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The Economics of Spatial-Dynamic Processes

Applications to Renewable Resources

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The Economics of Spatial-Dynamic Processes: Applications to Renewable Resources

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Abstract

Spatial-dynamic processes in renewable resource economics pose difficult conceptual, analytical, empirical, and institutional challenges that are distinct from either spatial or dynamic problems. We describe the challenges and conceptual approaches using both continuous and discrete depictions of space and summarize key findings. Using a metapopulation model of the fishery and simulated economic and ecological data, we show that it is possible in certain circumstances to recover both biological and economic parameters of a linked spatial-dynamic system from only economic data. We illustrate the application empirically with data from the Gulf of Mexico reef-fish fishery. We conclude with a discussion of key policy and institutional design involved in managing spatial-dynamic systems.

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The Economics of Spatial-Dynamic Processes: Applications to Renewable Resources

"When one tugs at a single thing in nature, he finds it attached to the rest of the world." John Muir

I. Introduction

A challenging class of environmental/natural resource problems emerges when ecological, physical, and economic systems are linked by spatial-dynamic processes. Some examples include epidemics, invasive species spread, animal disease transmission, subsurface contamination of porous aquifers, shoreline change, biological reserve site selection, provision of ecosystem services, and management of marine and terrestrial species. Each of these examples depend upon biophysical mechanisms that can be characterized by diffusion or dispersal processes. From a policy perspective, these problems pose familiar questions about when and how much regulatory effort should be used to mitigate the problems but also less familiar questions about **where** control efforts should be applied over spatial landscapes.

The individual components of spatial-dynamic problems, namely space and time, are not new. For example, natural resource economics has a long-standing and well developed set of concepts formulated to address **dynamic** aspects of resource use. Early analyses of optimal intertemporal use of specific resources include Faustmann for forest resources [26], Hotelling for mineral resource extraction [38],[1] Scott for conservation issues [71], and Crutchfield and Zellner for fishery resources [19]. These treatments were refined in the 1970s, using newly developed dynamic programming and optimal control methods, ultimately becoming core concepts of the field of natural resource economics [90].

In a similar manner, economics has a long-standing tradition dealing with **spatial** aspects of economic activity. Early work by von Thünen [89] shows how autonomous economic decisions produce spatial patterns of economic activity that exhibit, even on a flat featureless plain, heterogeneity in economic variables such as rents, crop choices, and production techniques. Modern variants of von Thünen models explain urban structure and the emergence of cities or patterns of production and consumption across space [28].[2] Other advances introduce environmental amenities to explain how patterns of urban development are altered as a consequence [92,93,94].[3]

In addition to conceptual work based on von Thünen, there is a considerable amount of research exploiting spatial variation and patterns in order to address important valuation questions. Using spatial sorting equilibrium concepts developed by Tiebout [84], a new class of models relies on spatial patterns in urban structure to infer values of local public goods (school quality) or public bads (air pollution) [25,52]. This line of inquiry has led to new methods for disentangling agglomeration and congestion externalities [5] and an empirical literature on valuing non-marginal environmental quality changes [73].

In two other papers in this issue, local environmental amenities play a central role. In Phaneuf et al. [57], environmental quality (of lakes) induces spatial sorting across recreation sites, but unlike traditional recreation demand models, the sorting process creates feedbacks on environmental quality.[4] In Irwin et al. [41], local environmental amenities are the drivers of regional development, but their paper focuses on how human-environment interactions give rise to different dynamic paths and steady states.[5]

While there are long-standing and evolving separate literatures on dynamic analysis of resource use and spatial processes in economic activity, there has been comparatively little analysis of problems for which spatial patterns are the outcome of the underlying dynamics. For a number of reasons, research addressing integrated spatial-dynamic processes is both needed and arguably overdue. For instance, many of the specific problems that motivate this general class of problems are increasingly in the public eye. While epidemics and invasions are not new, they are certainly more visible recently and likely to become more prevalent as globalization intensifies. In addition, technological developments in remote sensing, GIS, and enhanced computational capacity are generating spatially explicit data at a very fine spatial resolution. As scientists examine these data, they are discovering patterns in the organization of the biosphere and human activities that beg explanation. Also, most scientific disciplines from which environmental and resource economics draw have become more spatially focused over the past two decades [9]. Finally, problems governed by spatial-dynamic processes pose interesting questions about how to design policies and institutions that account for how problems unfold over landscapes with predictable spatial-dynamics.

This paper surveys recent and ongoing research on the economics of spatial-dynamic processes in renewable resources, provides an empirical application, and discusses opportunities for further analysis. Fundamental characteristics of spatial-dynamic problems in renewable resources include spatial heterogeneity in ecological features and the patterns of dispersal of organisms across space. For example, some habitats may be more productive or have special attributes that make them more suitable for some species than others. Spatial heterogeneity by itself, however, is not remarkable. The more important role is in conditioning patterns of dispersal. For example, if organisms disperse from high density to low density areas, population dynamics will be at least partially governed by movement and flow of organisms over the landscape. The dispersal processes that determine movement over space may reflect environmental forces, or they may be endogenous and dependent upon relative populations sizes over space. As we show, spatial heterogeneity and spatial interconnectivity pose special challenges on multiple fronts, from analytical and technical modeling, to derivation and interpretation of optimality conditions, to challenging empirical problems, to the synthesis of policy conclusions from analytical work.

In the next section, we discuss two analytical frameworks for spatial-dynamic problems, focusing particularly on the importance of dispersal and diffusion mechanisms. In the third section, we demonstrate, using a simulated data experiment, how coupled natural-human empirical modeling can be used to measure both economic and ecological parameters. Our particular focus is on whether we can recover the dispersal parameters in a discrete spatial model of fish population. We find that, in some circumstances, economic data alone are sufficient to understand linked spatial-dynamic systems. We then briefly illustrate the model with real data from the Gulf of Mexico reef-fish fishery. Though the application is a step towards empirically based spatial-dynamic management, converting it into practice for policy design will involve further empirical challenges. The final section discusses new institutional and policy design questions raised by spatial-dynamic processes.

II. Modeling Spatial-Dynamic Processes

The heart of spatial-dynamic models is the process that depicts the interaction between the object of study and time/space. When modeling these interactions, a methodological question arises on whether to model space continuously or discretely. The answer, of course, depends on the resource characteristics under consideration and the questions being posed. If the focus is rent gradients on land around a regional center, then a continuous framework might be appropriate. On the other hand, if the resource consists of sub-populations inhabiting patchy habitats with corridors linking sub-populations, then a discrete spatial formulation might be most appropriate. Mathematically, it is sometimes more convenient to work with continuous formulations when developing conceptual models. However, even with simple spatial-dynamic processes, researchers quickly reach the limits of finding analytical solutions. For insights about systems with even modest complexity, numerical methods using discrete approximations are necessary [8]. This is not uncommon in mathematical modeling and does not necessarily undermine the generality of results, because a discrete space can be thought of as an approximation of a continuous spatial domain [46].

In what follows, we begin with some models of diffusion based on a continuous spatial framework. We then switch to a discrete formulation in order to discuss specific results pertaining to realistic renewable resource systems.

A. Continuous spatial processes

Spatial-dynamic problems have characteristics that are relatively unfamiliar to economic modelers, namely 1) diffusion or dispersal processes; 2) boundary conditions; and 3) spatial geometry.

Real biophysical processes exhibit a range of qualitatively different kinds of dispersal or diffusion processes.[6] The simplest kind of diffusion process begins by assuming that a population (eg. cells, bacteria, animals, fish, insects) diffuses randomly over space. Consider a one-dimensional representation of space over a line. Suppose that the probability that a unit of the population $N(x,t)$ will move left or right is equal. Then such a random diffusion process can be represented by the partial differential equation (PDE):

$$\frac{\partial N}{\partial t}=\frac{\partial}{\partial x}D\frac{\partial N}{\partial x}=D\frac{\partial^2 N}{\partial x^2} \tag{1}$$

where time is indexed with t, space is indexed with x, and the (constant) diffusion coefficient is D. This well known PDE describes Fick's Law of diffusion. Equation (1) generates a process whereby the flux of a concentration of particles (individuals) at a point will be proportional to the gradient of the concentration.

Suppose now that we have a population that disperses in a way described by (1) and that there is a release of N_0 units at the origin. Then the concentration at some distance x at date t is:

$$N(x,t) = \frac{N_0}{2\sqrt{\pi Dt}} \exp\left\{\frac{-x^2}{4Dt}\right\} \tag{2}$$

Equation (2), which is a closed-form solution of (1), describes a process by which the population spreads over space (Figure 1). Notice that units of the population diffuse from high density locations to low density locations at a rate that depends upon the diffusion coefficient D.[7]

The diffusion process depicted by the partial differential equation (1) and its solution in (2) is essentially the simplest spatial-dynamic processes that one might imagine. One generalization is an increase in dimensionality to depict diffusion in a 2-dimensional plane or 3-dimensional spherical space. Another generalization is to make the diffusion coefficient density dependent. For example, many insect populations are attracted (via pheromones) to high concentrations rather than repelled. Let the diffusion coefficient be density dependent so that:

$$D(c) = D_0(N / N_0)^m \tag{3}$$

where D_0 and N_0 are constants and $m > 0$. The solution to a PDE with this type of dispersal is much more complicated than (2), and has a cross-sectional profile for which the concentration is more bunched near the original release point and there is no tail on the leading edge.

Another natural generalization particularly important for describing renewable resource populations involves combining the diffusion process that describes how something spreads over space with a differential equation description of a growth process that occurs at each point. The most famous is the so-called Fisher reaction-diffusion equation [27]:

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} + rN(1-N) \tag{4}$$

where *r* is the intrinsic growth rate. This spatial-dynamic equation describes a population as being influenced by random diffusion (the first part of the RHS) and density dependent growth at each point in space (the second part). This equation is impossible to solve in closed form, but the solution has been shown to exhibit a traveling wave characteristic, in that as time unfolds, the population moves as a wave front with a constant velocity $v = 2\sqrt{rD}$. The speed of the wavefront thus depends upon the product of the diffusion coefficient and the intrinsic growth rate.

Finally, physical forcing can affect the direction of movement in some biophysical media in an otherwise diffusive environment. For example, larvae in a marine environment may be influenced by dominant currents, so that whether an organism moves up or down-current is asymmetric. This is called advection. Suppose there is a small bias so that the probability of a particle moving right is larger than the probability of moving left, where *V* is the directional constant. Then the Fickian diffusion equation becomes:

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} - V\frac{\partial N}{\partial x} \qquad (5)$$

the solution of which exhibits an asymmetric spatial dispersal pattern relative to the origin [56].

B. Boundaries and Spatial Geometry

While the fundamental characteristic of spatial-dynamic processes is the diffusion or dispersal process, other important components are the geometry of space and the boundary conditions. In the real world, we see great diversity in both geometry and boundaries. One of the simplest and natural cases of a boundary condition for a terrestrial species is the perimeter of an island. The gypsy moth, which is radiating out in a wave front from its known point of introduction in 1869 near Boston, Massachusetts and moving at a rate of about 20 kilometers per year [49], will bump up against a fixed barrier when it reaches the Western edge of the continent.

Boundary conditions may be relevant because they influence the qualitative nature of the dispersal process, or they may be relevant because a policy setting suggests a boundary. For example, a government may view the relevant boundaries for control of an invasive as its political boundaries, even though the pest might actually move through these boundaries to neighboring political entities. As another example, plumes of subsurface contaminants spread through soils and into aquifers in ways well predicted by Fickian diffusion and hydrodynamic dispersion [43], calibrated by diffusion relationships that reflect the porosity and conductivity of soil. But the geometry and boundaries of particular cases may be fixed by aquifer edges, cap rocks, and other impermeable media. Similarly, every year flu epidemics spread from Asia to North America, entering at ports on the West Coast like Seattle and San Francisco, jumping to other airline hubs in Denver, Chicago and New York, and radiating out from those cities [88]. From a modeling perspective, some processes are sensibly modeled over an infinite one- or two-dimensional space that absorbs an asymptotically disappearing concentration of particles. For other processes, the actual physical boundary is important because it constrains the damages.

Modelers generally depict boundaries as absorbing, reflecting, or some hybrid characterized in terms of gradients. Absorbing boundaries imply that the state variable is zero at the boundary. This assumption is appropriate for species with passive dispersal that once pushed over a continental edge or boundary of an island can not return and experience 100 percent mortality. Reflecting boundaries bounce the diffusing particles back into the space (an enclosed aquifer), and zero flux boundaries depict a particle as orthogonal or at some other angle at the boundary. Finally, spatial geometry is important and dependent upon the mosaic that contains the spatial-dynamic process. It matters whether the medium is homogeneous, or whether it contains spatial character such as bottlenecks, edges, hostile patches, and heterogeneous productivity.

C. Bioeconomic Models with Continuous Spatial-dynamic Processes

Aside from characterizing the diffusion, boundary and spatial geometry of spatial-dynamic processes, the other analytical challenge relates to: 1) linking biological and physical system descriptions to economic system descriptions; and then 2) describing policy consequences, particularly under different institutional settings. We have models of open access, regulated open access, regulated restricted access, and sole-owner optimization that can be adapted to spatial-dynamic settings. Consider the case of the first-best optimal exploitation plan for a resource. Resource economists are familiar with applications of dynamic optimization theory to conventional resource use problems that express the dynamics of resource stocks as ordinary differential equations (ODEs). The mathematics of these problems yields well-known solutions that are also systems of ODEs in the stock equations and the control or co-state equations.

To illustrate how optimization of a system characterized by spatial-dynamic processes differs from conventional results, consider a renewable resource characterized by a Fisher reaction diffusion equation on a one-dimensional line. The population would then evolve over space and time in a manner determined by the harvest rate at each point, which we might assume to depend upon effort, $E(x,t)$, and a catchability coefficient, $q(x,t)$, and biomass according to:

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} + rN(x,t)(1-N(x,t)) - q(x,t)E(x,t)N(x,t) \tag{6}$$

Now, suppose that we define the relevant space over which this resource can survive in terms of some boundaries $[x_l, x_u]$. Then the optimization problem can be written as:

$$\max \int_{x_l}^{x_u}\int_{0}^{\infty} \exp(-\rho t)\{B[E,N]\}dtdx \tag{7}$$

$$\text{subject to: } \frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} + rN(1-N) - qEN \equiv D\frac{\partial^2 N}{\partial x^2} + g\{E,N\}$$

where the objective is to maximize some concave benefit function subject to the PDE state equation , spatial boundary conditions, and a set of initial conditions. Brock and Xepapadeas [10], hereafter B/X, characterize the solution to this problem. An important conclusion is that when the underlying system is a continuous spatial-dynamic system, the fundamental state and co-state equations of the optimized Hamiltonian are diffusion equations, expressed as partial differential equations (PDEs) in both time and space. The solutions to spatial-dynamic problems thus are derived from systems of PDEs that are notoriously more difficult to solve and characterize than systems of ODEs.

B/X find that the PDE system is “self-adjoint” in the sense that both PDEs have a common diffusion coefficient appearing with negative and positive signs. In the steady state, this property suggests that areas where the biomass variable generates flux (diffusion flowing from high biomass to low biomass areas) across a particular stretch of space, the corresponding co-state variables generates flux in the opposite direction (eg. from low shadow values to high shadow values). This mirrors a property of non-spatial systems, namely that low biomass levels imply high shadow values but it also suggests that the shadow value of another unit of biomass may differ depending upon where the biomass is located in space.[8]

Aside from the structure that emerges from the modified spatial Pontryagin conditions, the set of assumptions made about boundary conditions also influence the nature of the solution. Boundary conditions generally characterize how the system’s initial conditions are embedded, and they also characterize conditions at the boundary of the spatial domain and at the terminal period. B/X derive modified Pontryagin conditions for the above spatial-dynamic problem that encompass various special cases regarding boundary assumptions. For example, B/X show that an absorbing boundary is equivalent to the non-spatial case with a fixed endpoint and a reflecting boundary is equivalent to requiring a solution to terminate on a spatial manifold. Finally, if one wanted to eliminate the role of boundary conditions, it might be assumed that space is configured in a circle, so that the end point and beginning points are equal and the state and co-state variables do not jump at the boundary.[9]

Any of these may be appropriate in a particular setting, depending upon the nature of the geometry and other features of the setting. The important point is that B/X [10] derive spatial transversality conditions that are analogous to more familiar conditions for non-spatial intertemporal optimization problems. These spatial transversality conditions can be chosen to fit the particular geometry and boundary conditions appropriate to the problem at hand, and they will influence the nature of the optimal solution accordingly.

D. Discrete spatial-dynamics models

In modeling populations over space, ecologists and population biologists often use formulations that are discrete in space for at least three reasons. First, populations are often distributed in discrete patches that reflect the underlying spatial heterogeneity in habitats, currents, and other biophysical conditions. Second, even if populations are distributed continuously over space, it is unlikely that policy instruments would be developed that are continuous rather than discrete. Policies such as a zonal access charges are more feasible than, for example, spatial taxes on harvesting effort that vary continuously across an entire coast or terrestrial landscape. Finally, the mathematical challenges of solving PDEs almost always lead researchers to approximate the continuous spatial domain by a “sufficiently finely reticulated patchy environment” [46, p. 288].

A discrete approximation to the continuous Fisher reaction diffusion in equation (4) is

$$\frac{dN_j}{dt} = r_j N_j (1 - \frac{N_j}{K_j}) + \sum_{k=1}^{\Omega_j} d_{jk} N_k - q_j E_j N_j \tag{8}$$

where the spatial domain (x) is subdivided up into a set of discrete patches $j=1,\ldots,\Omega$ and the continuous dispersal process is replaced by the terms in the summation.[10] The dispersal coefficients, d_{jk}, reflect the rate at which biomass moves from one patch to another. The own dispersal rate (rate of emigration) is assumed negative ($d_{jk}<0$ with $j=k$) and the cross patch dispersal rates are positive when the patches are connected to each other ($d_{jk}>0$ with $j\neq k$). Restrictions can characterize various features of dispersal. For example, the "adding up" assumption that whatever leaves patch j for patch k arrives in patch k from patch j is consistent with no mortality in the dispersal process and no deviations in movement along the dispersal route.[11] Because not every patch need be connected to every other, Ω_j represents the set of patches in Ω that are connected to patch j.

A typical assumption regarding the dispersal mechanism in these models is that biomass moves from areas of high concentration to areas of low concentration, everything else being equal. This is a passive dispersal mechanism, as opposed to migration which is directed movement in space.[12] The simplest representation of such a process depicts the dispersal mechanism between patch one and two as $d_{11}N_1 + d_{12}N_2 \equiv a[(N_2/K_2)-(N_1/K_1)]$, and between patch two and one as $d_{22}N_2 + d_{21}N_1 \equiv a[(N_1/K_1)-(N_2/K_2)]$, where a is a common dispersal rate and K_j is the carrying capacity in patch j. The intuition is that patches with higher density generate greater competition for food and space, driving organisms to seek more favorable conditions in lower density patches.

In a discrete system, advection processes that led to organisms or particles moving in one direction with more likelihood than another can be modeled through differences in rates of dispersal. For example, a limiting case of advection is a source-sink system where the source patch j contributes biomass at rate d_{jk} to sink patch k ($d_{jk}>0$) but no biomass from patch k

disperses to patch j (d_{kj}=0). A stepping stone model, where patches are aligned linearly and dispersal is unidirectional from one end to the other, is an alternative structure that can capture an advection process. Other spatial configurations reflecting either spatial geometry or physical processes can be depicted with restrictions on the dispersal rates; examples include a circle, nearest neighbor, fully-integrated, and independent systems [65].

The patchy population dynamics depicted in (8) describe a class of models from ecology called metapopulation models. A metapopulation is a system of local populations occupying discrete habitat patches with significant demographic connectivity between patches [62].[13] While the concept of a metapopulation is the cornerstone of the main paradigms in terrestrial conservation biology [62], its application to the marine context is relative new. As Joan Roughgarden, a prominent mathematical ecologist stated, the “m[M]etapopulation concept is here to stay in marine ecology. Science demands it, fisheries management needs it, and it is the last hope for marine conservation. …it marks the most important milestone of marine ecology in more than 50 years.” [44, p. xix]

A *spatial bioeconomic metapopulation model* integrates the population dynamics in equation (8) with a model of user behavior that incorporates economic determinants of the distribution of effort across space and time. One determinant of the effort distribution is the institutional context within which exploitation takes place. If the ownership scale encompasses the whole range of the metapopulation, then we might expect that effort distributions are made to optimize utility or profits. Some noteworthy examples of models of optimization-based bioeconomic metapopulations include analyses of how to control dispersal of a pest population (beaver) from an unmanaged patch to a managed patch [6,7,8,39,45] and a model of the spatial movements of elephants that generate value from wildlife viewing but also create damages by destroying crops [70,75]. Clark presents an optimized two patch model of a biological population dispersing between inshore and offshore areas[13],[14] Brown and Roughgarden illustrate the optimal value of a larval pool to system wide fishery profits [11], and Janmaat investigates the implications of different governance regimes across a patchy system [42].[15]

In the marine context, it is often assumed that fishing is conducted under open access, where effort responds myopically to profitability via entry and exit [29,82]. Sanchirico and Wilen generalize the open-access entry/exit adjustment mechanism to a spatial-dynamic fishery to characterize the way effort moves across space and over time [66]. Other things equal, these spatial forces tend to redistribute effort in a manner that, in the long run, equalizes average net rents across all patches at the common opportunity cost. While the dynamic path in each patch exhibits oscillatory convergence that we see in a one-patch system [82], the interactions between the biology and profitability of each patch generate more intricate paths of convergence with this bioeconomic system. For example, patches that are closer to their natural carrying capacities will "feed" other patches via dispersal, thus speeding the process of system convergence to long run equilibrium. In addition, other things equal, patches with higher biomass levels will attract vessels from other patches with lower levels, also reinforcing the ability of low biomass patches to catch up with higher biomass counterparts. Biological and economic dispersal thus both act as system averaging forces, smoothing out the influence of bioeconomic heterogeneity, and linking the inherently dynamic process of convergence across space [67].

Once the system converges to the steady-state, the level of own biological growth in each patch will be exactly offset by the total net dispersal between the patch and other linked patches, and the harvest in the patch in question. In addition, in an open-access fishery, net rents will be identically equal to zero in each patch, leading to a rent-dissipated economic equilibrium over time and space. This *combined* bioeconomic equilibrium will be a *non-homogeneous* equilibrium in the sense that there will be some dispersal of the population across space in equilibrium, even though the population size and the fleet size in each patch is constant [66]. The flux in the system arises out of the biological system and not the economic system, however, since each patch's population size is maintained by the balance between own patch natural growth and harvesting, and system wide immigration or emigration to and from the other patches. This is not something we see regularly in economic models and it is a particular feature of some systems driven by spatial-dynamic processes. Finally, the open-access spatial equilibrium will not be the optimal way to distribute effort over space, of course, since it is the outcome of a myopic, open-access process and it will also be the case that too much effort will be drawn into the whole system.

III. Empirical Challenges and Opportunities

We argue in Sections I and II that a critical component of spatial-dynamic systems is the dispersal or diffusion mechanism linking space and time. The degree of scientific knowledge about these processes depends on whether the system is easily observed and measured. For example, measuring diffusion of liquids (water, oil, contaminants) in permeable soils is difficult because of the heterogeneities in subsurface soil structure as well as inclusions and barriers that are difficult to observe. Similarly, populations of adults and juveniles moving in time and space in marine systems are hard to measure because they often cannot be directly observed. But the manner is which spatial-dynamics are determined jointly from both biophysical and economic processes raises a provocative question: can bioeconomic observations be exploited in order to infer and measure unobserved dispersal coefficients? In other words, can we observe human users of a spatial-dynamic marine system and infer anything about the underlying biological structure generating their behavior?

The logic behind these questions exploits the fact that harvesting may perturb metapopulation dynamics in ways that generate useful variation in biomass levels and dispersal [66,68]. For marine populations, these perturbations may reveal system characteristics in ways that are measurable by observing the behavior of fishermen on the surface of the system. In this section, we demonstrate that it is indeed possible to observe fishing behavior in ways that facilitate estimating the parameters of a spatial-dynamic system.

There is a long history of estimating biological parameters from economic data in a fishery that dates back to Schaefer [69], but to our knowledge, fishery data has not been used previously to recover parameters of a spatial-dynamic process.[16] The essence of Schaefer's problem is that fish stocks are unobserved, but catches and fishing effort are observed. These quantities from the fishery are linked to fish stocks through a production function, and this linkage allows one to substitute observables recursively into the biological state equation and estimate parameters.[17]

In what follows, we generalize these methods to estimate bio-physical parameters of spatial-dynamic processes using a discrete-time version of the Sanchirico and Wilen model [66]. Using simulated data that represents the data often available in fishery settings, we estimate biological parameters of a three-patch source-sink and fully integrated system. We also show how in a second stage regression we can recover the relevant economic parameters. We then expand our analysis to consider observation error (e.g., error in the observed harvest rates) into the analysis to see how it affects parameter recovery in a spatial-dynamic context. Finally, we illustrate our method with real data from the Gulf of Mexico reef-fish fishery.

A. Modeling spatial-dynamic process with fishing micro-data

Let j index own patch population dynamics in a metapopulation system with J total patches. Following equation (8), the state equations are of the following form:

$$N_{jt+1} = N_{jt} + r_j N_{jt}\left(1 - \frac{N_{jt}}{K_j}\right) + d_{jj} N_{jt} + \sum_{k \neq j} d_{jk} N_{kt} - H_{jt} + \varepsilon_{jt} \qquad (9)$$

In the ecology literature, ε is known as a process error. As in (8), we use a Schaefer harvest function to link the economics:

$$H_{jt} = qN_{jt}E_{jt}^{TOT}, \tag{10}$$

where $E_{jt}^{TOT} = \sum_{i=1}^{n} E_{ijt}$ is the total effort in patch *j* at time *t* adding up across all *i*=1,..,*n* fishery participants, where i represents a fisherman. Defining the aggregate patch catch-per-unit effort as *z*, we can rewrite the state equation as:

$$\frac{z_{jt+1}}{q} = \frac{\left(1 + r_j + d_{jj}\right)}{q} z_{jt} + \left(\frac{-r_j}{q^2 K_j}\right)\left(z_{jt}\right)^2 + \sum_{k \neq j} d_{jk} \frac{z_{kt}}{q} - H_{jt} + \varepsilon_{jt}\,. \tag{11}$$

Note that we are assuming no observation error, i.e. the harvest functions hold without error.[18] Multiplying both sides by *q*, we have a linear estimating equation for each patch (with a total of *J* patches) that is solely in terms of observables:

$$z_{jt+1} = \sum_{k=1}^{J} \beta_{jk} z_{kt} + \beta_{jJ+1}\left(z_{jt}\right)^2 - \beta_{jJ+2} H_{jt} + \varepsilon_{jt}^{*} \tag{12}$$

Two notes are in order. First, the number of parameters in each equation grows with the number of patches, and the number of equations also grows with the number of patches. Together, the total number of parameters grows by the square of the number of patches. In a similar manner, a spatial weighting matrix in spatial econometrics grows with the square of spatial interconnections, increasing the computational burden. But in our case, the issue is identification and not necessarily computation. Second, the diagonal elements of the dispersal matrix are not separately identified from intrinsic growth. In what follows, we discuss various approaches to address this problem depending on the structure of the interconnectedness in the metapopulation.

One could proceed to generate simulated data from the biological state equations and generate random economic data as a Monte Carlo design. However, we are interested in querying the system to find circumstances—both bio-physical and economic—that are likely to generate data that will resolve the true structure. Thus, we choose a behavioral model structure that is consistent with empirical studies of fishing behavior over space and time [23,24,35,78]. To that end, we use a discrete choice framework to generate the economic data. Suppose that there are *n* permitted fishing vessels in a limited entry fishery. We index the vessels by *i*. For simplicity, we match the time scale of fishing choice occasions to the time scale of the biological dynamics, so *t* indexes the choice occasion.[19] Denote fishing site as *j* as in the biological model, and following Smith [76], we also model the alternative of not fishing ($j = 0$). The utility of each choice (U) can be broken into a deterministic and random component:

$$U_{ijt} = v_{itj} + \eta_{ijt} \tag{13}$$

For simplicity, as a starting point we will assume that the η_{ijt} 's are i.i.d. Type I Extreme Value. The deterministic portion of utility from not fishing is value of some outside opportunity (α), which reflects the value of leisure or wages from another employment activity. The deterministic portion of a fishing alternative is the profitability of fishing, which includes revenues from fishing, a fixed cost of taking a trip (bait, ice, etc.) denoted by *c*, and travel cost (ϕl):

$$v_{itj} = \begin{cases} \alpha, & for\ j = 0 \\ p_t h_{ijt} - c - \phi l_{ij}, & for\ j = 1,2,3,\ldots J \end{cases} \tag{14}$$

where *h* is individual expected harvest, *p* is price of fish, and l_{ij} is the pairwise length of roundtrip travel distance from individual *i*'s port to patch *j*. These distances introduce a source of spatial variation in the spatial gradient of costs that is potentially independent of spatial variation in the bio-physical gradient. Outside opportunities (α) could also vary systematically over space and time in ways that are uncorrelated with spatial-dynamic processes in the water, but we assume this away initially. Our assumption of no observation error effectively means that actual harvest is expected harvest, but it is important to note that in empirical settings the two are not equivalent. Given the Schaefer production function and noting that *E* takes on a value of 1 if the site is chosen and 0 otherwise, we can substitute to form the random utility:

$$U_{ijt} = \begin{cases} \alpha + \eta_{ijt}, & for\ j = 0 \\ p_t q N_{jt} - c - \phi l_{ij} + \eta_{ijt}, & for\ j = 1,2,3,...J \end{cases} \tag{15}$$

Here we see that the spatial bio-physical gradient enters through the patch-specific stocks.

In the static random utility maximization framework (RUM), the individual is assumed to select the choice with the highest utility for each choice occasion. The analyst observes components of deterministic utility but not the idiosyncratic error term. As a statistical problem, with data on trips to each location, prices (varying over time), stocks (varying over time and space), and travel distance (varying over space), one could estimate three parameters from this model: q, ϕ, and ($-c-\alpha$). In McFadden's conditional logit model [50], these parameters are only estimated up to scale. Note also that only the sum of the outside opportunity and the trip fixed cost can be identified because there is only one constant in the utility differences. In what follows, we use the RUM framework combined with the spatial-dynamic state equations to generate simulated data, then recover bio-physical parameters in a first stage using aggregate data, and recover economic parameters in a second stage using disaggregate data. Because catchability is identified in the first stage, we can recover the scale coefficient in a second stage by substituting in the stock index. This allows us to give an explicit structural interpretation to each parameter.

B. Modeling a source-sink system

As a starting place, we assume a 3-patch (j=3) source-sink dispersal system. The source-sink system captures the potential for oceanographic features such as currents and bathymetry to influence the spatial diffusion process by influencing flows of larvae and/or adults. In a source-sink system as long as the spatial adding up exists ($d_{jj} = -\sum_{k \neq j} d_{kj}$), the issue of identification is not a problem. In words, the outflow from patch *j* must exactly equal the inflow from patch *j* to all other patches. Appendix A describes the algorithm for generating simulated data.

To recover the bio-physical spatial-dynamic parameters from the simulated data set, we first estimate the reduced-form parameters in (12). Note that only aggregated catches and catch-per-unit-efforts enter the estimation equations, so in the first stage we add up across all of the individuals. Because the model is linear in all of the observables, estimation can be done using Seemingly Unrelated Regression (SUR) and imposing the cross-equation restriction $\beta_{jJ+2} = \beta_{kJ+2}, \forall j,k$ (to account for the assumption that catchability is the same over space). The next step is to transform the reduced-form parameters into the structural parameters using (11) and (12). See Appendix B.

Table 1 contains a summary of 100 simulated data experiments with 100 periods (T=100) and 100 individuals (n=100). Individuals are distributed randomly over space with mean travel distances of 3, 2, and 1 for patches 1, 2, and 3. The top set of results in Table 1 reports summary statistics of the recovered structural parameters assuming that we know the true connectivity structure of the spatial system. That is, we know which elements of the full dispersal matrix are zero. In this case, the form of the source-sink system imposes four restrictions. There are thus nine free parameters to estimate (compared to 13 in a system where each patch is connected to every other patch). For all parameters, the mean and median are close to the true value. Even the minima and maxima are qualitatively correct for all parameters except d_{21} and d_{31}, for which the minima are negative. As in any Monte Carlo experiment with an unbiased estimator, the spread of the resulting parameter estimates is a function of how much noise the analyst injects into the system. Thus, the top half of Table 1 primarily serves to illustrate that, in principle, one could recover all of the bio-physical parameters of a spatial-dynamic system from economic data alone. To our knowledge, this type of analysis is novel, though the availability and reliability of spatially-explicit fishing logbook data makes the exercise possible.[20]

The bottom half of Table 1 demonstrates that in some circumstances, a lack of information on the structure of the dispersal matrix does not preclude the recovery of the structural parameters. The structural coefficients do not appear to be biased in spite of including regressors that should not be included. This is a reflection of the underlying structure of our data generating process and the properties of SUR; inclusion of additional regressors should only affect efficiency. We can see this efficiency loss simply by comparing the standard deviations across sets of coefficients in the top and bottom half. There is more spread in the bottom half. Appendix C reports results for increased process error and a different set of source-sink parameters. Qualitatively, the same conclusions hold.

In principle, one could test down from the unrestricted model to the true model. Suppose that we know which joint restriction to test. In each 100 cases summarized in Table 1, we perform a likelihood ratio test and find that we fail to reject the restriction 98 times. That is, when we know the proper restriction to impose, we only incorrectly reject it 2 times out of 100. Nevertheless, it is important to consider that real world data will not necessarily conform to the data generating process of our simulated data environment. Quantitatively, we may be able to recover the parameters from economic data alone, but the efficiency of these estimates is hampered by spending degrees of freedom on incidental spatial parameters. This problem is likely exacerbated by the multicollinearity of stocks over space.

Our ability to understand bio-physical spatial-dynamic processes may require that metapopulation ecologists, population geneticists, and physical oceanographers specify the qualitative structure of spatial dispersal. With the expansion of remote sensing, GIS, GPS, and fish tagging technologies, the provision of qualitative information is not an unrealistic possibility. If scientists are able to tell us that the probability of something flowing from A to B is very low but the probability of something flowing from B to C is high,[21] economic data may be able to tease out how much.

In the absence of qualitative information about spatial structure, our simulated data experiment raises questions about the circumstances under which economic data can reveal the true structure under various spatial configurations. Given our data generating process, when we know the set of restrictions to test, we are able to test down accordingly. A natural question to ask is: is there is a logical order in which to test down from the general dispersal matrix when we do not know the restriction to impose? Since we have established that the economic data can, in principle, allow the recovery of spatial parameters, designing an econometric approach that will distinguish different types of spatial structure becomes an important question for future research. This endeavor will be complicated by empirical realities of matching spatial scales. Fishing grounds, as reported in logbooks, are not necessarily the same as patches in a metapopulation. Moreover, the stacked-equation approach that we develop above implicitly assumes a discrete rather than continuous space. Matching the discreteness of spatial locations in logbooks with a continuous-space model will provide a different set of challenges.

Though there are further issues to address in the recovery of bio-physical spatial-dynamic parameters, we can use a second stage to recover economic parameters. Continuing with the assumption that we do not observe stocks directly, we use catch-per-unit effort as a proxy in the second stage. Because $N_{jt} = \frac{z_{jt}}{q}$, q cancels in (15) and the coefficient on $p_t z_{jt}$ is one.[22] The simplicity of the stock index is a result of the Schaefer production function, but the result is general; we can substitute out the stock in individual expected harvest with an aggregate measure because individuals fishing in the same place at the same time are facing the same stock. By estimating the conditional logit model, we thus recover the otherwise unidentified scale coefficient. Note that whether we know the true structure of the bio-physical system does not affect the second stage estimation; the model and data are the same, and we need only know the linking function (a production function in this application). Table 2 contains results of 100 runs to recover structural economic parameters. The true scale coefficient is 2.0, so not surprisingly we see that the raw estimates are approximately one half their true values. After using the revenue coefficient to transform the remaining coefficients, the recovered structural parameters are close to the true values. These results, combined with Table 1, illustrate a complex sorting equilibrium that emerges from the interaction of human agents with a spatially heterogeneous natural system [57]. Our ability to measure all parameters of interest is not due to the system being in a spatial-dynamic steady state; instead, we are able to exploit a sequence of non-price equilbria that are imposed bio-physically by virtue of the state equations holding in each period and our knowledge of a bioeconomic link through the production function. Nevertheless, it is critical to note that by assumption we avoid cross-scale interactions studied in Irwin et al. [40]. Our human-environment interaction unfolds on the same time and spatial scale, an assumption that facilitates tractability but may be problematic for real systems.

C. Modeling a fully-integrated system

In contrast to a source-sink system, a fully-integrated system is expected to characterize spatial dispersal of adults where they can get from any patch to any other in the system directly. The dispersal mechanisms are due to ecological effects such as crowding and competition for food resources [66]. If the population in patch 1 relative to its carrying capacity is higher than the population in patch 2 relative its carrying capacity, then we expect flow from patch 1 to patch 2. Dispersal based on relative densities in a fully-integrated system imposes a particular structure on the dispersal parameters in equation (9). Because of symmetry in the state equations, we only illustrate the equation for patch 1 in a three-patch system:

$$N_{1t+1} = N_{1t} + r_1 N_{1t}\left(1 - \frac{N_{1t}}{K_1}\right) + a_1\left(\frac{N_2}{K_2} - \frac{N_1}{K_1}\right) + a_2\left(\frac{N_3}{K_3} - \frac{N_1}{K_1}\right) - H_{1t} + \varepsilon_{1t} \qquad (16)$$

Rearranging equation (16) and the correspond equations for the other patches, the dispersal system can be expressed with the following dispersal matrix *D*:

$$D = \begin{bmatrix} d_{11} & d_{12} & d_{13} \\ d_{21} & d_{22} & d_{23} \\ d_{31} & d_{32} & d_{33} \end{bmatrix} = \begin{bmatrix} -\left(\dfrac{a_1 + a_2}{K_1}\right) & \left(\dfrac{a_1}{K_2}\right) & \left(\dfrac{a_2}{K_3}\right) \\ \left(\dfrac{a_1}{K_1}\right) & -\left(\dfrac{a_1 + a_3}{K_2}\right) & \left(\dfrac{a_3}{K_3}\right) \\ \left(\dfrac{a_2}{K_1}\right) & \left(\dfrac{a_3}{K_3}\right) & -\left(\dfrac{a_2 + a_3}{K_3}\right) \end{bmatrix}. \qquad (17)$$

As in the source-sink system, there are three adding up restrictions. However, the complication of estimating this model with SUR is that the model is overidentified, and restrictions on the model to exactly identify it involve nonlinear implicit functions.

Table 3 reports results from the SUR estimates based on 100 Monte Carlo data sets generated by a fully-integrated system. In spite of overidentification, the means and medians of the parameter estimates track the true parameters. The true value of a_1 is 0.25. Using d_{21} and K_1 to recover a_1, we find 0.23019, whereas using d_{12} and K_2, we find 0.2569. Although these values differ, for purposes of optimizing the spatial-dynamic bioeconomic system (as in [68]), we need the dispersal matrix itself and not necessarily the underlying structural parameters of it (a_1, a_2 , and a_3). Thus, we argue that our numerical experiments provide some reason for optimism in using economic data to estimate bio-physical parameters of a spatial-dynamic system. Nevertheless, as the number of patches grows, the number of structural parameters in a density-dependent system also grows. Whether an estimated overidentified dispersal matrix diverges more or less from the true dispersal matrix requires further exploration.

Setting aside the qualitative spatial structure, our simulated data experiments provide quantitatively reasonable estimates of the true parameters because we build in sufficient variation in the data generating process. When will this be true for real-world data sets? Many systems are either limited entry (like our simulated data experiment), open access, or regulated open access. In all cases, participants over the long run have an incentive to dissipate rents over space [63]. For our particular setting, this generates spatial correlation in stocks. Biological and economic gradients may combine in a manner that generates large or small amounts of variation in economic data. One hypothesis worth examining is that offsetting biological and economic gradients will generate more variation and make it easier to recover spatial parameters from economic data.[23]

D. Incorporating observation error

The empirical population dynamics literature has long recognized that process error, i.e. stochasticity in stock-recruitment relationships, is just one complication; models that construct observable indices for the unobservable stock must also account for observation error. Here we conduct experiments in the fully-integrated system that include observation and process error.

In the context of using economic data from a fishery to recover stock dynamics, the observation error problem amounts to the production function, i.e. our equation (10), involving an error term. When the catch-per-unit effort is then substituted into the state equation, the resulting estimation problem will suffer from errors-in-variables bias. This problem was diagnosed in the fisheries literature by an economist [87] and has since drawn considerable intellectual attention from biologists, fisheries managers, and economists. To add observation error, we rewrite equation (10) with an individual-level error as:

$$H_{jt} = qX_{jt}\sum_{i=1}^{n} E_{ijt}\xi_{ijt} \tag{18}$$

where $\ln \xi_{ijt} \sim N\left(0, \sigma_{\xi}^{2}\right)$. While still a simple production function, this error structure is consistent with much of the fisheries production literature that estimates harvest functions in logarithms.[24] Because we know that intrinsic growth and carrying capacity in a single-equation model will be biased, we explore the spatial system with a larger number of simulations in order to see how significant these biases are.

Table 4 reports simulations of the fully-integrated system with 5,000 Monte Carlo data sets for three different levels of observation error σ_{ξ}: 0.1, 1.0, and 2.0. Not surprisingly, biases are small with low observation error. This is consistent with the literature that empirically estimates single-equation stock dynamics. As observation error increases, bias grows but in a way that is different across types of parameters. In particular, the traditional logistic growth parameters and catchability become nonsensical as observation error becomes very large ($\sigma_{\xi} = 2.0$). In these cases, median intrinsic growths and catchability are negative, and median carrying capacities are more than three times their true values. These results echo a principal concern of population biologists, namely that observation error can render the recovered population parameters misleading for management purposes [58]. However, the biases in the dispersal matrix remain relatively small even in the presence of very large observation error. Qualitatively, the means and medians all have the correct signs, and all of the dispersal parameter medians are within a factor of two of the true values. This suggests that economic data, even without accounting for observation error, can be helpful in understanding spatial-dynamic bio-physical processes. Although this result is surprising, our numerical experiments do not establish its generality, warranting further research.

E. An Empirical Example

We use data from the Gulf of Mexico reef-fish fishery to estimate the first stage of a three-patch model of population dynamics. The goal is to illustrate how spatial-dynamic parameters of the biophysical process can be recovered from economic data alone. As such, we do not attempt to control for observation error and simply acknowledge this as a limitation. The data set aggregates across individual vessels, species in the reef-fish complex (a collection of 60 species), and gear types reported in vessel logbooks (from NOAA Fisheries).[25] See Smith et al. [81] for a full description of the data. We also aggregate across days into monthly time steps and across space from thirteen National Marine Fisheries Service zones into three areas. Fishing effort is defined as a vessel trip day, and catch is the total pounds of reef-fish caught in the month. Our Area 1 contains NMFS zones 1-4 from the southern tip of the Florida Keys to roughly one third of the way up the peninsula. Our Area 2 includes NMFS zones 5-8 from the Tampa area up the rest of the peninsula and wrapping around to midway across the panhandle. Our Area 3 includes NMFS zones 9-13 extending west across Alabama and Mississippi to the mouth of the Mississippi River. By assumption, our total spatial domain neither interacts with areas further west in the Gulf nor with the South Atlantic and Caribbean.

The top panel of Table 5 reports reduced-form parameter estimates from the unrestricted SUR model on our empirical application, and the bottom panel reports the recovered structural parameters of the spatial-dynamic system. Unlike in the Monte Carlo experiments, we allow for spatially-explicit catchability coefficients. Moreover, to account for the fact that some reef-fish species aggregate to spawn (generally in the first four months of the year), we add dummy variables to introduce spawning variability in catchability. Because of how q enters the reduced-form equation (14), the seasonal feature adds two parameters to each estimating equation in the SUR system. We recover the structural parameters from the first five rows of the top panel and simply allow the other parameters to absorb seasonal noise. While admittedly somewhat ad hoc, this allows us to avoid estimating a structural model that is nonlinear in the parameters.

Conditional on our assumption above, the recovered parameters in the bottom panel of Table 5 are all reasonable. The intrinsic growth rates, cathabilities, and carrying capacities are all positive as theory predicts. The differences in these parameters across areas suggest that there is spatial heterogeneity in this system, though we do not do a formal statistical test. Examining just the point estimates, the spatial system is one in which the resource flows counterclockwise from Area 1 to Area 3 (note the negative own dispersals for Areas 1 and 2 and the positive own dispersal for Area 1). This apparent flow is in the opposite direction of the Loop Current in the Gulf of Mexico [34], though it is unclear how that current affects reef fish.[26] A closer examination shows that only three of the dispersal parameters are statistically significant. Both d_{21} and d_{12} are positive and significant, suggesting flows back and forth between these areas. This could be an indication of a fully-integrated system and flows based on relative densities. Perhaps the most interesting feature of the recovered parameters in Table 5 is that adding up the implied carrying capacities (roughly 35 million pounds) is consistent with spatially aggregated estimate from a naïve estimator in Zhang and Smith [96] (roughly 39 million pounds).[27]

IV. Institutional and Policy Design Issues

The purpose of modeling spatial-dynamic processes, estimating parameters, constructing simulation models, and subjecting these to various optimization techniques is not only to understand the nature of the human/ecosystem interactions, but also to suggest policies that might be used to control such systems. A few preliminary points have emerged from the small number of papers developed in this area to date. First, for renewable resource models, there is an optimal shadow price of biomass that varies over both time and space [68]. The shadow price at any point in space accounts not only for the contribution of a marginal biomass change to own profits at that point in space, but also to the marginal contribution (via diffusion or dispersal) to profits in all other patches. This implies that optimal policies must be determined over the entire landscape, or at least over subsets of systems that are linked and connected. The policy questions that are raised by this finding are several. What kinds of policies (e.g. taxes, quotas) are capable of resolving the spatial-dynamic externalities? How costly are spatially (and temporally) differentiated instruments to implement and monitor, and what is the efficiency payoff of doing so? How do the costs and benefits depend upon fundamental bioeconomic parameters and the structural nature of the diffusion system? What kinds of decentralized institutions are feasible and how should they be designed? Is there a role for decentralized cross-patch negotiation to resolve spatial externalities? What kinds of institutional designs would foster spontaneous decentralized arbitrage?

Given the complexity of these spatial-dynamic systems and the challenges of designing policies in such a context, another critical role for empirical work is to parameterize *ex ante* policy analyses of real spatial policy proposals. Even if real-world proposals do not originate with empirical estimates of spatial-dynamic processes, empirical estimates can answer positive questions about how these policies are likely to perform. Consider, for example, the proliferation of proposals from natural scientists to form new marine reserves or no-take zones. Most of these have been proposed with little concrete understanding of either the underlying spatial dynamics or information about economic costs and benefits.[28] In an empirically-based *ex ante* spatial-dynamic model, Smith and Wilen [79] show that conclusions about the fishery effects of marine reserves reverse when one accounts for fishing behavior, and these reversals are reinforced in a model that allows for spatial adjustments across fishing ports [80]. Sanchirico et al. [65] and Costello and Polasky [16] illustrate that the optimality of reserves hinges on the ability to control effort spatially in other locations.

Sanchirico and Wilen [68] examine conceptual issues of institutional design by characterizing first- and second-best optimal policies in a simple two patch metapopulation model. A system with bioeconomic heterogeneity will call for integrated system-wide solutions that account for parameter differences as well as the nature of interconnections. In an example with adult migration responsive to relative densities, it is optimal to adjust biomass so that dispersal flows from low profit to high profit patches. The equilibrium is a “flux equilibrium” in which effort and population densities are constant, but which maintains the equilibrium with flux across patch boundaries. The task of management in this spatial-dynamic system is thus one that jointly manages not only patch-specific profit differences, but also the flows of dispersal between patches in order to maximize system-wide returns.

These results suggest that the conventional “whole fishery” paradigm of managing a fishery as if it is a homogeneous single stock will be inefficient if it is a metapopulation. A metapopulation will require the spatial differentiation of policy instruments in ways that account for spatial externalities. For a fishery, this could mean, for example, patch-specific total allowable catches (TACs), or patch specific limited entry licensing programs, or patch specific landings taxes and/or individual quota programs. This kind of instrument proliferation would be costly of course, raising the question: what if the regulator is unable to set policies at the necessary spatially scale for a first-best outcome? Suppose that it is only possible to use one a single, undifferentiated instrument, such as a landings tax rather than spatially differentiated landings taxes. How would one optimally set such a tax and what would the implications be? In a two-patch fishery example, the inability to implement spatially explicit policies leads the regulatory authority to “over-conserve” the high cost patch and “under-conserve” the low cost patch where the magnitude depends on the degree and nature of connectivity in the system [68]. Similar conclusions are in Wilson et al. [92], who also investigate the policy implications of mismatched scales in a fishery context. In general, the results accord with intuition in the sense that optimal second best policies average or blend the spatially differentiated results. With an inability to utilize spatially differentiated instruments, the system cannot be as finely tuned as with first best instruments. As a result, overall fishery rents are lower, total effort is mismatched over space, and the biomass levels are not optimally adjusted to take advantage of the possibility of "farming" the system or aligning the dispersal and economic gradient.

These conceptual descriptions of optimal policies also raise important practical institutional design questions. How do we induce cooperation among autonomous agents and agencies in a system that is linked by spatial-dynamic processes? How do we reward users of patches that generate system-wide externalities to allow those external effects to propagate? Parkhurst et al. [55] investigate the potential for using an agglomeration bonus to get landowners to better coordinate land set-asides as a means to conserve contiguous parcels of habitat. While this research is illustrative of possibilities, it also raises many questions about possible uniqueness of Nash equilibria in a spatial context. More recently, Bhat and Huffaker [6] design self-reinforcing cooperative agreements within a differential game context for two landowners that share a biological resource (beaver population) that disperses between the properties.

Similar questions arise for point-input systems like invasive species problems [60,72]. How do we induce individuals who are first impacted to account for the spillover benefits of early control of invasions? What kinds of regional institutions are needed to tackle problems such as controlling invasive weed species? What kinds of international institutions are feasible to tackle phenomena like the avian flu or other potential pandemics? Many of these issues have features like the familiar commons game, but, in addition, they have structures such that the position of particular decision makers in time and space matter for the system outcome. As this frontier area is subjected to more analysis, the answers to these and similar questions will become clearer as economists synthesize principles from conceptual and empirical understanding.

An important aspect of our understanding of spatial systems undoubtedly will come from measuring the effects of spatial policies *ex post.* Our experience with marine reserves and other spatial policies is growing over time, and we will have opportunities to test whether policies to address spatial-dynamic features of coupled human-natural systems work as our *ex ante* models predict. Most evaluation of marine reserves is being done by non-economists who consider spatial policy interventions as if they are randomized experimental trials. However, the treatment and control groups in most of these policy interventions are not randomly assigned because, in coupled systems, humans interact with the resource base [81]. This suggests that program evaluation will also serve an important role for understanding spatial-dynamic systems. Program evaluation is now widely being used for environmental policy, and there are circumstances in which spatial variation or spatial geometry can be used to isolate policy treatment effects [31]. Spatial policies in renewable resource management will potentially generate the means to identify treatment effects through analyzing outcomes in spatially-explicit longitudinal data sets, whereas evaluating traditional non-spatial fishery management policies must identify treatment effects strictly from time series data. Program evaluation of spatial renewable resource policies will complement empirical work that is used either to design optimal spatial policies or predict the performance of second-best alternatives.

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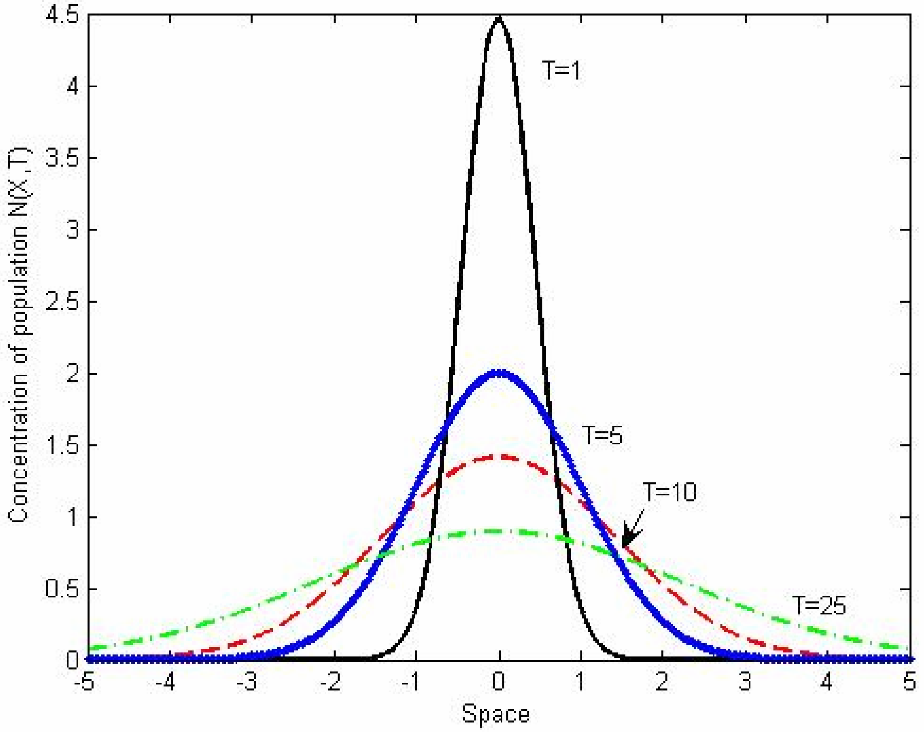

Figure 1 – Illustration of Fick's Law of Diffusion

Note: Derived with N_0=5 and D=0.1.

Table 1- Results of 100 Monte Carlo Simulations to Recover the Structural Spatial-Dynamic Parameters Using Seemingly Unrelated Regression in a Source-sink System

$J = 3, n = 100, T = 100, \bar{p} = 100, \sigma_p = 10, \sigma_\varepsilon = 0.075$

Parameter	True Value	Mean	Min	Max	Median	Standard Deviation
Restricted Model - Form of Dispersal Matrix Is Known A Priori						
q	0.015	0.0149	0.0124	0.0166	0.0150	0.0008
d21	0.15	0.1370	0.0239	0.2771	0.1398	0.0485
d31	0.05	0.0453	-0.0891	0.1740	0.0506	0.0573
r1	1.4	1.3755	1.0907	1.6550	1.3813	0.0995
r2	0.5	0.5467	0.1961	0.8646	0.5394	0.1306
r3	0.8	0.8160	0.4994	1.1835	0.8209	0.1409
k1	3	2.9935	2.4892	3.6546	2.9893	0.2082
k2	2	1.9986	1.3754	2.3138	2.0030	0.1414
k3	2	2.0047	1.7430	2.2530	2.0050	0.1143
Unrestricted Model - Form of Dispersal Matrix Not Known A Priori						
q	0.015	0.0149	0.0124	0.0166	0.0150	0.0008
d12	0	-0.0071	-0.1178	0.0833	-0.0012	0.0453
d13	0	0.0101	-0.0865	0.1128	0.0046	0.0451
d21	0.15	0.1360	0.0029	0.2874	0.1375	0.0516
d23	0	0.0049	-0.1182	0.1239	0.0044	0.0505
d31	0.05	0.0433	-0.1053	0.1939	0.0451	0.0588
d32	0	0.0094	-0.0962	0.1114	0.0092	0.0430
r1	1.4	1.3688	1.0324	1.6196	1.3689	0.1089
r2	0.5	0.5446	0.1303	0.8978	0.5591	0.1522
r3	0.8	0.8236	0.5004	1.2395	0.8149	0.1563
k1	3	2.9811	2.4832	3.7387	2.9893	0.2152
k2	2	1.9899	0.9033	2.8532	1.9905	0.3411
k3	2	2.0295	1.5785	2.9698	2.0286	0.2199

Table 2- Results of 100 Monte Carlo Simulations to Recover the Structural Economic Parameters in Second Stage

Parameter	True Value	Mean	Median	Min	Max	Standard Deviation
Raw Estimates						
$\alpha + c$	1.000	0.5211	0.5153	0.2823	0.9824	0.1165
ϕ	0.500	0.2491	0.2485	0.2263	0.2715	0.0090
Revenue	1	0.5095	0.5047	0.4129	0.7006	0.0519
Transformed by Estimated Scale - True Scale = 2.0						
$\alpha + c$	1.000	1.0115	0.9990	0.6837	1.4022	0.1252
ϕ	0.500	0.4944	0.4948	0.3274	0.6433	0.0562

Table 3 - Results of 100 Monte Carlo Simulations to Recover the Structural Spatial-Dynamic Parameters Using Seemingly Unrelated Regression

Density-Dependent System

$J = 3, n = 100, T = 100, \ \bar{p} = 100, \sigma_p = 10, \sigma_\varepsilon = 0.15$

Parameter	True Value	Mean	Median	Min	Max	Standard Deviation
Overidentfied Density-Dependent Model						
q	0.015	0.0149	0.0149	0.0133	0.0160	0.0006
d11	-0.250	-0.2380	-0.2364	-0.3828	-0.1039	0.0605
d12	0.083	0.0850	0.0866	-0.0487	0.1919	0.0472
d13	0.167	0.1690	0.1745	0.0714	0.2559	0.0404
d21	0.083	0.0771	0.0805	-0.0424	0.1786	0.0475
d22	-0.333	-0.3372	-0.3449	-0.4425	-0.1135	0.0661
d23	0.250	0.2438	0.2473	0.1206	0.3854	0.0480
d31	0.167	0.1609	0.1648	0.0414	0.2555	0.0488
d32	0.250	0.2522	0.2550	0.1302	0.3644	0.0478
d33	-0.417	-0.4127	-0.4104	-0.5947	-0.2390	0.0625
r1	1.000	0.9748	0.9471	0.5735	1.6273	0.1933
r2	1.000	1.0359	1.0473	0.4571	1.5451	0.1917
r3	1.000	1.0030	1.0034	0.6053	1.3843	0.1764
k1	3.000	2.9856	3.0147	2.4304	3.4663	0.2267
k2	3.000	3.0225	3.0523	2.4211	3.5426	0.2155
k3	3.000	2.9991	2.9926	2.3346	3.5571	0.2174

Table 4 - Results of 5,000 Monte Carlo Simulations to Recover the Structural Spatial-Dynamic Parameters Using Seemingly Unrelated Regression Density-Dependent System With Observation Error

$J = 3,\ n = 100,\ T = 100,\ \overline{p} = 100, \sigma_p = 10, \sigma_\varepsilon = 0.15$

Parameter	True Value	Mean	Median	Min	Max	Standard Deviation	Not a Number*
Overidentfied Density-Dependent Model - Observation Error Sig=0.1							
q	0.0150	0.0149	0.0149	0.0125	0.0172	0.001	0
d11	-0.2500	-0.2215	-0.2229	-0.5286	0.1075	0.082	0
d12	0.0833	0.0725	0.0728	-0.1332	0.2588	0.051	0
d13	0.1667	0.1492	0.1502	-0.0763	0.3360	0.050	0
d21	0.0833	0.0701	0.0689	-0.1373	0.2725	0.055	0
d22	-0.3333	-0.3015	-0.3010	-0.5594	0.0107	0.076	0
d23	0.2500	0.2275	0.2278	0.0700	0.4101	0.049	0
d31	0.1667	0.1514	0.1522	-0.0792	0.3720	0.059	0
d32	0.2500	0.2290	0.2285	0.0229	0.4117	0.053	0
d33	-0.4167	-0.3768	-0.3769	-0.6591	-0.1183	0.072	0
r1	1.0000	1.0669	1.0674	0.2314	1.8718	0.215	0
r2	1.0000	1.0717	1.0690	0.3119	2.0024	0.201	0
r3	1.0000	1.0556	1.0575	0.3460	1.8596	0.201	0
k1	3	2.8942	2.8875	1.5036	4.1394	0.279	0
k2	3	2.9116	2.9101	1.5285	3.9205	0.255	0
k3	3	2.9058	2.9027	1.7163	3.8868	0.254	0
Overidentfied Density-Dependent Model - Observation Error Sig=1.0							
q	0.015	0.0153	0.0153	-0.0037	0.0303	0.0044	1
d11	-0.250	-0.4309	-0.4194	-1.2442	0.1768	0.2015	1
d12	0.083	0.1350	0.1315	-0.1641	0.5095	0.0935	1
d13	0.167	0.1384	0.1344	-0.1314	0.5331	0.0853	1
d21	0.083	0.1872	0.1813	-0.1980	0.7879	0.1239	1
d22	-0.333	-0.3725	-0.3637	-1.1123	0.1563	0.1674	1
d23	0.250	0.1872	0.1815	-0.1210	0.6542	0.1011	1
d31	0.167	0.2433	0.2363	-0.2073	0.9236	0.1380	1
d32	0.250	0.2371	0.2308	-0.2282	0.7633	0.1232	1
d33	-0.417	-0.3260	-0.3193	-0.9288	0.1115	0.1431	1
r1	1.000	1.3427	1.3745	-0.4952	2.8021	0.4548	1
r2	1.000	1.1518	1.1821	-0.7502	2.7089	0.4609	1
r3	1.000	0.9287	0.9565	-0.8888	2.1696	0.4403	1
k1	3.000	2.9387	3.1285	-1605	61.2	23.4	1
k2	3.000	2.8915	3.1214	-1557.2	305.5	22.9	1
k3	3.000	2.7209	2.9505	-373.164	398.2688	11.3839	1
Overidentfied Density-Dependent Model - Observation Error Sig=2.0							
q	0.015	-0.0142	-0.0128	-0.3298	0.3686	0.0307	2
d11	-0.250	-0.4874	-0.3686	-12.9063	1.9023	0.6196	2
d12	0.083	0.1589	0.1037	-1.9886	7.5357	0.2772	2
d13	0.167	0.1281	0.0842	-3.5595	6.5235	0.2586	2
d21	0.083	0.2347	0.1601	-3.3590	9.7365	0.4143	2
d22	-0.333	-0.3597	-0.2644	-9.0540	7.7592	0.4699	2
d23	0.250	0.1478	0.0999	-4.3462	5.3882	0.2809	2
d31	0.167	0.2527	0.1757	-1.6992	11.8684	0.4032	2
d32	0.250	0.2008	0.1381	-8.4907	7.6496	0.3406	2
d33	-0.417	-0.2759	-0.2045	-6.8424	4.1885	0.4039	2
r1	1.000	0.0072	-0.0540	-6.7300	15.3708	1.1412	2
r2	1.000	-0.1438	-0.1668	-6.1892	11.0015	0.9329	2
r3	1.000	-0.2581	-0.2782	-5.6480	7.7297	0.8213	2
k1	3.000	25.7282	9.1508	-52890	105430	2390	2
k2	3.000	-16.6114	10.9632	-487770	107030	7540	2
k3	3.000	-483.906	12.0781	-398980	128510	6070	2

* Number of occurences out of 5,000 with a divide by zero error or other error in the estimation.

Table 5a – Raw Parameter Estimates from the Gulf of Mexico Reef-Fish Fishery Data

	Coefficient	t-stat	Coefficient	t-stat	Coefficient	t-stat
β_{j1}	0.9057	2.32	0.4497	3.589	1.3543	7.064
β_{j2}	-5.85E-04	-0.431	-1.50E-03	-3.441	-0.0032	-4.792
β_{j3}	0.542	2.24	0.7246	9.33	0.0815	2.099
β_{j4}	-0.1483	-0.687	0.0861	1.243	0.1189	1.09
β_{j5}	-1.25E-04	-1.008	-2.40E-05	-0.602	-3.98E-06	-0.097
β_{j6}	0.0002	1.237	-0.0001	-2.506	-0.0001	-1.472
β_{j7}	-0.0006	-0.478	0.0012	3.183	0.0015	1.652

Table 5b – Recovered Parameters from the Gulf of Mexico Reef-Fish Fishery Data

Parameter	Estimate	Parameter	Estimate
q1	1.25E-04	***d11***	-0.8061
q2	2.40E-05	***d12***	0.5420
q3	3.98E-06	***d13***	-0.1483
r1	0.7119	***d21***	0.7246
r2	0.1106	***d22***	-0.6235
r3	0.2921	***d23***	0.0861
k1	9.70E+06	***d31***	0.0815
k2	3.07E+06	***d32***	0.1189
k3	2.28E+07	***d33***	0.0622

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[1] Hotelling also explored questions about spatial equilibrium but in a context without dynamics [37].

[2] Emergence of urban features in the "new economic geography" often depends on a tension between economic forces that attract and repel [28]. See Irwin and Bockstael [40] for an early empirical application that accounts for environmental amenities.

[3] An important problem in conservation that hinges on spatial heterogeneity is the reserve site selection problem. To conserve biodiversity cost effectively, managers choose reserve sites based on spatially-varying conditions [2,59]. While the early literature focused on choosing sites in a static framework, recent extensions incorporate dynamics through the timing of site selection and risk of future development for unprotected sites [15], and through the feedbacks that local land markets can create when purchasing large areas for conservation [3].

[4] Phaneuf et al. [57] recover non-market values from the resulting spatial equilibrium assuming implicitly that the dynamics of environmental amenities are in equilibrium.

[5] Of particular importance in Irwin et al. [41] is how the presence of multiple time scales (some processes are faster/slower than others) affect results (see also [32]). They show that coupled economic and ecological models produce qualitatively different equilibria than those that would emerge from treating subsystems separately.

[6] For a comprehensive treatment of the mathematics of diffusion, see [51,54].

[7] Evolution of coastline shapes are also governed by spatial diffusion, where small perturbations can propagate over large spatial scales [4].

[8] Sanchirico and Wilen [68] illustrate this property in a discrete formulation of space. This property also resembles the manner in which agricultural rents depend upon transportation costs

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at that point in space in the original von Thünen model of the isolated town. See Fujita et al. [28] for a discussion.

[9] In the new economic geography, the circle setting is consistent with the geometry of the "racetrack" economy [28].

[10] See [64] for a discrete model of a fish population that includes other forms of dispersal processes.

[11] The assumption of no mortality in the dispersal process is not a requirement and one can easily assume that there is some loss in the dispersal process. In that case, the dispersal parameters would sum to less than one.

[12] For example, for some species, such as salmon or grouper, there is a seasonal migration to certain areas for spawning every year.

[13] The metapopulation concept is attributed to Levins [47,48], who focused on terrestrial species and considered only whether a patch was occupied or not. Over time, the concept has been expanded to consider within patch population dynamics and local abundances and is being applied and adapted for the marine environment. See also the work of Hanski [33].

[14] Using a similar formulation, Tuck and Possingham [86] and Supriatna and Possingham [83] investigate optimal management in a two-patch source-sink system with no economic heterogeneity

[15] Some recent work by other economists on the spatial implications of resource use include [1,12,30,36,61,92]. Costello and Polasky [16] consider a more general metapopulation structure that includes multiple types of random events that correspond to own growth and dispersal.

[16] A few noteworthy examples in economics include [14,21,91].

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[17] While our application is a fishery, the general requirements for adapting this type of analysis for other resource contexts are: 1) population growth and dispersal are additively separable; 2) there is a functional link between populations—which may not be directly observed—and human activities (e.g. a harvest or extermination function); and 3) spatially explicit time series data exist on inputs (e.g. harvest effort) and outputs (e.g. catches).

[18] In general, observation error that is not modeled in empirical settings will lead to errors-in-variables bias in the biological parameter estimates [87]. We assume initially no observation error to obtain a tractable starting point in our simulations. Ecologists are continuing to develop models that incorporate both process error and observation error [20]. Recent work by economists in a non-spatial system exploits the panel structure of fishery data to address simultaneously process error, observation error, and the limitations of the Schaefer production function [96].

[19] In general, the relative time scale over which the biological and economic processes unfold over space is an important factor in determining the underlying spatial-dynamic processes.

[20] It is important to note that the mandatory use of electronic logbooks is increasing throughout the world's fisheries, which makes one even more optimistic that such exercises will be more feasible in the future.

[21] See, for example, the recent work on connectivity structures [17,18].

[22] Recall that this result does hinge on the strong assumption of a Schaefer harvest function.

[23] A possible source of an offsetting economic gradient is the location of fishing ports relative to heterogeneous subpopulations. However, the intensity of effort fishing from a particular port in real systems can be endogenously determined by the overall spatial productivity of the resource [80].

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[24] Note that everyone fishing at the same time in the same place is facing the same stock. This is the sense in which disaggregated data can be used to estimate production functions, but it is also the key point that allows Zhang and Smith [96] to difference out the stock and use panel methods to account for observation and process error. This method has not yet been extended to the spatial domain.

[25] The authors thank Junjie Zhang for research assistance preparing the data.

[26] We are not in a position use our model to test hypotheses about physical oceanography. Our results are nonetheless provocative given the predominant Loop Current. Still, there is some evidence that deep water currents in the Gulf flow in the opposite direction [22], which is consistent with the flow of our dispersal matrix. Naturally, this raises questions about where in the water column fish larvae are transported.

[27] By correcting errors-in-variables bias and allowing curvature in the production function, Zhang and Smith [96] show that the implied carrying capacity is less than half that from the naïve estimator.

[28] Conceptual studies have shown that under some circumstances, reserves are part of the optimal policy [16,53,65]. However, theoretical predictions about reserve performance are sensitive to assumptions about how fishing effort is distributed over space in the remaining fishing area [77].

Appendix A – Simulated Data Algorithm

We use the following algorithm to simulate data from the bioeconomic model. First, we determine the number of individuals (*n*), choices (*J*+1), and choice occasions (*T*); assign true values to all of the bioeconomic parameters including the mean and standard deviation of price; draw a vector of prices; and set initial conditions on the stocks (N_{0j}). Second, we form the deterministic portion of utility at t=0 in (14) for each individual in each location. Third, we draw i.i.d. Type I Extreme Value errors η_{ijt} by inverting a uniform distribution (u~U[0,1]) using the cdf of Type I (denoted F(η) to recover the errors that we need: $\eta = b\left\{-\ln\left[-\ln\left(u\right)\right]\right\}$, where b controls the variance of the distribution). See Train (2003) for details on the inversion method for drawing from distributions. Fourth, we fill in the random component of utility in (14) and simulate individual choices:

$$E_{ijt} = \begin{cases} 1, & if\ U_{ijt} = \max\left(U_{i0t}, U_{i1t}, U_{i2t}, \ldots, U_{iJt}\right) \\ 0, & otherwise \end{cases} \tag{A}$$

Fifth, we add up individual-, space-, and time-specific effort in (A) and substitute into (10) to obtain total harvest by patch. Sixth, total harvest is substituted into (9). Finally, we draw an i.i.d. normally distributed process error in (9) and iterate the state equation. We return to step two and follow the process for t=1, and so forth.

Reference

Train, K.E. 2003. Discrete Choice Methods with Simulation.Cambridge: Cambridge Univ. Press.

Appendix B – Recovering Structural Bio-Physical Parameters in 3-Patch System

When adding up holds, we can recover all of the structural bio-physical parameters of the spatial-dynamic system from the reduced-form parameters. In the 3-patch system, there are thirteen total parameters.

$$q = -\beta_{15}$$

$$d_{11} = -\beta_{23} - \beta_{33} \qquad d_{21} = \beta_{23} \qquad d_{31} = \beta_{33}$$
$$d_{12} = \beta_{13} \qquad d_{22} = -\beta_{13} - \beta_{34} \qquad d_{32} = \beta_{34}$$
$$d_{13} = \beta_{14} \qquad d_{23} = \beta_{24} \qquad d_{33} = -\beta_{14} - \beta_{24}$$

$$r_1 = \beta_{11} - 1 + d_{21} + d_{31} \qquad r_2 = \beta_{21} - 1 + d_{12} + d_{32} \qquad r_3 = \beta_{31} - 1 + d_{13} + d_{23}$$

$$K_1 = \frac{-r_1}{q\beta_{12}} \qquad K_2 = \frac{-r_2}{q\beta_{22}} \qquad K_3 = \frac{-r_3}{q\beta_{32}}$$

Appendix C – Additional Experiments

Table C-1- Results of 100 Monte Carlo Simulations to Recover the Structural Spatial-Dynamic Parameters Using Seemingly Unrelated Regression

Increased Process Error

$J = 3, n = 100, T = 100, \bar{p} = 100, \sigma_p = 10, \sigma_\varepsilon = 0.3$

Parameter	True Value	Mean	Min	Max	Median	Standard Deviation
Restricted Model - Form of Dispersal Matrix Is Known A Priori						
q	0.015	0.0148	0.0071	0.0210	0.0149	0.0024
d21	0.15	0.1549	-0.0486	0.3172	0.1545	0.0777
d31	0.05	0.0387	-0.1192	0.2001	0.0376	0.0804
r1	1.4	1.3724	0.9752	1.8141	1.3855	0.1747
r2	0.5	0.5213	0.0981	0.9915	0.5074	0.2037
r3	0.8	0.8490	0.1103	1.4017	0.8477	0.2297
k1	3	3.1719	2.2285	5.5090	2.9961	0.5851
k2	2	1.9411	1.1134	3.3591	1.9378	0.3388
k3	2	2.0382	1.6438	3.0297	2.0135	0.2382
Unrestricted Model - Form of Dispersal Matrix Not Known A Priori						
q	0.015	0.0148	0.0071	0.0216	0.0147	0.0028
d12	0	0.0051	-0.2275	0.1809	0.0100	0.0756
d13	0	-0.0033	-0.1428	0.1599	-0.0029	0.0610
d21	0.15	0.1499	-0.0750	0.3449	0.1485	0.0839
d23	0	0.0140	-0.1321	0.1830	0.0145	0.0659
d31	0.05	0.0406	-0.1329	0.2234	0.0461	0.0876
d32	0	-0.0008	-0.1568	0.2764	-0.0037	0.0690
r1	1.4	1.3696	0.8398	1.7293	1.3782	0.2021
r2	0.5	0.5119	-0.1311	1.1734	0.5120	0.2263
r3	0.8	0.8552	0.0564	1.4827	0.8117	0.2645
k1	3	3.1719	2.2212	5.2493	2.9790	0.5951
k2	2	1.9034	-5.2289	4.9334	1.9727	0.9686
k3	2	2.0844	0.8823	4.1149	2.0019	0.4933

Table C-2 - Results of 100 Monte Carlo Simulations to Recover the Structural Economic Parameters in Second Stage

Increased Process Error

$J = 3, n = 100, T = 100, \overline{p} = 100, \sigma_p = 10, \sigma_\varepsilon = 0.3$

Parameter	True Value	Mean	Median	Min	Max	Standard Deviation
Raw Estimates						
$\alpha + c$	1.000	0.5211	0.5153	0.2823	0.9824	0.1165
ϕ	0.500	0.2491	0.2485	0.2263	0.2715	0.0090
Revenue	1	0.5095	0.5047	0.4129	0.7006	0.0519
Transformed by Estimated Scale - True Scale = 2.0						
$\alpha + c$	1.000	0.9996	0.9981	0.7372	1.1481	0.0704
ϕ	0.500	0.5008	0.4967	0.3972	0.6602	0.0437

Table C-3- Results of 100 Monte Carlo Simulations to Recover the Structural Spatial-Dynamic Parameters Using Seemingly Unrelated Regression

Fix r and K across patches

$J = 3, n = 100, T = 100, \bar{p} = 100, \sigma_p = 10, \sigma_\varepsilon = 0.15$

Parameter	True Value	Mean	Min	Max	Median	Standard Deviation
Restricted Model - Form of Dispersal Matrix Is Known A Priori						
q	0.015	0.0151	0.0090	0.0207	0.0151	0.0018
d21	0.15	0.1643	-0.1232	0.3690	0.1653	0.0843
d31	0.05	0.0397	-0.1563	0.2126	0.0387	0.0750
r1	0.8	0.8160	0.5247	1.1606	0.8292	0.1391
r2	0.8	0.7978	0.5183	1.0674	0.7924	0.1216
r3	0.8	0.8318	0.5434	1.2003	0.8168	0.1170
k1	2	2.1094	0.9652	5.8733	1.9296	0.7162
k2	2	1.9961	1.5963	2.7447	1.9769	0.1669
k3	2	1.9939	1.6107	2.5536	1.9663	0.1610
Unrestricted Model - Form of Dispersal Matrix Not Known A Priori						
q	0.015	0.0151	0.0096	0.0205	0.0151	0.0018
d12	0	0.0014	-0.1347	0.1400	0.0016	0.0569
d13	0	0.0057	-0.1421	0.1576	0.0038	0.0604
d21	0.15	0.1683	-0.1196	0.4054	0.1765	0.0883
d23	0	-0.0112	-0.1415	0.1542	-0.0153	0.0608
d31	0.05	0.0430	-0.1876	0.2428	0.0448	0.0801
d32	0	-0.0007	-0.1883	0.1491	-0.0026	0.0647
r1	0.8	0.8086	0.4944	1.2848	0.8091	0.1639
r2	0.8	0.8104	0.4527	1.1887	0.8281	0.1502
r3	0.8	0.8256	0.3595	1.1791	0.8327	0.1606
k1	2	2.1211	0.9737	5.9289	1.9667	0.7099
k2	2	2.0156	1.3369	3.2140	1.9766	0.3178
k3	2	1.9721	1.3677	2.8348	1.9422	0.2906