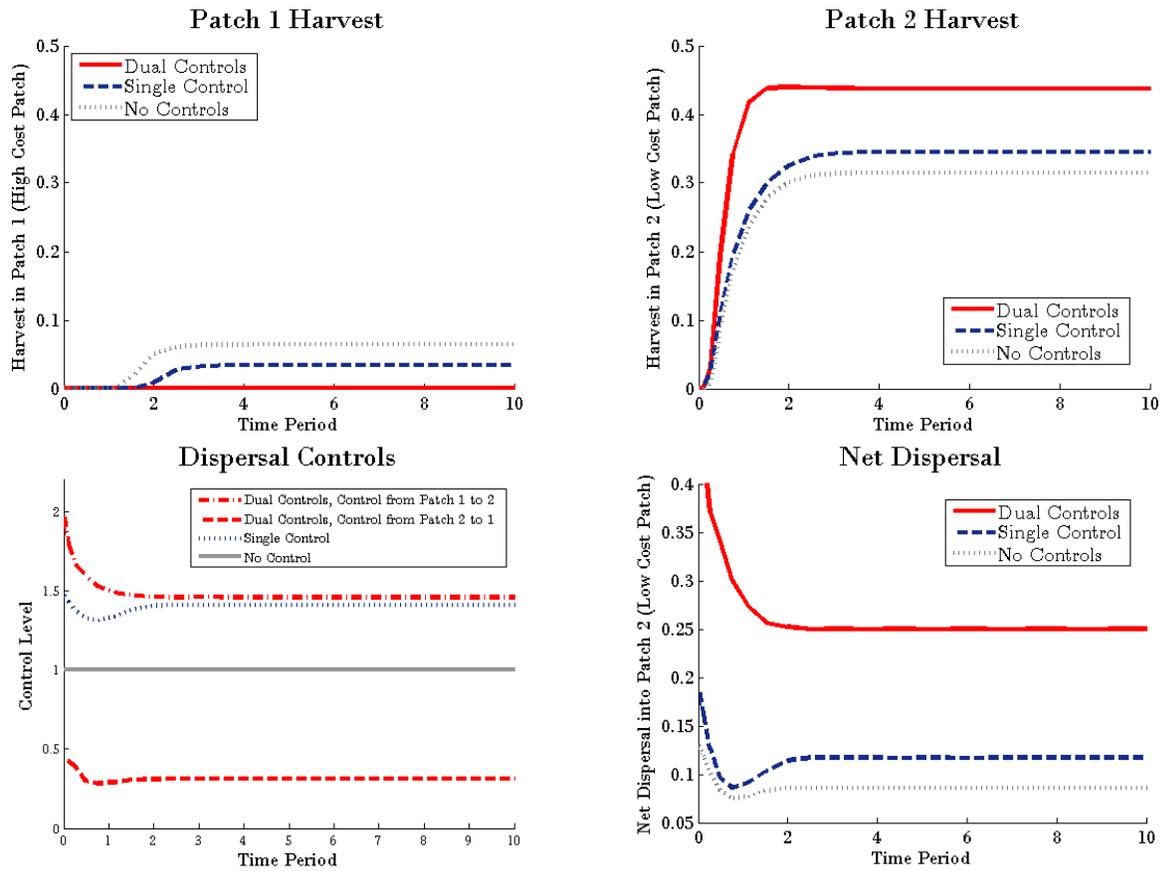


Figure 5. Example of optimal spatial-dynamics of rebuilding.

This figure explores the differences in rebuilding schedules in terms of profit-maximizing dispersal controls and harvest in each of three cases: dual controls, single control, and no controls. The stocks in both patches are rebuilding to their steady-state levels. Patch 1 denotes the high-cost patch, and patch 2 denotes the low-cost patch. See the Supplemental Text for information on the numerical parameters used to derive the figure.

## Supplementary Information

### *Spatial Bioeconomic Model*

We develop a simple 2-patch discrete space optimal control model to illustrate how the two features of spatial-dynamic problems combine to determine optimal policies. Traditional bioeconomic metapopulation models include harvest controls only. When only harvest controls are modeled it is (implicitly) assumed that the manager or regulator does not have control over the direction and magnitude of dispersal control. As such, the dispersal rate is exogenous (dispersal flows are often endogenous however due to relative densities of the population). Here we introduce controls on the dispersal process (e.g. fish ladders and terrestrial connectivity corridors) in addition to the harvest controls. With this addition, the choice not to control dispersal becomes a corner solution and will not be the optimal solution if controls are available at costs low enough to profitably employ.

The purpose of this model is to demonstrate the potential efficiency gains from addressing the spatial externality through dispersal controls. We frame the problem from the manager (sole owner) perspective where the objective is to maximize the net present value of rent from harvesting in the two patches, assuming a discount rate of  $\delta$ , subject to stock dynamics, harvest limits, dispersal control limits, non-negativity constraints on harvest and stock, and initial conditions. Then, the manager's objective is:

$$V = \max_{h_1(t), h_2(t), u_{12}(t), u_{21}(t)} \int_0^{\infty} e^{-\delta t} \sum_{i=1}^2 \left( \pi_i(h_i(t), x_i(t)) - \sum_{j=1, j \neq i}^2 g_{ij}(u_{ij}(t)) \right) dt \quad (S1)$$

In Equation (S1) the profit in patch  $i$ ,  $\pi_i$ , is a function of the population in patch  $i$ ,  $x_i(t)$ , and the harvest in the patch,  $h_i(t)$ . The per-period value also includes a second term, the cost for the dispersal control, represented by the  $g_{ij}(t)$  function. The function  $g_{ij}(t)$  is the cost of applying the dispersal control to the flows from patch  $j$  to  $i$ , and depends on the amount of control applied,  $u_{ij}(t)$ . In the model, there are four possible controls available to the manager: selection of harvest levels in each patch and dispersal control in each direction (i.e. from patch 1 to 2 and from patch 2 to 1).

We assume a Schaefer production function commonly used in fisheries where harvest is the product of a catchability term, effort, and stock  $h_i = q_i E_i x_i$ . We assume cost is quadratic in effort:  $cost_i = c_{1,i} E_i + c_{2,i} E_i^2$  to capture potential adjustment costs. The combination of our production function and cost function implies that per unit harvesting costs are decreasing in the stock. We also assume that the cost of dispersal control is convex (increasing at an increasing

rate) as dispersal is pushed further away from the natural dispersal conditions. For the numerical analysis, we assume the  $c_{2,i}$  term is the same in each patch. This results in marginal cost functions for the two patches having equal slopes, but different intercepts due to the  $c_{1,i}$  term. This type of functional form may be appropriate in a fisheries example to represent a case where there are different transportation costs associated with traveling to each patch, but once at the patch the opportunity cost of effort is the same.

The population in each patch grows logistically with growth rate  $r_i$  and carrying capacity  $K_i$  as shown in Equation (S2). We modify the symmetric dispersal process to include the possible controls on the dispersal process. Specifically,  $u_1$  controls dispersal of biomass from patch 1 (flowing to patch 2) and  $u_2$  refers to control of dispersal of biomass from patch 2 to patch 1. We impose constraints on  $u_i$  that are symmetric in the cost of dispersal control. In particular, the cost of applying an amount of control to reduce dispersal is equal to the same amount of control to enhance dispersal. We bound  $u_i, i \in [0, u_{max}]$ . Dispersal costs are incurred if you move off  $\frac{u_{max}}{2}$  in either direction. If  $u_i < \frac{u_{max}}{2}$ , then the dispersal control is decreasing the flow of biomass relative to the natural dispersal rate. At the limit of 0 no dispersal of biomass occurs. If  $u_i > \frac{u_{max}}{2}$ , then the control is increasing the rate of dispersal relative to the natural rate.

$$\begin{aligned}\frac{dx_1}{dt} &= r_1 x_1(t) \left(1 - \frac{x_1(t)}{K_1}\right) + b \left(u_2 \frac{x_2(t)}{K_2} - u_1 \frac{x_1(t)}{K_1}\right) - h_1(t) \\ \frac{dx_2}{dt} &= r_2 x_2(t) \left(1 - \frac{x_2(t)}{K_2}\right) - b \left(u_2 \frac{x_2(t)}{K_2} - u_1 \frac{x_1(t)}{K_1}\right) - h_2(t)\end{aligned}\quad (S2)$$

In our model patch heterogeneity can exist due to differences in the cost parameters, patch prices, growth rates, and carrying capacities. The dispersal control parameter  $\theta$  does not vary by patch, but extensions to our model could allow for this possibility.

We analyze 3 cases that differ in terms of the restrictions we place on the dispersal controls. In the first case, we allow controls on the flow to and from each patch; in other words,  $u_i$  is free, subject to the bounds. In the second case we only allow the magnitude of the natural dispersal rate to be manipulated. Finally, our third case requires  $u_1 = u_2 = \frac{u_{max}}{2}$ , and therefore replicates the traditional models used in the literature where it is assumed that no dispersal controls are applied. Specifically, the cases are:

### Case 1: Dual Controls

In our model, the dual control case is the first best case. In this case there are four controls in the system:  $u_1, u_2, h_1,$  and  $h_2$ . The dispersal term is:

$$u_2 b \frac{x_2(t)}{K_2} - u_1 b \frac{x_1(t)}{K_1}$$

This formulation allows the direction of dispersal to be altered such that net biomass can flow opposite to the density-gradient.

### Case 2: Single Control

We also explore a single control case, where  $u_1$  is equal to  $u_2$ , and therefore we identify the control parameter as  $u$  (without any subscript because it applies to both patches).

$$ub \left( \frac{x_2(t)}{K_2} - \frac{x_1(t)}{K_1} \right)$$

In this case,  $u$  is a unit-less multiplier on the rate of dispersal. The flow will always be from high density to low density, but the strength of the dispersal (the population dispersing per unit of time and per change in density) can be altered. This may be a relevant formulation when examining corridors between terrestrial populations.

### Case 3: No Controls

This case is the traditional case where dispersal is modeled as:

$$b \left( \frac{x_2(t)}{K_2} - \frac{x_1(t)}{K_1} \right)$$

### Long Run Steady State

We begin by examining the optimal long run steady-state to provide insight into the potential magnitude of profitability gains available through dispersal controls. The focus of this section is comparing the long-run profitability of the system with dual dispersal controls and with a single dispersal control to the traditional assumption of no dispersal controls.

The equilibrium of the first case is the solution to maximizing the integrand of  $V$ , which is the per-period-profit, assuming the stock levels are constant in the equilibrium. The integrand of  $V$  is:

$$\Pi(h_1(t), h_2(t), x_1(t), x_2(t), u_{12}(t), u_{21}(t)) = \sum_{i=1}^2 \left( p - \frac{c_{1,i}}{x_i(t)} - \frac{c_2}{x_i(t)^2} h_i(t) \right) h_i(t) - \theta(1 - u_i)^2$$

Solving the maximization problem yields equilibrium harvest levels, dispersal control levels, and stock levels in each patch. To obtain a solution we exploit the fact that in equilibrium  $dx_i/dt = 0$  and get closed form solutions for  $h_1$  and  $h_2$  in terms of  $x_1$  and  $x_2$ .

$$h_1(t) = r_1 x_1(t) \left(1 - \frac{x_1(t)}{K_1}\right) + b \left(u_2 \frac{x_2(t)}{K_2} - u_1 \frac{x_1(t)}{K_1}\right)$$

$$h_2(t) = r_2 x_2(t) \left(1 - \frac{x_2(t)}{K_2}\right) - b \left(u_2 \frac{x_2(t)}{K_2} - u_1 \frac{x_1(t)}{K_1}\right)$$

Then, by substituting the equations for  $h_1$  and  $h_2$  into  $\Pi$ , we have an equation in terms of unknowns  $x_1$ ,  $x_2$ ,  $u_1$ , and  $u_2$ . Differentiating with respect to each of these unknowns yields 4 first order conditions which jointly identify unknowns  $x_1$ ,  $x_2$ ,  $u_1$ , and  $u_2$  (and therefore also  $h_1$  and  $h_2$ ).

$$\frac{\partial \Pi(x_1(t), x_2(t), u_{12}(t), u_{21}(t))}{\partial x_1(t)} = 0$$

$$\frac{\partial \Pi(x_1(t), x_2(t), u_{12}(t), u_{21}(t))}{\partial x_2(t)} = 0$$

$$\frac{\partial \Pi(x_1(t), x_2(t), u_{12}(t), u_{21}(t))}{\partial u_1(t)} = 0$$

$$\frac{\partial \Pi(x_1(t), x_2(t), u_{12}(t), u_{21}(t))}{\partial u_2(t)} = 0$$

We also impose the non-negativity constraints on harvest and stock previously discussed.

The solution to case 2 mirrors that of case 1 with the exception that instead of  $u_1$  and  $u_2$  there is a single  $u$ . Finally, in case 3 only the harvest levels in each patch can be chosen. When  $u_1=u_2=1$  the problem is reduced to one similar to Sanchirico et al. (2006). In this case there are only two controls available ( $h_1$  and  $h_2$ ).

### **Numerical Analysis**

The values we use to obtain our numerical results are similar to those in Sanchirico et al. (2006).<sup>13,14</sup> We use pseudospectral collocation to solve for the optimal dynamics of harvest and

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<sup>13</sup> In this paper we choose  $u_{\max}$  so that no more than the patch population can be dispersed. Given the dispersal rate  $b=.5$ , we examine the maximum net dispersal from patch 2 that can occur. If, we assume dispersal control  $u_1 = 0$  (which results in the minimum dispersal from patch 1 of 0) then the maximum amount of dispersal from patch 2 that

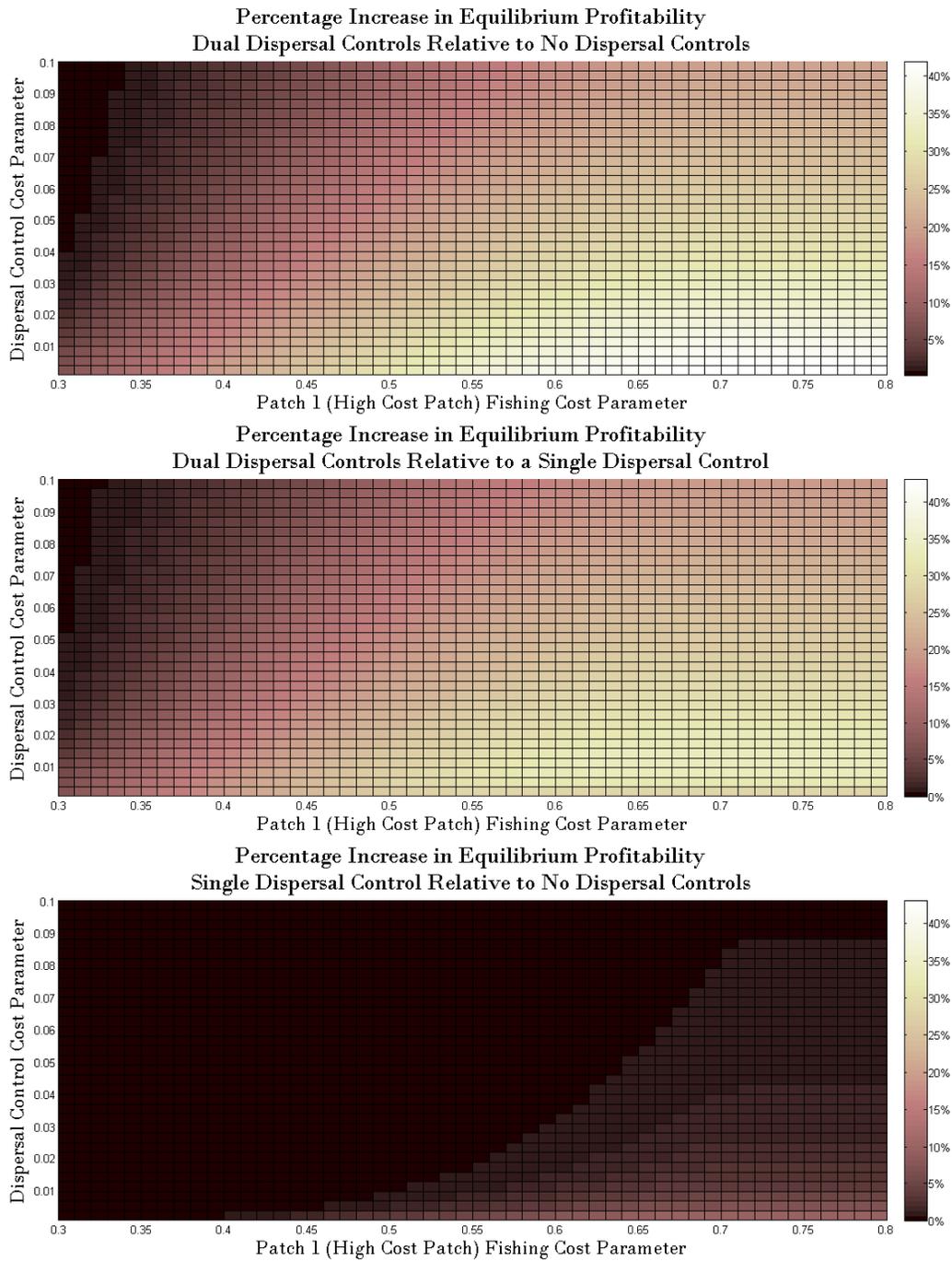
dispersal control over time (Garg et al 2010). Specifically, we approximate the infinite-time optimal control model with a finite-time non-linear programming (NLP) problem, where we assume that fishing harvest rates are approximated with a polynomial over a period from 0 to  $T$ . The algorithm ensures that the residual error of the state and non-negativity constraints are minimized at the collocation points. An advantage of this approach over, for example, shooting methods (Judd 1998) is that we can directly incorporate the non-negativity constraints into the problem. This feature enables us to find optimal solutions that might reside on the boundary of the control set for a period of time, which as we just highlighted could be an important feature of spatial-dynamic problems. The algorithm was implemented using TOMLAB (v. 7.8) (Holmström 2001, Holmström et al 2008) and the accompanying PROPT (Rutquist & Edvall 2009). The approximate NLP is solved using the general-purpose nonlinear optimization package SNOPT.

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is feasible is such that  $bu_2x_2 \leq x_2$ . Substituting  $b=.5$  and simplifying we find this occurs when  $u_2=2$ . The same reasoning applies to the limit on  $u_1$ . Therefore, we choose  $u_{\max}=2$ .

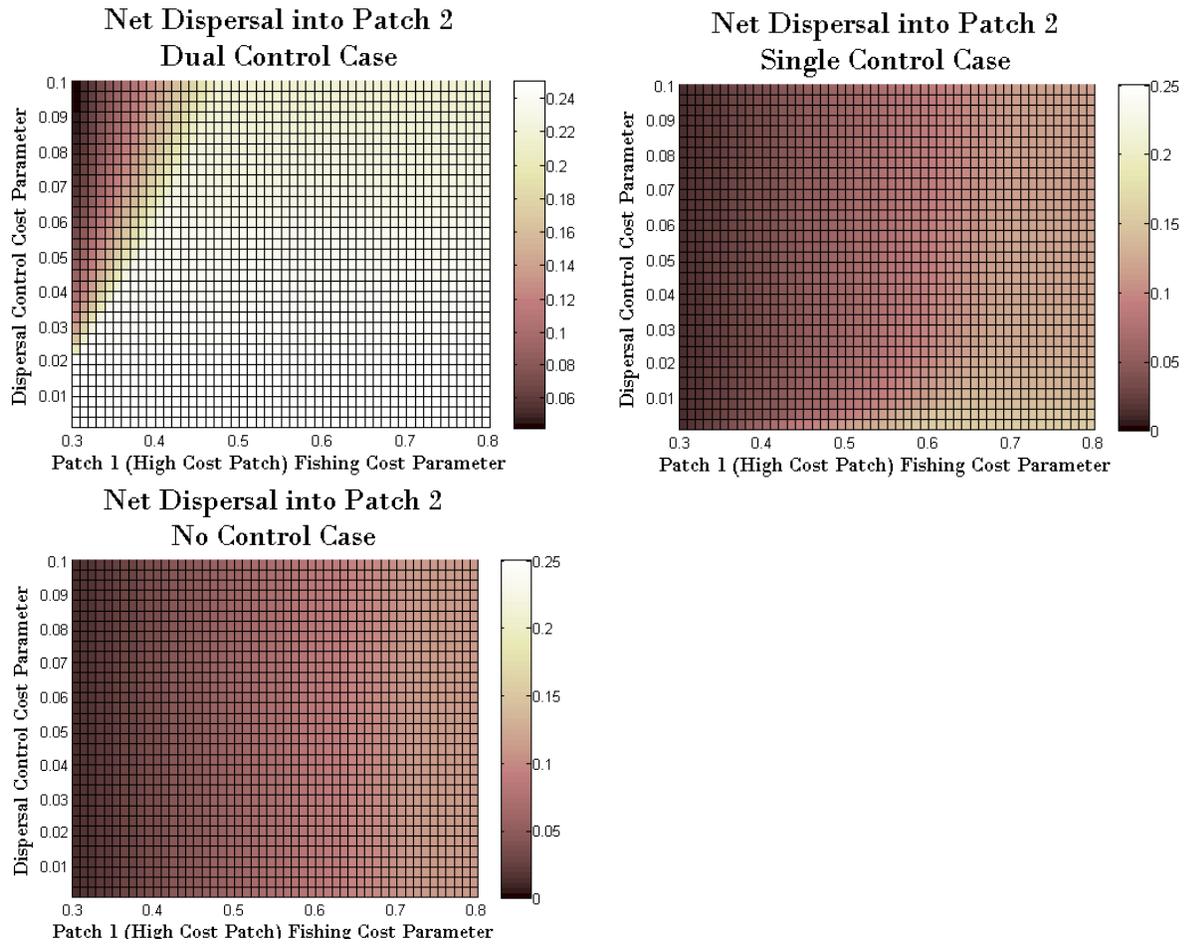
<sup>14</sup> Figure 4 in the main text is derived using the following parameters:  $c_{11}=.3-.8$ ,  $c_{12}=.25$ ,  $c_{21}=c_{22}=.1$ ,  $p=1$ ,  $k=1$ ;  $r=1$ ,  $b=.5$ ,  $\delta=.05$ ,  $u_{\max}=2$ ,  $\theta=.001-.1$ . The values used to derive Figure 5 are  $c_{11}=.6$ ,  $c_{12}=.25$ ,  $c_{21}=c_{22}=.1$ ,  $p=1$ ,  $k=1$ ;  $r=1$ ,  $b=.5$ ,  $\delta=.05$ ,  $u_{\max}=2$ ,  $\theta=.1$ .

**Additional Figures**



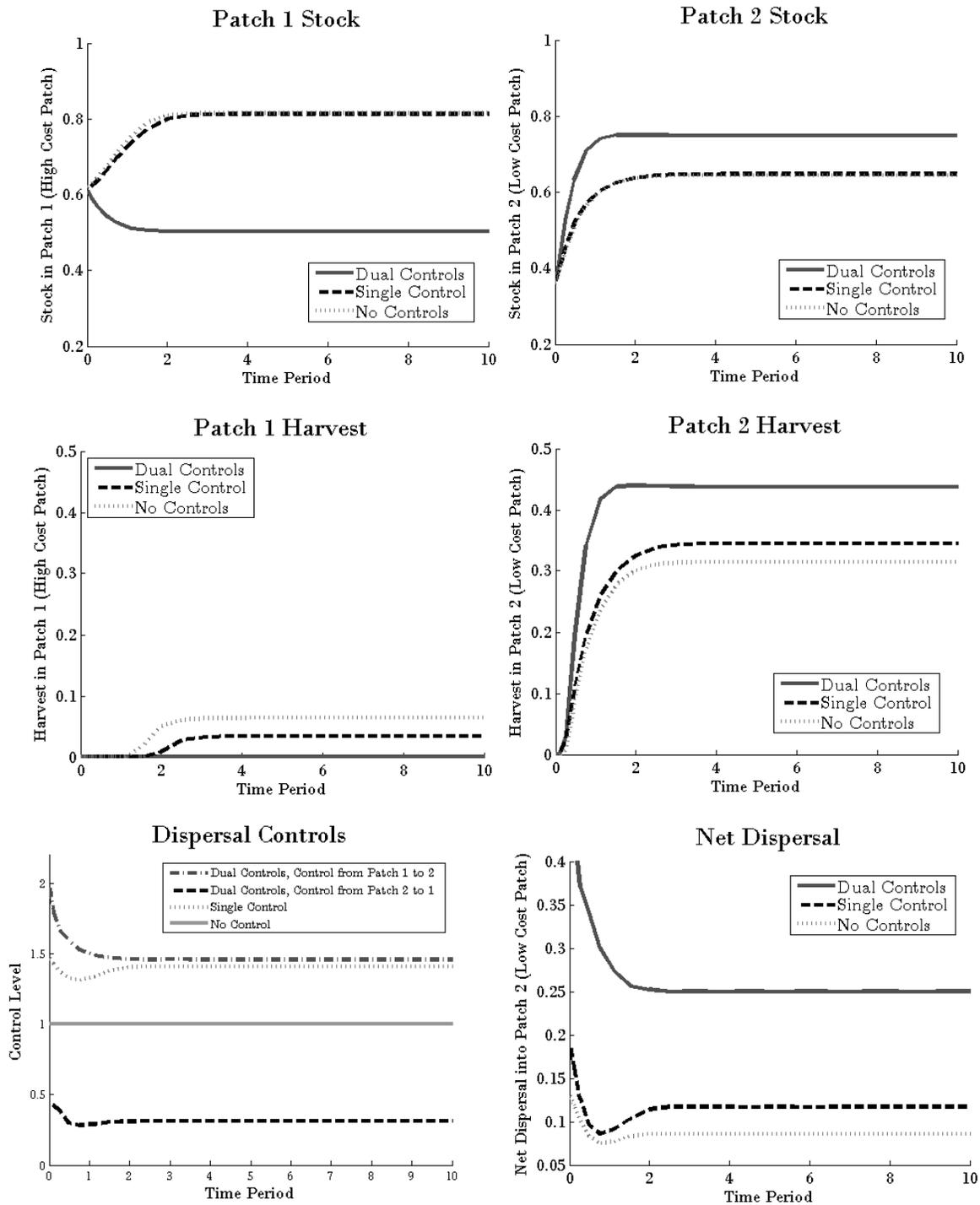
**Figure S1. Percentage increase in equilibrium profitability.**

Note: The figure is derived using the following parameters:  $c_{11}=.3-.8$ ,  $c_{12}=.25$ ,  $c_{21}=c_{22}=.1$ ,  $p=1$ ,  $k=1$ ;  $r=1$ ,  $b=.5$ ,  $\delta=.05$ ,  $u_{max}=2$ ,  $\theta=.001-.1$ .



**Figure S2. Net dispersal at the optimal equilibrium.**

Note: These set of figures shows the net dispersal flow into patch 2 (the low cost patch) under optimal management, for the three cases described in the text. Lighter shading represents greater dispersal flow. The figure is derived using the following parameters:  $c_{11}=.3-.8$ ,  $c_{12}=.25$ ,  $c_{21}=c_{22}=.1$ ,  $p=1$ ,  $k=1$ ;  $r=1$ ,  $b=.5$ ,  $\delta=.05$ ,  $u_{max}=2$ ,  $\theta=.001-.1$ .



**Figure S3. Optimal Rebuilding.**

Note: This set of figures explores the differences in rebuilding schedules in terms of profit-maximizing dispersal controls, stock, and harvest, in each of the three cases. The values used to derive Figure 5 are  $c_{11}=.6$ ,  $c_{12}=.25$ ,  $c_{21}=c_{22}=.1$ ,  $p=1$ ,  $k=1$ ;  $r=1$ ,  $b=.5$ ,  $\delta=.05$ ,  $u_{\max}=2$ ,  $\theta=.1$ .

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