Economics of habitat fragmentation: a review and critique of the literature[1]

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Abstract

Understanding the signficance of habitat fragmentation for ecological function has been a focus in the natural sciences for decades. More recently, the field of economics has begun to assess the drivers and impact of habitat fragmentation, as well as potential policy and market-based mechanisms to address fragmentation. We present a review of the existing economics literature that addresses habitat pattern/fragmentation and we define themes, issues, and next steps for this literature. First, this paper reviews economic modeling and empirical approaches to identifying drivers and patterns of fragmentation. The next section summarizes the literature on analysis of optimal land use patterns and the tradeoffs of managing for ecological and economic objectives. The last literature section contains description of policy and mechanisms for addressing habitat fragmentation in the context of single and multiple landowners who do not manage land for habitat benefits explicitly. We conclude with a discussion of unanswered questions and next steps for research and data analysis on habitat fragmentation.

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[1] The authors gratefully acknowledge the financial support of the Knobloch Wyoming Excellence Chair, and the research assistance of Aubrey Jones and Audrey Cheng.

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1. Introduction

Habitat fragmentation is the process of dividing a contiguous area of natural habitat into smaller, more isolated patches (Wilcove, Mclellan and Dobson 1986). Patches are separated by lands that are either degraded or transformed by land use change, which limits ecological interactions among patches. Natural events including wildfire, windfall, and disease outbreak events can cause fragmentation, but the largest driver is human-induced land use change (Burgess and Sharpe 1981; Hawbaker et al. 2006; Heilman et al. 2002).

The extent to which habitat area and spatial configuration independently affect species survival is still strongly debated (Fahrig 2017). Still, many studies describe negative impacts on species from fragmentation of habitat while others define the costs of "edge" area -- habitat that is in close proximity to converted habitat – on species that require interior habitat for survival (Paton 1994; Bevers and Hof 1999). Part of the impact of fragmentation derives from the reduced area of habitat for species that cannot reach other fragments, which, through species-area relationships, leads to a decline in species over time (Newmark et al. 2017; Lovejoy 1986; Terborgh 1974; Diamond 1972). In response to threats to biodiversity from habitat fragmentation, managers consider the potential impact of siting, sizing, and location decisions in establishing protected areas and in creating or protecting wildlife corridors between habitat fragments. In contrast, both ecological researchers and policy analysts find that increasing isolation of fragments can reduce risks to species by limiting the spread of disease or habitat-disrupting fire. These opposite sides of the impact of the pattern of conservation contribute to the SLOSS – single large or several small – debate about whether to conserve large contiguous areas or to separate many small conservation areas.

Despite a large literature within economics on habitat conservation and land use policy, only recently have economists begun to address fragmentation (Albers and Bu 2009). Several complicating factors have limited economists' attention to habitat pattern including: a lack of technical understanding of the relationship between habitat pattern and production of ecosystem services; availability of spatial imagery and data; and the computational challenges of spatial-dynamic analysis. Economists now explore various aspects of fragmentation including: spatial econometrics to identify the economic drivers of fragmentation; spatially optimal configurations of land conservation given spatial net benefit functions; land use/development models that contain spatially explicit ecological models; and policy analysis to induce conservation of acreage in socially beneficial spatial patterns.

Some economic analyses explore optimal habitat pattern through objectives to minimize fragmentation or through constraints on connectivity, but other economic work on fragmentation does not begin with the assumption that fragmentation is negative. Instead, the tools and methods used in the field of economics are well-equipped to analyze tradeoffs among the choices that define the spatial configuration of conservation. As a result, economic analysis of fragmentation contributes to our understanding of the process of fragmentation and outcomes of land use policies, desired and undesired, because of its emphasis on understanding human decisions as actors in a landscape's ecosystem.

This paper provides a review of the existing economics literature that addresses habitat pattern and defines some themes, issues, and next steps for analyzing the economics of habitat fragmentation. The following section provides an overview of non-economic research in habitat fragmentation. The third section reviews the econometrics literature on identifying drivers and patterns of fragmentation. Section 4 details economic modeling and empirical approaches to defining optimal patterns of habitat and the impact of land use decisions on creating habitat fragmentation. Section 5 outlines policy mechanisms and frameworks for addressing habitat fragmentation in the context of multiple landowners who do not manage land for habitat benefits explicitly. The final section develops a discussion of the literature's themes and indicates appropriate directions forward.

2. Understanding and measuring fragmentation.

a. Monitoring and measuring habitat fragmentation

Humans cause habitat fragmentation and are impacted by its consequences, making both monitoring and measuring land use patterns critical aspects of economic questions and research. Accurately quantifying habitat fragmentation is essential for analyzing both its drivers and impacts. Geographic Information Systems (GIS) technology and remote sensing facilitate the collection of spatial statistics to describe patterns and rates of fragmentation. Satellite imagery has been collected since the early 1970's, and is primarily available through space and governmental agencies. The process of habitat fragmentation is monitored by identifying differences between two or more classified sets of land cover data over time. Land cover data may come from field-based mapping data, but most current analyses rely on interpretation of images collected by satellites across time. Interpretations of the raw satellite images may be based on either human ("supervised") or automated ("unsupervised") classification into land cover types. Ideally, fragmentation process analyses rely on satellite images with the same resolution and scale and from the same type of instrument, collected at different points in time. Over time, resolution of commonly available imagery has increased from 125m during first collection to, recently 30m resolution (Hansen et al. 2013), allowing for increasing detailed measurement and analysis. The cost of images and interpretation has also decreased dramatically over time, allowing for analysis of habitat fragmentation across numerous countries. Now truly a global endeavor, fragmentation patterns have been analyzed in China (Li et al. 2010, Gong et al. 2013, Liu et al. 2016), Greece (Gounaridis, Zaimes and Koukoulas 2014), Chile (Echeverria et al. 2008), Italy (Bruschi et al. 2015), Brazil (Arima et al. 2008), Ecuador (Tapia-Armijos et al. 2015), Thailand (Sims et al. 2014), Costa Rica (Sánchez-Azofeifa et al. 1999), Nepal (Nagendra et al. 2008), and more.

Using classified land cover data, habitat fragmentation levels can be assessed using metrics that vary in spatial and temporal scale (Turner 1989; McGarigal 2006; Kindlmann and Burel 2008; Leitao et al. 2012). The scale of analysis, metric type, and metrics chosen in an analysis depend on the overall research question. Table 1 summarizes frequently used metrics in measuring habitat fragmentation. Composition metrics assess the amount of each type of land class and the diversity of classes while configuration metrics focus on the spatial arrangements of these land classes. There are a limited number of software programs available to calculate fragmentation statistics. The FRAGSTATS software program is commonly used for quantifying fragmentation metrics and computes an array of statistics at the patch, local landscape, and global landscape scales, allowing the user to choose the spatial scale that is appropriate for each analysis (McGarigal and Marks 1995). Users may also calculate metrics directly from spatial data.

The number of metrics available to characterize habitat fragmentation creates inconsistencies in conceptualization and measurement of fragmentation across studies, which is problematic in understanding its ecological and economic impacts. Fahrig (2003) performs a meta-analysis of the ecological fragmentation literature, specifically papers testing the impacts of fragmentation on ecological processes, and finds that most studies do not distinguish between their measure of loss of habitat area and the creation of isolated habitat patches. In addition, because habitat must be measured at a landscape scale, most field experiments are not large enough to make inferences about the effects of fragmentation on species and ecosystems.

Table 1. Examples of metrics used in measuring fragmentation

Metric	Metric type	Description
Habitat class abundance	Composition	Amount of habitat type relative to entire map
Richness	Composition	Number of habitat types
Evenness	Composition	Relative abundance of habitat types
Diversity	Composition	Combined measure of richness and evenness
Patch size distribution and density	Configuration	Summary statistics of habitat sizes
Patch shape complexity	Configuration	Complexity of patch geometry, related to perimeter-to-area ratio
Core area	Configuration	Interior area of patch
Isolation	Configuration	Measure of distance between habitat patches
Dispersion	Configuration	Heterogeneity of patches
Contagion	Configuration	Measure of patch aggregation
Subdivision	Configuration	Separation between patches of a certain habitat type

Connectivity	Configuration	Connections among patches
Interspersion	Configuration	Connectivity of heterogeneous habitat types

b. *Is Fragmentation Economically Harmful or Beneficial?*

From an economic perspective, interest in fragmentation stems from questions about its impact on the costs or benefits of land use change. These impacts are a function of how land use patterns affect economic values (above and beyond the changes in value due to changes in land use quantities) and ultimately rest on the underlying biological relationships between habitat fragmentation and ecological health. Much of the biological literature suggests increasing returns to scale in larger habitat patches, through mechanisms such as increased species viability (Armsworth, Kendall and Davis 2004; McGarigal and Cushman 2002; Fahrig 2002; Bender, Contreras and Fahrig 1998; Turner 1996; Robinson et al. 1995) or resilience to shocks from severe weather or disease (Opdam and Wascher 2004; Allan, Keesing and Ostfeld 2003; Kramer et al. 2001; Boose, Foster and Fluet 1994). Connectivity between patches is also important (Debinski and Holt 2000; Krauss et al. 2010): the combined value of parcels that create contiguous or well-connected habitat may be greater than the sum of an identical set of parcels that create dispersed or isolated habitat. Yet some species or ecological processes may actually benefit from increased patchiness, additional edge habitats, or more mixed landscapes (Fahrig 2017; Christensen 1997; Turner 2005; Galvin et al. 2008). Several small distributed areas may help to spread the risk of environmental stress across sub-populations (Hof and Flather 1996). This idea of tradeoffs between ecological outcomes and related economic impact has been incorporated in a limited set of studies but is likely to gain more attention as the underlying ecological understanding of fragmentation improves.

3. **Econometric Assessments of the Drivers of Fragmentaton**

Magnitude and patterns of land use change can be influenced by a number of drivers. Identifying which of these drivers are most influential in fragmentation is key to addressing future land use change and developing policies to guide land use patterns in socially preferred directions. The availability of spatial data allows economists to use spatially explicit regression analysis to uncover the drivers of fragmentation, often within the context of examining other aspects of the landscape. The goals of econometric analyses have included understanding why patterns of fragmentation have emerged, predicting patterns of and high-risk areas for future fragmentation, and evaluating policy effectiveness in addressing habitat fragmentation. Underpinning most of these econometric analyses of the drivers of habitat fragmentation are the core assumptions of a von Thunen style land rent model in which all land units go to their highest value use. Key drivers tested include both natural land characteristics related to rents—such as soil quality or slope—and human-induced characteristics such as roads and tenure patterns.

a. Roads and Habitat Pattern.

Roads are clearly a potential driver of habitat fragmentation. While all land conversion alters the pattern of habitat types, roads directly reduce the contiguous area of any natural habitat (Chomitz and Gray 1996; Nelson and Hellerstein 1997; Pfaff 1999; Forman and Alexander 1998). Fragmentation via road construction is also unique in that roads cut across large areas of land, creating breaks and fragments (Hawbaker et al. 2005), and the existence of roads partially determines and encourages subsequent land conversion. In one of the earliest explorations of how road building affects deforestation and forest fragmentation, Chomitz and Gray (1996) develop a spatially explicit model of land use in Belize. Using the standard Von Thunen framework, they model clearing probabilities as a function of distance to markets, land and soil characteristics, topography, climate, and tenure arrangements. A key finding is that subsistence farmers are highly responsive to soil quality, suggesting small economic returns where soil quality is low. That result signals that road location decisions should consider the response of farmers to those roads in order to direct the pattern of land use. Although not examining fragmentation itself, Pfaff et al. (2007) perform a regression analysis of road networks in the Brazilian Amazon, finding that roads in one location increase the deforestation in both that location and neighboring locations, which suggests strong spatial spillovers on forest cover from road creation. Saunders et al. (2002) find that road density contributes to fragmenting the landscape by increasing the number of patches and patch density and by decreasing the patch size.

Hawbaker et al. (2005) use generalized least-squares (GLS) regression models to analyze the dynamic relationships among road density, landscape patterns, and housing density change in northern Wisconsin. They conclude that both road density and fragmentation increased significantly over time, with roads causing substantial landscape change and driving fragmentation. They also explore the drivers of road placement in order to predict habitat types most likely to be threatened by future fragmentation. They find that both road density and the resulting landscape pattern are positively correlated with suitable soils for forming road subgrade, which correlates with existing residential, agricultural, grassland, and coniferous forest areas (and less with wetlands, deciduous forest, mixed forest, and lake areas). Similarly, Freitas, Hawbaker and Metzger (2010) explore the drivers of forest fragmentation in the Brazilian Atlantic Forest. They find that forest fragmentation correlates with topography, land use, and road density. They also examine the dynamics of forest cover and find that older road networks have more impact on forest fragmentation than newer roads, highlighting the persistent impacts of roads on land use patterns and thus the importance of road siting decisions for long-term ecological health.

Heilman et al. (2002), in building a fragmentation dataset covering the full coterminous U.S., argues that fragmentation by roads is so important that they use highway data to define landscape units. Their analysis highlights different regions of the U.S. that remain relatively less fragmented, such as the Northwoods of Maine, the Boundary waters area in Minnesota, and the Olympic Mountains of Washington. It also emphasizes a core question in the analysis of fragmentation: what scale and grain of detail is useful in evaluating fragmentation? More detailed data often increases measured fragmentation levels for the same area as smaller roads or more patchiness of individual habitat types are revealed. For example, the authors describe Jeffery pine forests (common to the Klamath-Siskiyou region) that are a single habitat type that is naturally patchy.

A major ecological impact of roads is the amount of edge habitat they create. Edge habitat can only be used by certain species, meaning that the overall effect of road creation on habitat area and patch isolation can be much larger than the actual area of the road. Saunders et al. (2002) discuss the importance of determining depth-of-edge influence, the amount of habitat around the road that becomes edge habitat, in measuring the impact of roads on habitat availability. The authors use data from northern Wisconsin to determine the effects of roads on habitat patch size and density and find habitat disturbance occurring 300 meters away from the road.

An issue carried throughout these analyses is how to best measure the features of roads that lead to fragmentation: is it their effect on access to markets, thus changing land rents, is it the total density of roads and their relationship with housing patterns, or is it the pattern of roads themselves? Stoms (2000) points out that density measures treat all road segments equally and ignore patterns, while factors such as road width, traffic volume and noise levels are all important for impacts on biodiversity. Their "roadedness" index sums areas potentially affected by roads, allowing differences in impact for different road types. Theobald (2001) and Theobald (2003) use this index to describe the areas affected by roads in Colorado and conclude that roadedness and housing density indeed contribute to landscape change and threaten biodiversity. Albers et al. (2012) also argues that even modified measures of road density do not capture aspects of road pattern that could drive fragmentation. They develop a measure of the pattern of roads, the Road Network Agglomeration Index (RNAI), based on the coefficient of variation of road distances from landscape points, and find that RNAI correlates highly with the degree of fragmentation of California's reserve network, explaining more of the variation of fragmentation than road density alone.

b. Land Characteristics and Habitat Pattern.

The possible specific human uses of and ownership structures for land also contribute to the pattern of habitat or fragmentation of a landscape. Early work by Irwin and Bockstael (2002) proposed and estimated a model of land use conversion that explained sprawl patterns (low density, non-contiguous residential/commercial development) as a result of negative externalities between spatially distributed agents. Abdullah and Nakagoshi (2007) demonstrate that different agricultural crops lead to different levels of fragmentation, with oil palm plantations generating high levels of wetland fragmentation but rubber plantations within forest landscapes generating far less fragmentation. Butler, Swenson and Alig (2004) use a land rent model and find that forest fragmentation is positively correlated with population density, income, and percent agriculture, and negatively correlated with distance to highways, federal land, and slope in the U.S. Pacific Northwest. Alig, Lewis and Swenson (2005) use measures of the spatial pattern of soil quality, which is a key determinant of possible uses, to explain forest fragmentation. They find that capturing soil quality configuration instead of more aggregate measures improves the statistical fit of the regressions and that this spatially descriptive explanatory variable proves particularly important in regressions with a dependent variable that addresses pattern. Echeverria et al. (2008) analyze spatial patterns of forest loss in Chile between 1976 and 1999 to predict likely loss by 2020. They establish that clearance of forest for pasture/agriculture and logging for fuelwood and timber is driving most fragmentation and that these patterns are highly correlated with soil type and gentle slopes.

In the Oregon Coast Range, Stanfield, Bliss and Spies (2002) find that characteristics of the land ownership patterns correlate with characteristics of forest cover, including that forest cover diversity increases with land ownership diversity, forest patch size increases with land ownership unit size, and forest patch connectivity increases with land ownership unit connectivity. Turner, Wear and Flamm (1996) examine the influence of different land owners – federal, state, and private – on landscape pattern in two forest-dominated regions: the Olympic Peninsula, Washington, and the southern Appalachian highlands of western North Carolina. They compare patterns and changes across a 16-year period, predicting transitions between forest, grassy and unvegetated land cover classes as a function of ownership and determinants of rents such as slope, distance to markets, and population density. They find that land-cover transitions differ between ownership types with private lands are more fragmented than public lands, and that the importance of land cover change variables differed between the two study regions.

Rapid urbanization is also an important determinant of habitat fragmentation, particularly in high growth rate countries (Li et al. (2010), Gong et al. (2013), and Gao and Yu (2014)). Liu et al. (2016) demonstrate dramatic forest cover loss and fragmentation from 1979 to 2014 close to an urban zone in the Ningbo region of China. New drivers of fragmentation are likely to continue to emerge as well: for example Abrahams, Griffin and Matthews (2015) document substantial fragmentation threats from natural gas development, particularly when gas lines do not follow existing roadways. Recent research (in China—Gong et al. (2013) and in Puerto Rico—Gao and Yu (2014)) has also highlighted that fragmentation may either decrease or increase as a result of reforestation, particularly in peri-urban areas.

Although these analyses of the drivers of habitat fragmentation contribute considerable insight for understanding landscape patterns, two aspects limit their policy applications. First, the parcel-specific characteristic of these analyses means that patterns of land uses that generate higher value than the sum of the individual parcel values cannot be assessed. Future work should include more use of spatial lags or other ways to model synergies and spillovers between parcels. In addition, given the focus of these analyses on pattern, further development of explanatory variables that themselves reflect pattern should prove useful. Second, this type of regression analysis relies on characteristics of parcels, with an assumption that each parcel will be put into its highest valued use. While the assumption of individual parcels being put to highest and best use may play out well where factor markets are well-functioning, situations where landowners face subsistence, labor, capital, or skill constraints may be better modeled by a framework that depicts individual decisions about locations of different land uses. In addition, because many of the parcel characteristics such as soil quality and slope cannot be directly altered with policy, these analyses may be better at prediction or explanation than at informing policy. Still, understanding both natural and human characteristics driving fragmentation can identify areas at risk for fragmentation and may be useful in decisions about road siting or tenure institutions. In addition to responding to new threats, future analysis of fragmentation drivers will need account for processes of reforestation driven by forest transitions.

4. Decisions and the Pattern of Conservation Areas within a Landscape

4.1 Reserve site selection and optimal reserve design.

Reserve site selection (RSS) models use techniques from operations research to allocate parcels on a landscape to reserves with the ecological goal of conserving species. Early RSS models focused on identifying the minimum reserve size (number of sites) to provide habitat for the defined number of species or the maximum number of species "covered" by a specific number of reserve sites, but did not account for spatial pattern of the reserve sites beyond heterogeneity in the location of species on the landscape (Kirkpatrick 1983).

While most RSS models do not specifically address fragmentation in reserve design (Church, Stoms and Davis 1996), connectivity and corridor patterns have been included within some models (Moilanen and Cabeza 2002). To address fragmentation in RSS, spatial rules or constraints have been added to modeling frameworks as proxies for spatial ecological processes that contribute to species persistence. Seeking less fragmented or more compact reserve networks, approaches may minimize the perimeter area of reserves, optimize over compactness, or impose connectivity constraints (Fischer and Church 2003; Önal et al. 2016; Önal 2004). In situations where connected reserves might lead to the spread of disease or other threats to species, researchers define constraints against connectivity such as minimum distances or buffers between reserve sites, to force more dispersed sites within a reserve network (Williams 2008; Hamaide, Williams and ReVelle 2009). Whether in order to provide agglomerated or dispersed reserve networks, the use of spatial constraints limits the ability to balance tradeoffs between the species protection benefits on a site and the risks or benefits of the spatial configuration of reserve sites. Albers et al. (2016) use expected species coverage in an RSS framework that evaluates the risks to species in contiguous reserve sites when fires can spread. For this fire case, in theory and in an application to part of Oregon, the analysis demonstrates that reserve site distance constraints produce a too-dispersed reserve network and force the exclusion of high value sites from the reserve network in comparison to the reserve network defined where proximity or distance-based risks are evaluated against the possible gains from including contiguous sites in the reserve network.

A criticism of early RSS models was the fact that sites were selected in a static framework, with no consideration for species survival through habitat suitability or evolution of the reserve. Costello and Polasky (2004), Visconti et al. (2010), and Dissanayake and Önal (2011) incorporate dynamics into RSS. Meir, Andelman and Possingham (2004) and Newburn, Berck and Merenlender (2006) explore RSS in a dynamic setting under uncertainty about degradation of unprotected land parcels and species survival. As the field has developed, the complexity of analysis has increased to also include species survival and dispersal. Moilanen and Cabeza (2002) include a single-species metapopulation model of a butterfly species in their RSS design to ensure that the sites selected result in long-term persistence. Jiang, Swallow and Paton (2007) and Nicholson et al. (2006) evaluate the outcome of the RSS model by applying the selected site configurations to multi-species metapopulation models.

While most modeling analyses of determining optimal patterns of conservation abstract away from the budgetary source, Ando and Shah (2010) models a scenario in which the demand for conservation determines the budget of the conservation organization. People's willingness to pay for conservation declines with distance from the conserved location, which implies that conservation organizations can generate larger budgets if they locate their activities near population centers. In some settings, locations close to large populations may not provide high conservation benefits as compared to more distant locations, which sets up tradeoffs between the generating larger budgets for conservation and conserving more productive sites. This analysis finds that planners may optimally produce more fragmented reserve site patterns in finding a balance between conservation activities near people and near ecologically productive locations.

4.2 Economic Spatial Optimization by a Single Decision-maker.

One way for managers to directly address habitat fragmentation is to choose land parcels for conservation in a way that incorporates spatial patterns. Economists approach this problem differently than most of the RSS literature by incorporating real-world costs and complexities into the decision of conservation siting and land allocation. Decisions about land use are made by maximizing the value of land parcels or groupings of land parcels on a landscape, while considering the opportunity costs. Here land value includes both its private productive value and its social value in terms of recreation opportunities, ecosystem services production, and maintenance of biodiversity. Economists use spatial optimization to determine the best pattern of land uses, including habitat conservation, for a sole decision-maker to implement to provide the highest societal benefits. Within the context of such a sole decision-maker perspective, economic research may rely on a model of net benefits that reflects the fragmentation or pattern of habitat, may adapt a RSS method that includes an emphasis on pattern rather than individual species, or may incorporate an ecological simulation to determine the relationship of pattern and benefits. Other optimization approaches employ a spatial response function of land/ecosystem users to a conservation policy.

a. *Spatial Benefits Functions.*

When the decision maker knows how the pattern of habitat conservation contributes to the landscape habitat benefits, the spatial optimization of habitat benefits requires allocating different land uses to different locations. In an implicitly spatial framework, Wu and Boggess (1999) find that nonconvexities in the forest-watershed protection relationship imply that when budgets are limited, conservation activities should be focused on one watershed rather than split across multiple watersheds. Albers (1996) develops a stylized spatial-dynamic optimization model over a set of land units of tropical forest land management for a single land owner making land use decisions across several contiguous land parcels. Each parcel has its own value but the framework's incorporation of an additional value for creating contiguous preserved area leads to less fragmented habitat than without such connectivity values. That value does not always dominate and create an unfragmented landscape, however, because the value of configuration is one consideration in the land use decision rather than a constraint. A modified version of that optimal land allocation framework applied to Khao Yai National Park, Thailand finds that preserving the inner core and the contiguous ring of forest – a low level of fragmentation of habitat -- leads to the highest net benefits (Albers and Robinson 2007).

b. *Wildlife and Simulation Models within Optimization Models.*

In part because benefits from a pattern of habitat derive from wildlife's response to that pattern, many frameworks combine a model of wildlife behavior with a land use optimization framework rather than valuing habitat configuration directly. Hof, Bevers, and co-authors develop tools to find the optimal pattern of a landscape while accounting for ecological processes (e.g. Hof and Bevers (2002)). In one example, Hof and Flather (1996)'s framework selects the size and location of habitat patches on a coordinate plane to maximize the expected population of a species dispersed on the landscape, subject to constraints on the total area and number of patches conserved. The pattern of habitat matters because the expected species population is a function of the probability that patches are connected – reflecting an assumption about the impact of connectivity on species populations but not requiring contiguity for the definition of connected, which is based on distance. In addition, the analysis considers that the edges of any individual habitat patch can provide less effective habitat than more central areas, which tends to lead to larger patches and a less fragmented habitat in optimal land use patterns. In contrast, spreading habitat patches apart – creating a more fragmented habitat – can reduce the variance of the landscape's total population when threats to viability such as disease or fire are spatially correlated. The examples considered find optimal habitat locations to follow a "mixed strategy" of some "connected" or close-proximity habitat patches at a distance from other groups of patches.

Bevers and Hof (1999)'s spatial optimization model determines the best arrangement and timing for forest management in order to maximize species populations when forest edges lead to both positive and negative habitat impacts for the forest's wildlife populations. The analysis incorporates a model of wildlife habitat needs, such as nest sites, forage, and dispersal, and a reaction-diffusion structure into a constrained optimization problem with static and dynamic examples. Hof and Raphael (1997) use a static optimization model to determine the amounts of habitat per cell to protect in order to maximize owl protection. They estimate a "connectivity function" for their study area that is based on first order (meaning nearest neighbors only) queen (meaning neighbors in all directions) connectivity conditions and habitat conditions. They find optimal patterns of conservation for protecting owls and then critique these solutions based on the land ownership patterns of government and private lands in their study region.

c. *Resource Demand's Impact on Optimal Conservation Patterns.*

An extension of the land allocation literature considers the effects of neighboring human populations on nearby land preserves. For example, in low income countries where conservation area property rights may be imperfectly enforced, areas near the boundaries of parks often contain degraded ecosystems. Because the conservation benefits accruing from a park are a function of how (illegal) resource extraction degrades the habitat, the reaction of resource extractors to a park should optimally be considered within the siting decision (Albers, Maloney and Robinson 2017). Establishment of buffer zones – land surrounding preserves that can be exploited by local populations – can facilitate development and enhance the quality of the protected area. In a series of papers, Robinson, Albers and various co-authors model the spatial impact of such extraction on forest and park quality, which might be viewed as human-induced edge effects. Albers (2010) explores optimal buffer zone size under different assumptions about enforcing conservation of the protected area. In this, and related work, buffer zones create distance between populations and conserved land parcels, increasing the cost of extracting resources from the preserve, and disincentivizing habitat fragmentation.

Robinson, Albers, and Williams (2011) optimally divides a forested area into a protected area and a buffer zone, with legal extraction in the buffer zone causing resource degradation there, in a case with the park and buffer zone both generating ecosystem benefits. The model reveals tradeoffs between the size of the park and buffer zone that are sensitive to the functional form of the relationship between the level of extraction in the buffer zone and the resulting ecological services. Using a similar framework, Robinson, Albers, and Busby (2013) addresses the relationship between the size of the buffer zone and the level of illegal extraction, and thus degradation and fragmentation, of the park, in addition to discussing the interaction of enforcement and buffer zone size on landscape ecosystem service provision. The analysis demonstrates that policies to limit human-induced edge effects, such as planting or restoring degraded areas, can provide further protection to the core park area under some conditions but can also backfire in terms of increased degradation of the core area at some levels of resource restoration and buffer zone size. This line of research emphasizes that the optimal siting/sizing of parks and other protected areas in low-income countries requires incorporating the spatial processes of human extractors into decisions, just as ecological processes are considered in such decisions (Bode et al. 2015; Albers et al. 2017).

Several similar models of resource extraction decisions form a base to analyze how a protected area alters the location and amount of resource extraction through the displacement of leakage of extractor effort to other forest areas. That leakage (partially) offsets the conservation gains from the PA, but the impact of leakage on fragmentation or forest pattern remains less well-studied. Albers and Robinson (2011) demonstrate how managers can improve the pattern of forest degradation resulting from resource extraction by making spatially strategic choices about the location of beekeeping projects and enforcement patrols to control the pattern of leakage. Bode et al. (2015) combine a landscape model, a spatial resource extraction model, and a household utility model to examine the location and amount of leakage resulting from various protected area (PA) locations/sizes when biodiversity is distributed heterogeneously across the landscape. Their modeling results mimic observations in that the leakage often occurs near boundaries of new PAs, but the heterogeneous distribution of biodiversity complicates assessments of how costly the leakage is to biodiversity conservation. This framework does not measure fragmentation nor pattern's impact on biodiversity directly but makes a strong case for incorporating the reaction of people to PAs in the siting of PAs.

Recognizing that human activities cause disturbances that alter the pattern of habitat within protected areas, Sims (2014) uses a von Thunen-inspired framework of human-induced forest change to consider how patterns of enforcement within protected areas may lead to fragmentation. The analysis recognizes that human disturbances occur in response to attributes of the land but also of the management, particularly the level of enforcement against ecosystem-disrupting activities. All three considered patterns of enforcement (uniform, boundary, core) can lead to lower fragmentation than in unprotected areas but with different levels of success in different regions of the protected area. Enforcement in the core decreases fragmentation in the forest interior more than other enforcement approaches, in addition to creating the largest forest patch sizes, while boundary enforcement leads to the highest forest patch perimeter to area ratio (a measure of edge effects). In this analysis and presumably in many parks worldwide, fragmentation within protected areas occurs as resource extractors or land demanders make their location decisions based on the natural and economic characteristics – such as accessibility – of sites and in response to the perceived management or enforcement's impact on the expected value of activities at different locations. Just as Bode et al. (2015) and Albers et al. (2017) emphasize that park siting decisions must reflect the reaction of people in terms of their resource use, Sims (2014) demonstrates the importance of incorporating that response in the determination of management and enforcement location decisions to prevent fragmentation.

Though the largest driver of land use change and threat to biodiversity is human activity, RSS largely ignores the impact of humans on conservation efforts. Establishing a reserve in an area where humans are dependent on natural habitats for survival will have implications for the human population and success of the reserve. If the reserve is not well-protected, poaching could undermine conservation efforts. If the reserve is well-protected, human activities can be displaced to areas surrounding the reserve, degrading those habitats and isolating the reserve patch. As a result, economically and ecologically efficient RSS requires considering human responses to the established reserve in the optimization process (Albers, et al. 2017).

4.3 Patterns of Conservation with Multiple Agents.

While the decisions of a single conservation actor – whether private or public – form a significant portion of the academic literature and make a large contribution to the total amount and pattern of conservation worldwide, the overall pattern of conservation in a landscape often derives from the coordinated and uncoordinated activities of many groups.

a. *Multiple Conservation Actors.*

In some settings, individual landowners aim to manage land to provide conservation or amenity benefits that may be a function of the land use and conservation in the landscape beyond their parcel. Swallow, Talukdar and Wear (1997) extend Hartman (1976) in an optimal timber rotation model with non-timber forest amenity benefits to include multiple stands of different owners, with spatial interactions in the production of amenity benefits. The modeling framework is spatially implicit, and highlights how the interdependence between stands in the creation of amenity benefits alters timber management through changes in the optimal rotation length on a given stand. Similarly, many conservation organizations or agents undertake conservation activities on the same landscape, including settings with national to local government conservation agencies and private land trusts. Albers, Ando and Batz (2008) use a game theoretic model of private and public organizations' decisions about the location and amount of conservation to undertake on a landscape to provide the conservation public good. Analyzing the impact of the functional form of the production conservation benefits on whether public activities crowd in or crowd out private conservation, the model analysis examines the spatial pattern – agglomerated or fragmented – that results from the uncoordinated activities of sets of private and public actors. When both organizations value agglomerated patterns, sequential move games result in the social optimum while simultaneous move games can face a coordination failure and produce a more fragmented landscape than either organization desires. In contrast, when organizations have opposite values for agglomerated conservation, the order of actions largely determines the degree of fragmentation or agglomeration in the landscape. Across many settings, conservation agents make spatially strategic decisions in their conservation location choices in order to increase the total amount of conserved area and to create desired patterns. Using this modeling framework, Albers, Ando and Chen (2008) test how the relationships between private and public conservation in three U.S. states contribute to the pattern of conserved land. That analysis finds a high degree of agglomeration in private conservation overall but a range of public-private spatial relationships. In two states, public land conservation appears to "spatially repel" private conservation, generating a more fragmented reserve network, while in one state, California, public conservation "spatially attracts" private conservation, creating larger concentrations of reserves. Analysis of California's private and public network of reserves at a finer scale, however, finds that private conservation often increases the degree of fragmentation of the reserve network, albeit while increasing the total area conserved (Albers et al. 2012). A recent paper by Lawley and Yang (2015) builds on this literature by analyzing interactions between agencies purchasing conservation easements for prairie pothole habitat in Western Canada. Using high resolution panel data, they are able to assess how immediate adjacency crowds in or crowds out additional conservation, and how spatial interactions differ when there are multiple conservation agencies with similar mandates. They find crowding-in among private easements, with neighboring easements substantially increasing the probability of additional easements, but a small crowding-out effect of government protection.

b. *Patterns of Conservation from Multiple Non-Conservation Agents on a Landscape with Development or Land Conversion.*

Although conservation organizations making optimal location/pattern decisions contribute to the resulting landscape of conservation, the patterns of conservation in many landscapes may be largely determined by landowners making land conversion or development decisions without the goal of creating conservation public goods. A fruitful line of research uses models of development and land use decisions that incorporate a spatially-explicit ecological model to examine the impact of decisions and policies on the ecological system. In Bauer, Swallow and Paton (2010), a town planner maximizes the sum of development benefits – Ricardian land rents – subject to land use and ecosystem constraints on the likelihood of species persistence on the landscape and to social goals concerning several measures of ecosystem quality. To link the level and pattern of development to species survival, the analysis develops a spatially-explicit metapopulation model that incorporates both habitat patches and species dispersal matrix patches, with species moving through the dispersal matrix but facing connectivity issues due to development creating dispersal barriers. Although this analysis doesn’t target fragmentation directly, the species dynamics are a complex result of the spatial pattern of the intensity of development, including its fragmentation and connectivity. Using a similar model, Bauer and Swallow (2013) compare the optimal patterns of conservation in an urban-rural fringe setting to the preservation outcomes from other models, including the reserve site selection framework with its emphasis on full protection of habitat patches without limiting development in the dispersal matrix. Reflecting earlier optimization models that contain an ecological model, Lewis (2010) combines an econometric model of land use decisions with a simulation model of those stochastic decisions evolving the landscape (Polasky et al. 2008) across time, and then incorporates an ecological model to produce forecasts of localized and aggregate species extinctions that result from patterns of development.

In contrast to analyses that optimize particular objective function to be optimized, in an influential paper, Polasky et al. (2008) identify an efficiency frontier between economic production and expected species protection for the Willamette Valley, Oregon. Although the economic values accrue linearly from adding up parcel production values, the framework defining species persistence incorporates species-specific habitat requirements and a connectivity score based on the distance between habitat patches and the dispersal characteristics of the species. The efficiency frontier enables comparison of landscape patterns that produce different combinations of economic and species outputs, with the species levels defined by the spatial characteristics of habitat within those patterns, in addition to efficiency comparisons between current or past land use patterns with the frontier's patterns.

c. *Agent based modeling*

Understanding and explaining historic patterns of fragmentation using existing preferences and incentives can assist in the design of future policy to reduce environmentally costly land use patterns. Agent based models (ABMs) simulate numerous simultaneous decisions of individual "agents", incorporating local and regional institutions and interactions (often with lags) among agents, at the micro-level, to produce patterns observed at the macro-level. The interactions of decisions and the natural and social systems modeled can generate unanticipated results and emergent properties. The decision rules for agents reflect varying degrees of economic theory about agent decisions and interactions among those decisions. Within the habitat fragmentation literature, ABMs are used to model one-way interactions and/or feedback loops between individual behavior and environmental conditions. Spatial ABMs allow for heterogeneity in the natural landscape, making them useful for analyzing how fragmentation patterns occur, given human behavior. Models can be parameterized using stylized theories from the social sciences or empirical observations, and allow for various assumptions about preferences, rationality, adaptation, and learning.

While not explicitly measuring the impact of habitat fragmentation, a large number of ABMs explore how patterns of fragmentation occur. This body of work suggests that if the decision frameworks that create patterns of fragmentation is understood, policies can be designed to change how future fragmentation occurs. Parker and Meretsky (2004) model patterns of land use when conflicts between agricultural and urban land uses affect the land rents and development. They find that conflicts between rural and urban land uses can create inefficiently large areas of urban-rural edges and sprawl. The results of their work have implications for urban development and land use planning.

Assumed agent preferences and distribution of those preferences play a large role in ABM simulation outcomes. Earlier work, including Brown et al. (2004), assume agents have homogeneous preferences. Brown and Robinson (2006) incorporate survey results of attribute preferences (i.e. aesthetics, distance to services) into an ABM of residential development. The authors test how different distributions of preferences affect fragmentation in residential development. Modeling preference heterogeneity resulted in greater fragmentation and larger edge areas. Arima et al. (2008) simulate the emergence of road networks and fragmentation patterns through logging activity in the Brazilian Amazon. The authors use geospatial data to identify areas containing high-valued timber and simulate resulting dendritic patterns of road construction. The simulations generally replicate the observed patterns of road building, but do not include key realistic elements such as spatial heterogeneity in road building cost. To understand a different pattern of development, Arima et al. (2013) model radial patterns of road networks developed around existing settlements.

ABM frameworks have been used to test hypotheses about patterns of land use, measure landscape function, and perform policy analysis. A number of articles model the impact of industry production decisions or policies on fragmentation. How measures of fragmentation translate to ecological outcomes varies significantly across the literature. Parry et al. (2013) simulate the effect of crop choices on fragmentation patterns, and bird survival. Another approach is to simulate the effects of policies on individual behavior. Polhill, Gimona and Gotts (2013) evaluate how conservation policies in combination with decisions made based on crop prices affect landscape-level species richness. ABMs can also be used to compare fragmentation outcomes under various policy designs and scales (global, regional, local) (Caillault et al. 2013). Bell et al. (2012) use ABM to understand how monitoring of logging concessions may reduce illegal timber harvesting but drive more fragmentation. Timber operators who are forced to harvest more selectively to comply with legal requirements will harvest over a larger area in response, creating more road networks that drive fragmentation.

ABMs are often criticized for the assumptions made about agent decision-making and the use of spatial and temporal lags in place of optimization or game theoretic interactions among agents. In addition, the institutional and individual realities of low income countries, such as subsistence, incomplete markets, and unique property rights settings, would need to be added to an ABM framework to accurately represent land use decisions in developing countries. Methods besides optimization can be implemented to simulate decision-making. However, varying assumptions across different ABM models complicates the interpretation of ABM output. Sensitivity analyses are critical to understanding how results depend on chosen behavioral assumptions, and for validation and verification. Because many ABMs are large, additional simulations are computationally expensive and produce large datasets. Failure to validate or verify applications of ABMs with empirical evidence poses the question of whether ABM simulations represent socio-ecological systems well enough to justify such a complex method.

5. Economic analysis for policy and mechanism design for land use patterns

Socially optimal patterns of land use may often be different from those arising from individual landowner decisions, so managers must use policy tools to influence the allocation of land for specific uses. Landowners who are compelled or choose to preserve land must forgo the benefits of alternative land uses (agriculture, housing development, resource extraction) and incur an opportunity cost from this forgone use. Identifying landowners' willingness to accept (WTA) a payment to retire land parcels that reverse or reduce fragmentation is an ongoing challenge, because neither the landowner nor the manager has complete information about this opportunity cost. The economics literature takes a variety of approaches to developing and testing theories of private landowners' land use decisions to achieve conservation and reduce fragmentation. These include ex-ante models of policy, often drawing on econometrically-based models of past conversion behavior; as well as ex-post evaluation of policy using quasiexperimental comparisons between areas with and without policies that have already been implemented.

a. Direct regulation: Protected Areas and Zoning Requirements

A core justification for land set-asides is that they can protect large, contiguous areas of habitat. Yet as suggested by the modeling literature, interactions between resource users and protected area managers complicate this assumption, particularly when policies are incompletely enforced. Some of the first empirical literature on fragmentation sought to understand protected area impacts. Sánchez-Azofeifa et al. (1999) find the extent of fragmentation inside protected habitats is significantly lower than in unprotected habitats in Costa Rica. Liu et al. (2001) find a policy failure in China; they find more fragmentation occurred in habitat reserved for giant panda conservation. Nagendra et al. (2008) compare transitions across land cover categories and fragmentation patterns from 1989 to 2000 in the Chitwan valley district of Nepal. They find that areas of forest under community management were more successful at protecting forest cover, limiting fragmentation and allowing regrowth. Southworth et al. (2004) calculate multiple fragmentation metrics within the core zone, boundary zone and outside of a national park in Honduras and find substantially lower fragmentation in the core area. As they point out, however, the core area is also one with very high elevation and steep slopes, and this inaccessibility may explain much of the difference across land management types.

Responding to concerns that these analyses do not account well for underlying differences in the landscapes where parks tend to be placed, Sims (2014) illustrates how causal inference techniques can be brought to the fragmentation literature. The research divides landscapes into "microlandscapes" and compares fragmentation metrics between matched microlandscapes in and out of northern Thailand's protected areas. Sims (2014) finds that wildlife sanctuaries and national parks prevent both forest loss and fragmentation. Consistent with the theoretical framework described earlier, the higher level of restriction and core-focused enforcement in wildlife sanctuaries than national parks are associated with higher levels of avoided forest fragmentation. Recent research in the US uses historically de-gazetted areas that were originally part of Yosemite to evaluate fragmentation impacts. They also find that protection within the national park led to substantially less fragmentation than both formerly protected and never protected areas (Golden Kroner, Krithivasan and Mascia 2016).

Zoning is another form of direct regulation with substantial potential impacts for fragmentation. Freeman and Bell (2011) compare buildout patterns under two types of zoning: “cluster subdivision” in which a fixed percentage of land must be left as open space, versus “conservation subdivisions” in which land of the highest ecological value must be identified and protected. They find that the conservation-oriented zoning can increase habitat connectivity (in this case for wood frogs in Maine), even when the amounts of land development versus protection are the same. This highlights the importance of zoning processes that explicitly incorporate spatial planning. Wrenn and Irwin (2012) also find that zoning is a more effective way to ensure less fragmented outcomes of land development than relying on market-based incentives. The authors use data on residential development near Baltimore, Maryland and heterogeneity in zoning and land prices to model and predict development with additional land development fees or changes in the allowable density of development. The key reason for the greater effectiveness of quantity-based regulation is the highly-inelastic demand for land by developers.

b. *Incentive-based mechanisms: Subsidies, Taxes, and Payments for Environmental Services*

Property tax incentives have been used to enhance habitat conservation, particularly in forests in the United States. Locke and Rissman (2012) measure the fragmentation outcomes that develop on landscapes containing mosaics of public and privately owned forests in Wisconsin. They find that although connectivity was not a goal of the tax policy, private landowner enrollment in the forest tax program clustered around public lands. Although not aimed specifically at habitat fragmentation, Cho, Roberts and Lambert (2016) use a spatial discrete-choice model for land conversion decisions and data concerning land development to evaluate the potential impact of a dual-rate property tax on the pattern of urban development including open space and sprawl, with implicit impact on the degree of habitat fragmentation.

Paying landowners for retiring or conserving land through “Payments for

Ecosystem Services" programs is the most straightforward approach to increasing conservation and ecosystem services on private lands. For example, the Conservation Reserve Programs (CRPs) is a US governmental payment for ecosystem services that operates through incentives for land retirement, where landowners submit bids for enrollment of acreage. Farm operators enrolled in the program receive annual rental payments for retiring environmentally valuable acreage for 10 to 15 years. Initially, CRPs were intended to mitigate soil erosion, but have since been developed for water conservation and wildlife habitat conservation. Other payments for ecosystem services programs that offer fixed payments in exchange for maintaining or improving natural resources are now a global phenomenon, with national-scale programs operating for at least five years in Mexico, China, Costa Rica, Ecuador, Peru, and Vietnam, and hundreds of small-scale programs in operation. Core concerns about payments programs in the context of fragmentation include how to design payments and targeting, and whether they can successfully slow fragmentation, given the focus on private owners and the difficulty of enrolling contiguous parcels. The spatial pattern of retired land parcels is directly related to the ecological value of the natural habitat; and larger areas protected by payments programs can support more species than smaller ones. If private landowners are free to choose but do not coordinate which parcels of land are designated for conservation, the resulting habitat patches may be small and isolated. A challenge in designing payments is incentivizing landowners to voluntary contribute parcels in ways that increase spatial connectedness of habitat. Additional payments to landowners for reserving land parcels that are adjacent to other conserved parcels—in order to increase the overall size of the preserve--have been explored both theoretically and experimentally.

Lewis and Plantinga (2007) compare the cost-effectiveness of incentive-based land conservation using a uniform subsidy and a spatially heterogeneous subsidy. The analysis combines an econometric model with a GIS-based landscape simulation to determine forest fragmentation outcomes in the coastal region of South Carolina. Although the spatially heterogeneous subsidy leads to less fragmented patterns of forest, it is more expensive than the uniform policy, which partially offsets the additional conservation benefits achieved with lower fragmentation. This analysis also reveals that the marginal costs of reducing fragmentation are significantly lower on landscapes with larger initial amount of forests. Lewis, Plantinga and Wu (2009) develop a model of spatially heterogeneous optimal afforestation subsidy levels, based on initial landscape conditions. Due to the convexity of marginal costs, corner solutions of converting all or none of a landscape to forest emerge. These results suggest that areas targeted for afforestation should be those with a large amount of existing forest.

Nelson et al. (2008) integrates econometric models of land use, policy simulation models, carbon sequestration models, and species conservation models to simulate the response of landowners to incentive-based policies to increase carbon sequestration and/or species conservation in the Willamette Valley, Oregon. They compare results from two species conservation models, one that simply relates species conservation to the proportion of the area conserved and one that incorporates the spatial habitat configuration needs of the species. The species conservation success of a policy with the more complex species model proves quite sensitive to which landowners participate in the incentive policy. Complicating the incentives schemes further, the optimal conservation payment varies across landowners and can be a function of both the landowner and the landowner's neighbor's land use decisions.

Smith and Shogren (2002) propose an additional payment, an agglomeration bonus, when neighboring landowners retire land at their shared property border. Parkhurst et al. (2002) tests the effectiveness of using an agglomeration bonus in an experimental setting. They find that additional payments can result in the first-best outcome. Introducing communication between players increased the likelihood of arriving at the first-best outcome and efficient spatial pattern of conservation. Experiments by Parkhurst and Shogren (2007), Warziniack, Shogren and Parkhurst (2007), and Parkhurst and Shogren (2008) vary the complexity of the desired spatial pattern of conservation, ability of players to communicate, and available information sets. The success of the agglomeration bonus is dependent on information and communication. In a real-world setting, both information and communication are critical to successful conservation using agglomeration bonuses.

Implementing agglomeration payments in conservation programs requires further understanding of how realities of land ownership such as number of neighbors that need to coordinate and uncertainty affect the success of agglomeration payments. Banerjee, Kwasnica, and Shortle (2012) test the effect of group size by varying the number of players that need to coordinate in an experiment using agglomeration payments. They find that smaller groups can arrive at the optimal land reservation configuration, while the larger groups often fail to achieve the desired reserve configurations. Another potential shortcoming of agglomeration payments is the presence of information rents and rent-seeking behavior among landowners. Banerjee et al. (2014) vary information given to players about desired spatial configurations in an iterative auction experiment, and find that sharing information on the spatial configuration reduces cost-effectiveness due to rent-seeking behavior, but does not reduce the efficiency of the auction format. Overall, this line of work demonstrates that mechanisms that encourage landowner coordination or revelation of costs and actions can improve the patterns of land conservation and the provision of spatially-based ecosystem services (de Vries and Hanley 2016).Versions of agglomeration payments occur in a number of real-world applications. For example, when enrolled in a Conservation Reserve Enhancement Program (CREP), landowners receive a one-time additional payment when they retire land near other acres that are already enrolled in a conservation program. Starting in 2010, Mexico's federal Payments for Hydrological Services Program has awarded extra priority points to applicants who are in the same watershed as others receiving payments for ecosystem services (Sims et al. 2014). When incentives are correctly designed, contiguous habitats can be created, but at what cost? Drechsler et al. (2010) evaluate whether agglomeration payments are cost effective in a butterfly conservation program in Germany. They find that agglomeration payments were cost effective and elicited better conservation outcomes than homogeneous payments. Wätzold and Drechsler (2014) find that spatially homogeneous payments reduced the cost-effectiveness of conservation programs.

Developing efficient spatial land conservation payment mechanisms is problematic because landowners' WTA compensation for conservation is unknown. A large economics literature describes the difficulties of defining payment or subsidy schemes that arise due to asymmetric information between land owners and the payment program organizations. Much of that literature emphasizes the use of auctions to reveal landowners WTA for conservation contracts. In a competitive auction, participants are less likely to overstate their WTA for land preservation. In theory in uniform-price auctions, competitive bidding nearly eliminates information rents, increasing cost-effectiveness but budget constraints complicate the effectiveness of auctions. Latacz-Lohmann and Van der Hamsvoort (1997) model a bidding framework for conservation contracts. They find single-round auctions are effective in eliciting WTA from individual landowners. When multiple round auctions are used, bidders gain information about the common value of land, and do not bid based on their own perceived land value. Schilizzi and Latacz-Lohmann (2007) design an experimental framework to compare the performance of auctions and fixed- subsidies in conservation. The evaluation criteria used in the analysis are cost-effectiveness, existence of information rents, and economic efficiency. The authors find that using these criteria, auctions perform better that fixed subsidies but the advantages vanish as the auction is repeated and bidders learn to bid strategically.

Asymmetric information also creates uncertainty in the resulting spatial pattern of conservation that will arise for a given policy. Lewis et al. (2011) measure the effectiveness of incentive-based voluntary land conservation policies in combination with a spatially explicit model of biological benefits. The authors combine an econometric estimation of returns to land use to estimate distributions of landowners' WTA for conserving land. These estimates are then used in a spatially explicit optimization model to determine the pattern of land use that will generate the highest overall biodiversity score. The ecological outcomes of several different incentive-based policies are evaluated in the framework. The authors conclude that using a mechanism such as an auction that elicit landowners' WTA with spatially explicit environmental/ecological modeling frameworks can produce the most efficient patterns of conservation. In the absence of auction mechanisms, payments can still be differentiated across space. Wätzold and Drechsler (2014) find that spatially homogeneous payments reduced the cost-effectiveness of conservation programs.

Auctions also create opportunities for improving outcomes from payments/subsidies in settings in which spatial configuration of land uses contributes to the conservation benefits produced – whether these configuration goals are simply given or are derived as an optimal pattern. Iftekhar and Latacz-Lohmann (2017) compares a two price mechanisms in auctions and four bid selection criteria to generate contiguous wildlife zones across multiple land holdings, both in a framework and case study. In addition to exploring the relative performance of different auction types, the analysis reveals the importance of uncertainty about the number of competing groups and conservation costs, and the role of information, in achieving conservation. Polasky et al. (2014) develop an auction mechanism that allows the managing organization to employ a payment scheme that achieves the socially preferred pattern of conservation with spatially-dependent ecosystem services because it induces land owners to reveal their true cost information. Lewis and Polasky (unpublished) develop a framework in which a land use planner can implement their optimal landscape pattern based on an auction mechanism that reflects changing ecosystem service provision over time through climate change. Drechsler (2017) compares social welfare and budget efficiency outcomes between (agglomeration) payment and auction frameworks in a theoretical framework. The author concludes that there is a tradeoff between increased welfare and budget efficiency; the agglomeration payments achieve greater budget efficiency, while auctions improve social welfare. For a desired spatial pattern of dispersed reserve sites within agriculture, Bamière, David and Vermont (2013) compare an auction scheme to an agglomeration "malus" program (akin to a negative agglomeration bonus) and determine that the auction improves cost-efficiency of uniform subsidies while the malus performs best for achieving the spatial pattern albeit at higher cost.

Despite their widespread application, little empirical analysis of existing incentive-based policies' effectiveness in reducing habitat fragmentation exists. Hellerstein (2017) provides a detailed analysis of CRP enrollment mechanisms and trends, and discussion of alternative bidding mechanism, but without focus on the CREP impact on fragmentation. Work by Ramirez-Reyes et al. (unpublished) evaluates the impacts of Mexico's Payments for Hydrological Services program on fragmentation using forest cover change from 2000 to 2012 and comparisons between landscapes with a high share of PES versus similar, matched landscapes with a low share of PES. They find that the number of forest patches, amount of forest edge, forest islets and the largest area of forest loss increased by only half as much across time in areas with PES versus control areas.

c. Incentive-based mechanisms: Tradeable development rights.

Tradeable development rights (TDRs) build on the conceptual success of tradable permit programs in generating efficient outcomes in other environmental settings, including fisheries and pollution. A regulator determines the maximum number of development projects that can occur within a given region and allocates development permits to landowners within the region. Landowners can buy and sell their development rights, depending on whether development in their region is below the maximum number of projects. The goal of TDRs is to make development rights scarce, so that development projects occur on lands with the highest development values. TDRs do allocate development permits efficiently from a development perspective, by moving permits from low value to high value areas, but they do not discriminate between natural habitat qualities, and can result in environmental degradation.

Mills (1980) proposes zoning regulations can be used in combination with TDRs to include ecological value in the decision to locate development. Government agencies determine which lands should be protected, and landowners are “compensated” for the loss of use of those lands by selling their development rights. An example of a successful TDR program is the New Jersey Pinelands Development Credit program, which sought to redirect residential and commercial growth from the Pinelands area (a key state watershed area) to defined regional growth areas (New Jersey Pinelands Commission 2017; Tripp and Dudek 1989).

One potential issue with heterogeneity in environmentally valuable land is the ‘shoot, shovel, and shut up’ treatment of the environmental problem; if it is costly for landowners to participate in conservation efforts relative to development, landowners have incentive to alter land attributes to reduce the value for conservation. Parkhurst, Shogren and Crocker (2016) propose that land management goals should be twofold, design incentives for 1) retiring land area 2) desired spatial configurations of retired land. The authors propose a system of tradeable set-aside requirements (TSARs), with agglomeration bonuses. Landowners are assigned TSARs, and each TSAR requires landowners to conserve one unit of land. TSARs can be traded between landowners and the agglomeration payment incentivizes landowners to coordinate on the spatial arrangement of conserved parcels. The authors test this framework in an experimental setting and find TSARS increase cost-effectiveness and economic efficiency in conservation efforts.

TDRs can be difficult to practically implement. Legal, financial, and administrative capacities need to be developed before development rights can be traded. Interdisciplinary efforts also need to be employed to determine the number of permits to be transferred and measure the effectiveness of the TDR program. Low transaction costs are important in the efficiency of the program, which suggests that the method for distributing and trading permits needs to be carefully designed.

6. Comments and Directions for the Economics of Fragmentation

Insights about the economics of habitat fragmentation are found in many types of research including: empirical characterization of fragmentation; analysis to understand land use patterns, with or without an emphasis on habitat pattern; policy analysis that addresses land use patterns; and frameworks that directly or indirectly examine the role of habitat pattern in providing species protection and other ecosystem services. As described above, that research includes empirical analysis, optimization, and simulation analysis – often in combination.

In recent years, environment and natural resource (ENR) economics – including land economics – has increasingly embraced spatial economic or econometric models in general. Still, spatial economics poses challenges to traditional analytical modeling and to data analysis. Given the importance of the temporal aspects of resource use and management, research into the economics of habitat fragmentation often requires integrating spatial and dynamic analysis, which generates still further complications. In contrast to ecological models' depiction of large landscapes and long timeframes, forward-looking human decisions and policy analysis involve incorporating dynamic-spatial optimization for many small parcels, which leads quickly to dimensionality issues that the ecological models don't face. Solving these models to inform spatial-dynamic policy often involves sophisticated computational methods. As ecologists, economists, and computer scientists work together, economic policy analysis of landscape and habitat patterns will continue to improve.

Although the SLOSS debate identifies both pros and cons to more fragmented habitat, much of the ecological literature emphasizes the downsides to fragmentation, and much of the policy literature follows that direction by establishing objectives or constraints that consider fragmentation to be negative. For example, surprisingly little Reserve Site Selection research incorporates both the countervailing forces of benefits from connected habitat areas, such as broader reproductive options, and the benefits from separated habitat units, such as lower disease transmission. Economic models are well-suited to assessing tradeoffs, evaluating the dominance of particular forces in various situations, and revealing the outcome from the sum of a range of interacting factors. In particular, optimization models that incorporate an ecological simulation model can allow for sets of ecological and economic factors to reveal their relative importance and/or synergistic interactions. For both modeling and empirical analysis, economic models that determine the optimal habitat pattern or policy as the result of complex interactions without assuming that fragmentation is negative should prove more useful than constraint-based or fragmentation-minimizing frameworks that do not permit tradeoffs. These frameworks will also better inform future empirical analyses, which to date have generally assumed that fragmentation is economically undesirable because of the lost social benefits from ecological health.

Some optimization models for land conservation base decisions on costs and benefits of different conservation configurations, which requires spatial ecosystem service production functions or other benefit relationships as a function of both size and pattern of habitat. In simpler landscapes or ecosystem services like carbon storage, these benefit functions of configuration may be readily represented with metrics of patterns or bonus values to neighboring habitat areas that reduce edge. In more complex settings, spatially explicit ecological simulation models embedded in optimization models obviate the need for simple functional relationships between pattern and outcome because the integrated model captures the relationships. Still, spatial-dynamic optimization over a complex, stochastic simulation model can prove much more complicated to solve and evaluate than the more direct pattern to benefits frameworks. One direction for future work includes regression analysis of the outputs of pattern-specific simulation models to estimate functional relationships between outcomes – such as wildlife populations – and habitat patterns that could then be incorporated directly into optimization or policy frameworks to lower the computational requirements of finding solutions. In an additional complication, however, different species respond to habitat configuration differently, which makes the choice of species considered in the simulation analysis an important driver of the optimal landscape structure.

Economic analysis of fragmentation or landscape habitat pattern differs from other disciplines' approaches in several ways but most importantly in that people's decisions and activities, often in response to policies, contribute to the landscape. Ecologically-focused research to define the size/shape of conservation areas or to target fragmentation prevention activities often abstracts away from how these goals can be achieved or at what cost. The costs of purchasing land may not reflect the true total costs of preserving a habitat parcel because people may require disincentives provided by monitoring and penalties in order to reduce their resource and land use despite having no legal right to that land, which implies ongoing monitoring and enforcement costs. For example, as above, spatially explicit models of people's decisions to degrade or convert habitat reflect the people's response to the resource quantities/characteristics, costs, and enforcement. Similarly, even econometric analyses of habitat fragmentation often have limited policy levers because explanatory variables are site-specific rather than specific to people's decisions. Future empirical analysis will have higher policy relevance as analysts incorporate more pattern-based explanatory variables and more economic data about people's behavior, which will require collecting less aggregated socioeconomic information. In addition, economic models of people's decisions about both location and pattern of land use, paired with data about those decisions, will improve our understanding of the drivers of fragmentation and the likely impact of policies on landscape pattern.

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