ALLOCATION OF LAND AT THE RURAL-URBAN FRINGE USING A SPATIALLY-REALISTIC ECOSYSTEM CONSTRAINT

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INTRODUCTION
Development in rural-urban fringe communities is increasing with the potential to damage healthy ecosystems and endanger the long-term persistence of resident flora and fauna (Heimlich and Anderson 2001; Daniels 1999; Maestas, Knight, and Gilgert 2003; Miltner, White, and Yoder 2004). Development affects all species of wildlife including mammals (Harrison 1997), birds (Lindsay, Gillum, and Meyer 2002), and amphibians (Woodford and Meyer 2003). Environmental impacts of development include loss, degradation, and fragmentation of wildlife habitat, increased air and water pollution, increased soil erosion, and decreased aesthetic appeal of the landscape (Johnson 2001). Roads, in particular, have a dramatic impact on wildlife by blocking migration routes, making habitat near roads unacceptable due to noise and pollution and road kills from passing traffic (Forman and Deblinger 2000; Haskell 2000; Romin and Bissonette 1996; Trombulak and Frissell 2000). Habitat loss and fragmentation is thought to be one of the primary causes of species extinction today, and is considered a research priority for conservation biologists (Davies, Gascon, and Margules 2001).

The largest growth in development is currently occurring in exurban communities (Davis, Nelson, and Dueker 1994; Lamb 1983). Exurban communities are heterogeneous landscapes made up of farms, suburban-style subdivisions, large-lot residential developments, commercial centers, and undeveloped open spaces (Nelson 1992). Exurban areas have increasingly become zones of conflict as conservation and development uses compete for the same finite land resource and wildlife habitat becomes increasingly fragmented (Wiens 1996). Concern over conflicting land uses has reached all the way to the federal level in the United States (United States Senate 2003).

Current land use policies rarely incorporate features of landscape-scale ecosystem health (Burke and Gibbons 1995; Miltner, White, and Yoder 2004; Willson and Dorcas 2003). For example, wetland policies focus on protection of individual wetlands, but at the same time provide incentives for higher-intensity development of upland habitat (Hardie et al. 2000; Swallow 1994; Semlitsch 1998; Semlitsch and Bodie 2003). Many wetland species, such as pond-breeding amphibians, spend much of their life cycle in these upland habitats either over-wintering or dispersing to other wetlands across the landscape (Semlitsch 2000). Development and fragmentation of upland areas decreases the long-term viability of these species by reducing the quantity and quality of upland habitat and decreasing dispersal success (Arnold and Gibbons 1996; Lehtinen, Galatowitsch, and Tester 1999; Vos et al. 2001; Vos and Chardon 1998). Similar problems occur in the preservation of reserve networks where only core reserves are protected without consideration for the quality of the intervening landscape.

Solutions to these problems require an ecosystem management approach that achieves combined ecological and economic objectives. The research reported here evaluates the potential for development in exurban communities while simultaneously maintaining a sustainable level of ecosystem health.[1] The study develops a spatially-realistic conceptual model that integrates economic and ecological principles to determine the optimal allocation of land between development and preservation uses.

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[1] We distinguish here between ecological integrity, a pristine condition which applies to wilderness areas, and ecosystem health, a flourishing condition which applies to areas shared jointly by human and non-human species (Karr 1996, 2000; Rapport, Costanza, and McMichael 1998).

Historically, two different economic theories have been used to explain land allocation decisions: (1) von Thunen's locational rent model (Hall 1966; von Thunen 1875; Alonso 1964), from which the bid-rent model evolved, and (2) Ricardo's differential rent model (Ricardo 1911). In the von Thunen model, land is homogeneous in terms of quality and land rent is a function of distance from the city center, with the basic assumption being that the farther away from the city the greater the transportation costs. Higher-valued land uses (i.e., those that accrue the highest rents) are found closest to the city core. In contrast, the Ricardian (or differential) rent model uses parcel quality rather than distance to city center in determining land rents. In this model, parcels located at the same distance from the city center may be heterogeneous in terms of land quality. Higher quality land receives higher land rents than lower quality land, for the same land use. Factors affecting land quality include type of soil, slope of terrain, amount of forest cover, presence of scenic vistas, and availability of public services, among others. The importance of particular quality factors varies by land use type. For example, scenic vistas would be valued more highly for residential land use than for agricultural land use. In the analysis performed here, the von Thunen land rent model identifies the geographic area of concern (exurban communities at the urban-rural fringe), while the Ricardian land rent model identifies the heterogeneous land values *within* the geographic area of concern.

While economic models typically focus on monetary benefits and costs, ecological models typically focus on long-term viability of species or other indicators of ecosystem health. A number of approaches have been used to incorporate ecological "values" into economic analyses. For example, hedonic housing studies, recreational travel-cost models, and contingent valuation surveys have all been used to estimate values of non-market public goods such as open space (Bates and Santerre 2001; Geoghegan 2002; Irwin 2002; Johnston et al. 2001; Lutzenhiser and Netusil 2001; Rosenberger and Loomis 1999). Unfortunately, attempts to quantify the entire economic value of ecosystem services are often difficult to accomplish or generate substantial controversy (Swallow 1996; Toman 1998; Berrens 1996). Because of the difficulty in measuring non-market benefits of ecosystem health, an alternative "safe minimum standard" approach may be used (Bishop 1978; Randall and Farmer 1995; Ciriacy-Wantrup 1952). With this approach, a government agency establishes a standard or constraint that guarantees a particular level of safety. For example, a safe minimum standard approach is used by the Clean Water and Clean Air Acts to protect human health, whereby various pollutants are not allowed to exceed specified levels. Similarly, the Endangered Species Act protects non-human species from extinction. As society increases its understanding of ecological processes and environmental conditions, standards are modified (strengthened or relaxed) to reflect this new information.

One way of modeling a safe minimum standard is through the use of an ecological constraint. Ecological constraints have been used in the modeling of both renewable and non-renewable resources (Albers 1996; Roan and Martin 1996; Yang et al. 2003). Albers (1996) models management of tropical forests using ecological constraints to reflect both spatial interactions across forest plots and the irreversibility of some forest land uses. Roan and Martin (1996) model mineral production and waste reclamation as joint products subject to the traditional ore depletion constraint and an additional ecosystem constraint that limits the amount of water pollution released. Yang et al. (2003) model the cost-effective retirement of cropland subject to a constraint that limits sediment loading of local rivers. In each of these studies, the ecological constraint provided insights that weren't available from the corresponding traditional model

without the constraint. This study develops a theoretical model that incorporates an ecological constraint on the development of land at the urban-rural fringe.

Some economists view a spatial component as critical for land use modeling and policy analysis (Bockstael 1996; Bockstael et al. 1995; Irwin and Geoghegan 2001). A small number of ecological-economic studies have utilized metapopulation dynamics as a spatially-explicit ecological component (Brown and Roughgarden 1997; Sanchirico and Wilen 1999, 2001, 2001; Smith and Wilen 2003). Metapopulations consist of groups of local subpopulations distributed throughout a patchy environment, with each subpopulation occupying its own patch and exchanging individuals through a dispersal process (Hanski 1999). Local subpopulations can go extinct and patches can be re-colonized without threatening the overall viability of the entire metapopulation.The land allocation model developed here establishes links between long-term metapopulation persistence and of development through an ecological constraint. A social planner seeks to maximize the benefits of development (or, alternatively, minimize the opportunity costs of foregone development) while guaranteeing a certain likelihood of long-term metapopulation persistence across the landscape that accounts for the changes to habitat patches and species dispersal success brought about by development.

METAPOPULATION MODEL
Metapopulation theory has been used to analyze and predict population processes for a variety of species including mammals (Moilanen, Smith, and Hanski 1998; Sweanor, Logan, and Hornocker 2000; York, Merrick, and Loughlin 1996), birds (Akcakaya and Atwood 1997; Akcakaya et al. 2004; Foppen, Chardon, and Liefveld 2000; Gutierrez and Harrison 1996), insects (Briers and Warren 2000; Wahlberg, Moilanen, and Hanski 1996), and amphibians (Carlson and Edenhamn 2000; Gill 1978; Pope, Fahrig, and Merriam 2000; Sjogren-Gulve 1994; Vos, Ter Braak, and Nieuwenhuizen 2000). The majority of these metapopulation studies focus on the conservation of endangered species. However, metapopulation theory can also be used to develop conservation strategies for common species.

<u>A Spatially-Realistic Metapopulation Model</u>
Ilkka Hanski and colleagues have developed a metapopulation model that allows patch areas and distances between patches to vary according to a spatially-realistic landscape structure (Hanski 1999; Hanski and Gyllenberg 1997; Hanski and Ovaskainen 2000; Moilanen and Hanski 1998; Moilanen and Nieminen 2002; Ovaskainen 2003; Ovaskainen and Hanski 2003, 2001; Hanski and Ovaskainen 2003). The Hanski model is an *occupancy model*, based on the presence or absence of a species, rather than a *count model*, based on the number of individuals. One of the major advantages of occupancy models is that they only require one or two years of empirical data collection and variables for which data are easy to collect (Hanski 1999; Sjogren-Gulve and Hanski 2000). Occupancy models are particularly useful for ranking patch-scale management alternatives, such as which patches to preserve in a conservation reserve network. The "size" of an occupancy-based metapopulation is measured by the proportion of occupied patches in the habitat patch network or, alternatively, the probability that patches will be occupied (Hanski 1999). In the deterministic, spatially-realistic metapopulation model, the change in probability

that any given patch is occupied is a function of local colonization and extinction rates that are different for each patch:

$$\frac{dP_i}{dt} = C(\mathbf{P})_i(1 - P_i) - E_i P_i \qquad \text{for i=1 to N} \qquad (1)$$

where P_i is the probability of patch i being occupied, $C(\mathbf{P})_i$ is the probability of patch i being colonized, E_i is the probability of patch i going extinct, and $\mathbf{P}$ is the vector of occupancy probabilities for all N patches in the network. The equilibrium (i.e., long-term) probability of occupancy of patch i, determined by setting equation (1) equal to zero, is given by:

$$P_i^* = \frac{C(\mathbf{P}^*)_i}{C(\mathbf{P}^*)_i + E_i} = 1 - \left[\frac{E_i}{C(\mathbf{P}^*)_i + E_i}\right]. \qquad (2)$$

Thus, the long-term probability of persistence of an individual patch is dependent upon the long-term probability of persistence of all the other patches.

Colonization of Empty Patches

Colonization of an empty patch depends on three things: (*i*) the number of dispersers leaving currently occupied patches, (*ii*) the ability of these dispersers to successfully traverse the landscape between patches, and (*iii*) the ability of these dispersers to find and become established in the empty patch. The patch-specific colonization rate, $C(\mathbf{P})_i$, may be represented as a sum of the contributions to colonization from each of the other patches:

$$C(\mathbf{P})_i = cg(A_i, H_i)\sum_{j \neq i} P_j g(A_j, H_j) f(d_{ij}, B_{ij}) \qquad (3)$$

where $g(\cdot)$ is the *effective area* of patch i, $f(\cdot)$ is the *effective distance* between patches i and j, P_j is the probability that patch j is occupied, and c is the species-specific colonization rate parameter that measures the ability of the species to colonize empty patches. Effective areas are functions of patch size, A, and habitat quality, H, allowing for heterogeneity of patches across the landscape. Thus, effective areas act as proxies for the number of individuals in a given patch; larger patches and patches with higher quality have larger local populations and thus produce more emigrants (Fleishman et al. 2002; Moilanen and Hanski 1998). Larger patches and patches of higher quality also attract more immigrants and are more likely to support successful re-colonization. One possible functional form for effective area is given by $(H_i A_i)^{\zeta_{im}}$ and

$(H_i A_i)^{\zeta_{em}}$ where H_i is some type of habitat quality index and ζ_{im} and ζ_{em} are species-specific immigration and emigration rate parameters that scale effective area to reflect the number of immigrants reaching patch i and the number of emigrants leaving patch j, respectively (Moilanen and Hanski 1998).

The *effective distance*, $f(\cdot)$, sometimes called the *dispersal kernel*, reflects the ability of the species to disperse across the landscape incorporating the effect of distance on colonization success. The shorter the distance between two patches, the more likely a migrant will survive the dispersal process. An exponential form of the dispersal kernel, $\exp(-\alpha d_{ij})$ is commonly used (Fleishman et al. 2002; Moilanen and Nieminen 2002; Hanski 1999). With this functional form, the value of the dispersal kernel ranges between 0 and 1. The species-specific parameter, α, reflects the dispersal ability of the focal species ($1/\alpha$ is the average dispersal distance). The larger the dispersal ability of the species, the smaller the value of α and, thus, the larger the

effective distance. Dispersal abilities may vary depending on the type and quality of land being traversed (Aberg et al. 1995; Gustafson and Gardner 1996). Thus, the dispersal kernel can also be adjusted for heterogeneity in the intervening landscape between patches by including a *barrier function*, B_{ij}, that measures the dispersal permeability between patches (Moilanen and Hanski 1998). The greater the barrier between two patches, the smaller the contribution of those patches towards long-term persistence of the metapopulation. Removing the summation from equation (3), we see that the individual contribution of patch j to the colonization rate of patch i is given by:

$$C_{ij} = c(A_i H_i)^{\zeta_{im}} P_j (A_j H_j)^{\zeta_{em}} B_{ij} \exp(-\alpha d_{ij}) \tag{4}$$

In this model, successful colonization does not require a minimum threshold of immigrants arriving at the same time.

Extinction of Occupied Patches
The extinction rate of patch i, E_i, is also a function of the effective area of patch i:

$$E_i = \frac{e}{g(A_i, H_i)} = \frac{e}{(A_i H_i)^{\zeta_{ex}}} \tag{5}$$

where e is the species-specific extinction rate parameter that measures the ability of the species to persist as a local population and ζ_{ex} is a species-specific parameter that relates decreases in the extinction probability to increasing effective area (Hanski 1992). The extinction rate of patch i varies as an inverse function of effective area, because larger patches usually mean larger local populations and risks of extinction tend to decrease with larger local populations (Gilpin and Diamond 1976; Lande 1993). This model assumes no rescue effect (Brown and Kodric-Brown 1977); that is, the probability of extinction in patch i is not affected by the other patches in the network or the corresponding number of immigrants that could "rescue" the local population from extinction.

The Landscape Structure Matrix
An NxN landscape structure matrix, **M**, can be derived from the N patch-specific differential equations in (1):

$$\begin{aligned}
\frac{dP_i}{dt} &= C(\mathbf{P})_i (1 - P_i) - E_i P_i \\
&= \frac{c}{e} E_i \left[\frac{e}{c} \frac{C(\mathbf{P})_i}{E_i} \right] (1 - P_i) - E_i P_i \\
&= \frac{c}{e} E_i [\mathbf{MP}]_i (1 - P_i) - E_i P_i
\end{aligned} \tag{6}$$

where $[\mathbf{MP}]_i$ is the ith element in the column vector resulting from the multiplication of the landscape matrix, **M**, by the column vector of occupancy probabilities, **P** (Ovaskainen and Hanski 2001, 2002). Each element of the landscape structure matrix, m_{ij}, is a function of effective areas and effective distances (Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2002):

$$m_{ij} = \left(\frac{e}{c}\right)\left(\frac{c(A_iH_i)^{\zeta_{im}}(A_jH_j)^{\zeta_{em}}B_{ij}\exp(-\alpha d_{ij})}{\dfrac{e}{(A_iH_i)^{\zeta_{ex}}}}\right)$$

$$= (A_iH_i)^{\zeta_{im}+\zeta_{ex}}(A_jH_j)^{\zeta_{em}}B_{ij}\exp(-\alpha d_{ij}) \qquad \text{for } i \neq j \qquad (7a)$$

$$m_{ij} = 0 \qquad \text{for } i = j \qquad (7b)$$

Each element of the landscape structure matrix gives the contribution that patch j makes to the colonization of patch i when patch i is empty multiplied by the expected lifetime of patch i when it is occupied (Ovaskainen and Hanski 2003).

Metapopulation Capacity

From the landscape structure matrix, **M**, a constructs for comparing or ranking different landscapes can be derived (Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2003, 2001). The *metapopulation persistence capacity*, or metapopulation capacity for short, is a measure of the landscape's ability to support a viable metapopulation over the long term. It is analogous to the carrying capacity in traditional population models, such as the logistic growth model. The metapopulation capacity takes into account both the quantity and quality of habitat available, the spatial configuration of the habitat patch network, and natural and human-created barriers to dispersal. A species is predicted to persist in a landscape if the metapopulation capacity of that landscape is greater than a critical threshold determined by characteristics of the focal species. The larger the metapopulation capacity the greater the long-term probability of persistence. The metapopulation capacity can be used to rank different landscapes in terms of their capacity to support viable metapopulations. It is possible to calculate how the metapopulation capacity is changed by removing patches from or adding new patches to a specific location in a given landscape. It is also possible to calculate the effect on metapopulation capacity caused by increasing or decreasing patch sizes, patch quality, and dispersal barriers. Habitat destruction, habitat deterioration, and increased dispersal barriers all lower the metapopulation capacity of the patch network and, therefore, also lower the long-term probability of metapopulation persistence.

Mathematically, the metapopulation capacity, K_M, is the leading eigenvalue of the non-negative landscape structure matrix, **M** (Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2001). Thus, the metapopulation capacity provides "a one-dimensional approximation of the equilibrium state of the N-dimensional system" (Hanski and Ovaskainen 2003). The metapopulation capacity defines the spatially-realistic threshold condition for long-term metapopulation persistence as (Hanski and Ovaskainen 2000):

$$K_M > \frac{e}{c}. \qquad (8)$$

Destruction of an entire habitat patch leads to a rank modification of matrix **M**, the effect of which on the metapopulation capacity may be derived from eigenvector-eigenvalue relations (Ovaskainen 2003). For example, the contribution of patch i to the metapopulation capacity, K_i, may be calculated as the difference between the metapopulation capacity with patch i in the network and the metapopulation capacity with patch i removed from the network.

The effect of gradual habitat deterioration or gradual increases in dispersal barriers is given by the derivative of K_M with respect to the various patch attributes (Ovaskainen and Hanski 2003, 2001). For example, the effect on metapopulation capacity of a small reduction in the area of patch i is given by:

$$\frac{\partial K_M}{\partial A_i} = \sum_{i,j} \frac{\partial K_M}{\partial m_{ij}} \frac{\partial m_{ij}}{\partial A_i} \ . \tag{9}$$

Similar sensitivities can be derived for other landscape structure components (Ovaskainen and Hanski 2003). See the Appendix for a two-patch illustration of the calculation of metapopulation capacity and the threshold condition for metapopulation persistence.

LAND ALLOCATION MODEL
As stated earlier, exurban communities are increasingly becoming zones of conflict as ecological preservation and economic development compete for the same finite land resources. As development increases, wildlife habitat is becoming scarce, degraded, and fragmented. In most cases, conversion from developed uses back to a natural environment is economically infeasible. Thus, development and its corresponding environmental impacts may be considered irreversible. As indicated by the increasing number of open space referenda that have passed in recent years (The Trust for Public Land 2005), there is a general concern that the current regulatory environment will not adequately protect the environment; that is, there will be too much development or development will occur in the wrong places. This section presents a land allocation model that combines ecological and economic objectives in providing a solution to the exurban "sprawl" problem. The model identifies both the allocation of land uses and the costs of changing the current regulatory structure, if needed, to achieve both objectives.

Model Components
The basic problem is one of a social planner (e.g., town planner, regional planning council) who wants to determine the optimal allocation of land to various uses while guaranteeing a certain likelihood of long-term metapopulation persistence. The economic objective is to maximize the net benefits of heterogeneous land use, measured by Ricardian land rents, across the landscape. The ecological objective is either the protection of an endangered species (or group of species) or the maintenance of a common species (or group of species) acting as an indicator for ecosystem health.

In many exurban communities, particularly those in the northeastern United States, land use is controlled by local zoning regulations. The town is divided into "zones" with each zone being designated for particular uses (e.g., business, industrial, residential, agricultural). Historically, zoning was used to separate conflicting land uses (e.g., residential and industrial) in order to protect human health. For development-type land uses, zoning can also dictate the density of development. Other types of regulations (e.g., wetland, easement, water quality, subdivision) also restrict land use. The term "full buildout" refers to the state at which no more development can legally take place under the current set of regulations. Unless specifically prohibited, most agricultural land can legally be converted to some developed use and would be considered "developable" in a buildout analysis. In situations where land cannot be legally converted to developed uses, the term full buildout can be expanded to include the long-term expected land use or the worst-case (from an ecological perspective) land use for all undeveloped, unpreserved

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land. Thus, full buildout represents the final state beyond which no changes of land use occur. The question for the social planner becomes one of determining whether the full buildout state that will result under current regulations meets both economic and ecological objectives or whether current regulations need to be changed to achieve an optimal end state. If full buildout under current regulations does not meet the ecological objective, then regulations will need to be changed such that some land will not be developed. The foregone land rents associated with this undeveloped land represent the opportunity cost to society for achieving the ecological objective.

Because it is the terminal state that is important for determining whether enough undeveloped land remains to guarantee the long-term viability of the target species, a static analysis of the landscape at the terminal state is appropriate. A static model focuses on the spatial implications of the ecosystem constraint and examines the costs associated with varying the restrictions of this constraint. This view essentially assumes that society has agreed to purchase outright the required land today. Thus, a static model also avoids the complexities of endogenous land rent changes that can occur with land use policies that purchase land over time.

Landscape Management Units
Current zoning may or may not result in zones that are of an appropriate scale for the desired analysis. For example, some zones may be deemed too big, such as the case of "no zoning" where the entire region (town or county) is one big zone. Alternatively, zones may contain varying levels of land use quality and corresponding land rents. In these cases, *landscape management units* can be defined such that each landscape management unit is homogeneous in land use quality, where quality is based on the land's highest valued use, and of an appropriate size for the analysis. In most exurban communities, the highest valued land use is residential development. In this case, the community would be divided into landscape management units based on residential development quality with perhaps a high residential land rent for high-quality residential land and low residential land rent for low-quality residential land. Landscape management units may be larger than, smaller than, or equal to zoning units.

Habitat Patches
Habitat patches are defined by the habitat requirements of the target species and vary in size and quality. Habitat patch sizes may be on a larger scale, smaller scale, or the same scale as the landscape management units depending on the problem. That is, the ecological scale may not match the economic scale. For this analysis, a single patch is assumed to be homogeneous in habitat quality and also "zoned" for a single land use type. This requirement for homogeneity within habitat patches simplifies the analytical analysis, but could be removed in numerical simulations if the size scale of patches are dramatically larger than those of landscape management units such that a single patch could have multiple land use types within it. Habitat patches and landscape management units are mutually exclusive but, together, make up the entire landscape.

Objective Function
To achieve the economic objective, the social planner maximizes the sum of land rents across all habitat patches and landscape management units:

$$\text{Maximize } V(\mathbf{Q}) = \sum_w \left[R^w(\cdot) \times \left(\sum_{i=1}^{N} Q_{Ai}^{w} + \sum_{j=1}^{J} Q_{Zj}^{w} \right) \right] \tag{10}$$

where **Q** is the vector of all land parcel units assumed to be of uniform size (e.g., acres, hectares), w is the land use type (e.g., commercial development, residential development, agriculture, forestry, recreation lands, preserved open space), $R^w(\cdot)$ is the per land parcel unit (e.g., per-acre) Ricardian land rent of land use type w, Q_{Ai}^w is the quantity of land parcel units in habitat patch i that is in land use type w, Q_{Zj}^w is the quantity of land parcel units in landscape management unit (zone) j that is in land use type w, N is the number of habitat patches, and J is the number of landscape management units. $R^w(\cdot)$ is a function of land quality factors and reflects the value of all future land use. Q_{Ai}^w and Q_{Zj}^w will be zero for all but one land use type in this model.

Non-Renewable Resource Constraints

The model assumes that land is not created or destroyed. Therefore, each landscape management unit and habitat patch are, by definition, a non-renewable resource of finite size. Thus, the quantity of land parcel units within a given habitat patch or landscape management unit that can be put to productive use is limited by its finite size. It is not possible to develop more land than exists.

$$Q_{Ai} \leq A_i - Q_{Ai0} \quad \text{for all } i=1\ldots N \text{ habitat patches} \tag{11a}$$

$$Q_{Zj} \leq Z_j - Q_{Zj0} \quad \text{for all } j=1\ldots J \text{ landscape management units} \tag{11b}$$

A_i and Z_j are the size of (i.e., total quantity of land parcel units in) habitat patch i and landscape management unit j, respectively. Q_{Ai0} and Q_{Zj0} represent the current state of development within the region. That is, the model does not assume a pristine landscape at a starting condition.

The Ecosystem Constraint

The social planner also wants to achieve the ecological objective of protecting an endangered or indicator species or group of species. Using the metapopulation theory presented earlier, the social planner achieves the ecological objective by maintaining long-term metapopulation persistence for the target species, as indicated by the metapopulation capacity, K_M, above a socially-determined safe-minimum-standard (SMS) which may be greater than that required to avoid extinction:

$$K_M \geq K_{SMS}. \tag{12}$$

Recall that the metapopulation capacity is based on a landscape structure matrix with matrix elements consisting of habitat patch effective areas and effective distances between habitat patches. In the land allocation model developed here, the effective areas and effective distances are modified to account for the changes to habitat patches and species dispersal brought about by development. The metapopulation capacity is, therefore, a function of the development vector, $K_M=K_M(\mathbf{Q})$. It is expected that development has a negative impact on metapopulation capacity.

For an N-patch landscape, the landscape structure matrix is given by:

$$M = \begin{bmatrix} 0 & g_1^{\zeta_{ex+im}} g_2^{\zeta_{em}} f_{12} & \cdots & \cdots & g_1^{\zeta_{ex+im}} g_N^{\zeta_{em}} f_{1N} \\ g_2^{\zeta_{ex+im}} g_1^{\zeta_{em}} f_{21} & 0 & & & \vdots \\ \vdots & & \ddots & & \vdots \\ \vdots & & & 0 & g_{N-1}^{\zeta_{ex+im}} g_N^{\zeta_{em}} f_{N-1,N} \\ g_N^{\zeta_{ex+im}} g_1^{\zeta_{em}} f_{N1} & \cdots & \cdots & g_N^{\zeta_{ex+im}} g_{N-1}^{\zeta_{em}} f_{N,N-1} & 0 \end{bmatrix} \qquad (13)$$

where $g_i = g(Q_{Ai})$ is the effective area of patch i as a function of the amount of development occurring in patch i, $f_{in} = f(\mathbf{Q_Z})$ is the effective distance between patches i and n as a function of the amount of development occurring between the two patches, and ζ_{ex}, ζ_{im}, and ζ_{em} are the species specific patch-area scaling parameters. Residential development decreases the effective area of a habitat patch by both reducing the quantity and degrading the quality of habitat within a given patch, $\frac{\partial g_i}{\partial Q} < 0$, and increases the effective distance between habitat patches by increasing dispersal barriers, $\frac{\partial f_{in}}{\partial Q} < 0$. Note that $\mathbf{Q_Z}$ is the vector of development occurring in all landscape management units, because more than one landscape management unit may exist between any two patches. Also note that f_{in} is not necessarily the same as f_{ni}. Slope of terrain, local wind patterns, and water currents may result in dispersal in one direction to be more difficult than dispersal in the opposite direction even if following the same linear path.

Multiple ecosystem constraints could be used to achieve a multi-species ecological objective that protects multiple endangered species or implements a multi-species index of biodiversity or a multi-species indicator of ecosystem health. Multiple ecosystem constraints could also be used to guarantee species persistence "across the landscape" for situations of large habitat patch networks in which a single cluster of patches dominates the metapopulation capacity as it approaches the threshold condition.

It is expected that the ecosystem constraint (or group of constraints) drives the optimization; otherwise there would be no conflict between productive land uses and meeting ecological objectives. Therefore, it is assumed that the ecosystem constraint is binding and replaces full buildout as the terminal condition:

$$K_M = K_{SMS}. \qquad (14)$$

If the constraint is not binding, full buildout results without jeopardizing the ecosystem, no policy changes are required, and all the concern about sprawl is much ado about nothing.

The Basic Homogeneous Model
The following assumptions hold for the basic homogeneous model:
1. Development is irreversible. That is, once land has been developed, it is economically infeasible to convert it back to an undeveloped use.
2. Ricardian land rents are constant, reflecting all future net revenues, and determined exogeneously.
3. All land is ecologically and economically homogeneous. Both habitat quality and landscape management unit quality are constant across the landscape.

4. All land is zoned for one type of land use and, thus, the effects of development on effective area and effective distance are homogeneous.
5. There are no stock effects on land rents. That is, the amount of undeveloped land does not factor into the Ricardian land rent.
6. There is only one ecosystem constraint and the constraint is binding.
7. Zoning is fixed and determined exogenously. A_i and Z_j are constants with a given land use type.
8. There are no overlapping development effects. That is, development within patches does not impact the effective distance between patches and development within landscape management units does not impact the effective area of nearby patches.

The social planner maximizes the sum of benefits from development subject to a series of non-renewable land resource constraints and the ecosystem constraint.

$$\text{Maximize } V(\mathbf{Q}) = R^D \left(\sum_{i=1}^{N} Q_{Ai} + \sum_{j=1}^{J} Q_{Zj} \right) \tag{15}$$

$$\text{Subject to} \quad Q_{Ai} \leq A_i - Q_{Ai0} \qquad \text{for } i = 1 \ldots N \tag{16}$$

$$Q_{Zj} \leq Z_j - Q_{Zj0} \qquad \text{for } j = 1 \ldots J \tag{17}$$

$$K_M(\mathbf{Q}) = K_{SMS} \tag{18}$$

where D is homogeneous development land use type across the landscape. The Lagrangian for this problem is:

$$\begin{aligned}
\mathsf{L} \;=\; & R^D \left(\sum_{i=1}^{N} Q_{Ai} + \sum_{j=1}^{J} Q_{Zj} \right) + \sum_{i=1}^{N} \lambda_{Ai} \left(A_i - Q_{Ai0} - Q_{Ai} \right) \\
& + \sum_{j=1}^{J} \lambda_{Zj} \left(Z_j - Q_{Zj0} - Q_{Zj} \right) + \lambda_K \left(K_{SMS} - K_M(\mathbf{Q}) \right)
\end{aligned} \tag{19}$$

where λ_{Ai}, λ_{Zj}, and λ_K are the Lagrangian multipliers that measure the sensitivity of $V(\mathbf{Q})$ to changes in the respective constraints. $\lambda_{Ai} \geq 0$ and $\lambda_{Zj} \geq 0$ are the shadow prices associated with making patch i or landscape management unit j one land unit bigger. $\lambda_K \leq 0$ is the shadow price associated with making the safe-minimum-standard one unit stricter. This multiplier is negative due to the negative impact of the ecosystem constraint on the objective function. The larger the value of K_{SMS}, the stricter the constraint and the lower the value of benefits from development.

The first-order conditions for the homogeneous problem are:

$$\frac{\partial \mathsf{L}}{\partial Q_{Ai}} = R^D - \lambda_{Ai} - \lambda_K \frac{\partial K_M}{\partial Q_{Ai}} \leq 0 \qquad Q_{Ai} \geq 0 \qquad Q_{Ai} \frac{\partial \mathsf{L}}{\partial Q_{Ai}} = 0 \quad \text{for all i} \tag{20}$$

$$\frac{\partial \mathsf{L}}{\partial Q_{Zj}} = R^D - \lambda_{Zj} - \lambda_K \frac{\partial K_M}{\partial Q_{Zj}} \leq 0 \qquad Q_{Zj} \geq 0 \qquad Q_{Zj} \frac{\partial \mathsf{L}}{\partial Q_{Zj}} = 0 \quad \text{for all j} \tag{21}$$

$$\frac{\partial \mathsf{L}}{\partial \lambda_{Ai}} = A_i - Q_{Ai0} - Q_{Ai} \geq 0 \qquad \lambda_{Ai} \geq 0 \qquad \lambda_{Ai} \frac{\partial \mathsf{L}}{\partial \lambda_{Ai}} = 0 \quad \text{for all i} \tag{22}$$

$$\frac{\partial \mathsf{L}}{\partial \lambda_{Zj}} = Z_j - Q_{Zj0} - Q_{Zj} \geq 0 \qquad \lambda_{Zj} \geq 0 \qquad \lambda_{Zj} \frac{\partial \mathsf{L}}{\partial \lambda_{Zj}} = 0 \quad \text{for all j} \tag{23}$$

$$\frac{\partial \mathsf{L}}{\partial \lambda_K} = K_{SMS} - K_M(\mathbf{Q}) = 0 \qquad\qquad \lambda_K < 0 \qquad\qquad (24)$$

The Kuhn-Tucker conditions in equations (20) thru (24) are due to the inequality constraints in equations (16) and (17) which state that some land may be left undeveloped. There are three possible outcome scenarios: (*i*) an interior solution consisting of some, but not full, development in all habitat patches and landscape management units; (*ii*) a corner solution with no (further) development in some habitat patches or landscape management units; or (*iii*) a different corner solution with full development in some habitat patches or landscape management units.

Case (i): Interior Solution. $0 < Q_{Ai} < A_i - Q_{Ai0}$ and $0 < Q_{Zj} < Z_j - Q_{Zj0}$ for all i and j. Because all development quantities are positive, the first sets of equations in (20) and (21) are equalities. Because there is no full development in, the first set of equations in (22) and (23) are inequalities and, therefore, the second set of equations must be equalities (i.e., the Lagrangian multipliers in (22) and (23) are zero). The static efficiency conditions in equations (20) and (21) can be re-written:

$$R^D = \lambda_K \frac{\partial K_M}{\partial Q_{Ai}} \quad \text{for all i} \qquad\qquad (25)$$

$$R^D = \lambda_K \frac{\partial K_M}{\partial Q_{Zj}} \quad \text{for all j} \qquad\qquad (26)$$

The marginal benefit of development (the Ricardian land rent) is equal to the marginal cost of damages to ecosystem health in each habitat patch and landscape management unit. Because of the homogeneous landscape, the development land rent, R^D, is the same everywhere. Thus, equations (25) and (26) can be combined to give:

$$\frac{\partial K_M}{\partial Q_{Ai}} = \frac{\partial K_M}{\partial Q_{An}} = \frac{\partial K_M}{\partial Q_{Zj}} = \frac{\partial K_M}{\partial Q_{Zm}} \qquad\qquad \text{for all i}\neq\text{n and j}\neq\text{m} \qquad\qquad (27)$$

The marginal effect of development on the metapopulation persistence capacity is the same across the landscape. Thus, the solution to the homogeneous problem is determined solely by ecosystem (landscape and species) elements.

Case (ii): Corner Solution with No Development in Patch n. $Q_{An} = 0$, $0 < Q_{Ai} < A_i - Q_{Ai0}$, and $0 < Q_{Zj} < Z_j - Q_{Zj0}$ for i≠n and all j. In this case, the first equation in (20) for patch n is an inequality:

$$\frac{\partial \mathsf{L}}{\partial Q_{An}} = R^D - \lambda_K \frac{\partial K_M}{\partial Q_{An}} \leq 0$$

which can be re-written as:

$$R^D \leq \lambda_K \frac{\partial K_M}{\partial Q_{An}} \qquad\qquad (28)$$

Equation (3.18) now becomes:

$$\frac{\partial K_M}{\partial Q_{An}} \leq \frac{\partial K_M}{\partial Q_{Ai}} = \frac{\partial K_M}{\partial Q_{Zj}} = \frac{\partial K_M}{\partial Q_{Zm}} \qquad\qquad \text{for all i}\neq\text{n and j}\neq\text{m} \qquad\qquad (29)$$

Once again, the solution to the homogeneous problem is determined solely by ecosystem elements. However, now the marginal effect of development on the metapopulation capacity in patch n is less than (i.e., more negative than) the marginal effect of development elsewhere in the landscape. That is, the marginal damages from development in patch n are so much greater than damages that no development occurs in patch n. Figure 3.1 shows this graphically.

Case (iii): Corner Solution with Full Development in Patch n. $Q_{An} = A_i - Q_{Ai0}$,

$0 < Q_{Ai} < A_i - Q_{Ai0}$, and $0 < Q_{Zj} < Z_j - Q_{Zj0}$ for i≠n and all j. In this case, the first equation in (20) for patch n includes the shadow price for land in patch n ($\lambda_{Ai}>0$):

$$\frac{\partial \mathbf{L}}{\partial Q_{An}} = R^D - \lambda_{An} - \lambda_K \frac{\partial K_M}{\partial Q_{An}} = 0 \tag{30}$$

Equation (3.18) now becomes:

$$\frac{\lambda_{An}}{\lambda_K} + \frac{\partial K_M}{\partial Q_{An}} = \frac{\partial K_M}{\partial Q_{Ai}} = \frac{\partial K_M}{\partial Q_{Zj}} = \frac{\partial K_M}{\partial Q_{Zm}}$$

which gives:

$$\frac{\partial K_M}{\partial Q_{An}} \geq \frac{\partial K_M}{\partial Q_{Ai}} = \frac{\partial K_M}{\partial Q_{Zj}} = \frac{\partial K_M}{\partial Q_{Zm}} \qquad \text{for all i≠n and j≠m} \tag{31}$$

Once again, the solution to the homogeneous problem is determined solely by ecosystem elements. However, now the marginal effect of development on the metapopulation capacity in patch n is greater than (i.e., less negative than) the marginal effect of development elsewhere in the landscape. That is, the marginal damages from development in patch n are so much less than damages elsewhere that full development of patch n occurs. This is the exact opposite scenario as Case (*ii*). Figure 3.1 shows this graphically.
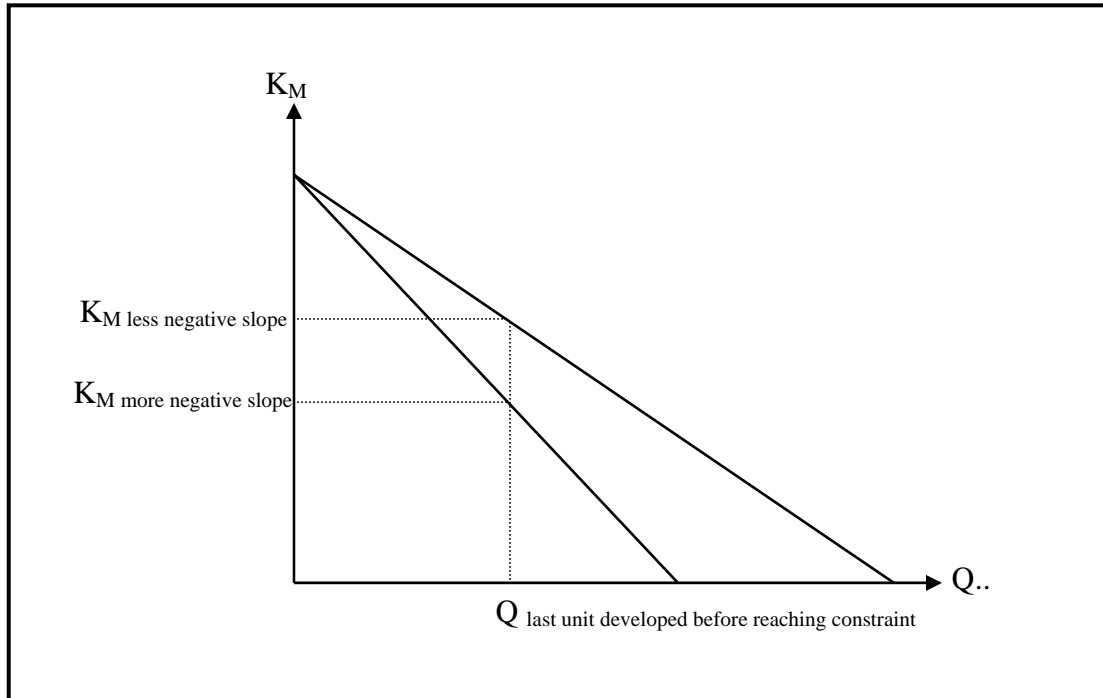

Figure 3.1 Unequal marginal effects of development on metapopulation

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Two-Patch Example

A two-patch illustration provides some insights into which ecosystem elements play an important role in determining the allocation of development among patches and landscape management units. The landscape structure matrix for a two-patch environment with one landscape management unit is given by:

$$M = \begin{bmatrix} 0 & g_1^{\zeta_{ex}+\zeta_{im}} g_2^{\zeta_{em}} f_{12} \\ g_2^{\zeta_{ex}+\zeta_{im}} g_1^{\zeta_{em}} f_{21}) & 0 \end{bmatrix} \tag{32}$$

where $g_1=g(Q_{A1})$, $g_2=g(Q_{A2})$, $f_{12}=f(Q_Z)$, and $f_{21}=f(Q_Z)$. For simplicity of analysis, this illustration assumes $f_{12}=f_{21}=f(Q_Z)$. The characteristic polynomial for this landscape matrix is:

$$F(\mathbf{Q}, K_M) = K_M^2 - g_1^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} g_2^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} (f_{12})^2 = 0 \tag{33}$$

the solution of which results in two eigenvalues. Recall that the metapopulation persistence capacity, K_M, is equal to the leading eigenvalue of the landscape matrix, which from equation (33) is:

$$K_M = g_1^{\frac{\zeta}{2}} g_2^{\frac{\zeta}{2}} f_{12} \tag{34}$$

where $\zeta = \zeta_{ex}+\zeta_{im}+\zeta_{em}$, the species-specific patch-area scaling parameter. Taking the derivative of K_M with respect to Q gives the following:

$$\frac{\partial K_M}{\partial Q_{A1}} = \frac{\zeta}{2} g_1^{\frac{\zeta}{2}-1} \frac{\partial g_1}{\partial Q_{A1}} g_2^{\frac{\zeta}{2}} f_{12}$$

$$= \frac{\zeta}{2g_1} \frac{\partial g_1}{\partial Q_{A1}} K_M \tag{35}$$

$$\frac{\partial K_M}{\partial Q_{A2}} = \frac{\zeta}{2} g_2^{\frac{\zeta}{2}-1} \frac{\partial g_2}{\partial Q_{A2}} g_1^{\frac{\zeta}{2}} f_{12}$$

$$= \frac{\zeta}{2g_2} \frac{\partial g_2}{\partial Q_{A2}} K_M \tag{36}$$

$$\frac{\partial K_M}{\partial Q_Z} = g_1^{\frac{\zeta}{2}} g_2^{\frac{\zeta}{2}} \frac{\partial f_{12}}{\partial Q_Z}$$

$$= \frac{1}{f_{12}} \frac{\partial f_{12}}{\partial Q_Z} K_M \tag{37}$$

From equation (27), the first-order conditions for the two patch network are:

$$\frac{\partial K_M}{\partial Q_{A1}} = \frac{\partial K_M}{\partial Q_{A2}} \text{ and } \frac{\partial K_M}{\partial Q_{A1}} = \frac{\partial K_M}{\partial Q_Z} \tag{38}$$

Substituting equations (35) through (37) into equation (38) gives the following:

$$g_2 = \frac{\dfrac{\partial g_2}{\partial Q_{A2}}}{\dfrac{\partial g_1}{\partial Q_{A1}}} g_1 \tag{39}$$

$$f_{12} = \frac{2}{\zeta} \frac{\dfrac{\partial f_{12}}{\partial Q_Z}}{\dfrac{\partial g_1}{\partial Q_{A1}}} g_1 \qquad (40)$$

Recall that when the ecosystem constraint is binding $K_M(\mathbf{Q}) = K_{SMS}$, thus equation (34) becomes:

$$K_{SMS} = g_1^{\frac{\zeta}{2}} g_2^{\frac{\zeta}{2}} f_{12} \qquad (41)$$

With specific functional forms for the effective areas of habitat patches 1 and 2 and the effective distance between them ($g_1 = g(Q_{A1})$, $g_2 = g(Q_{A2})$, $f_{12} = f(Q_Z)$), equations (39), (40), and (41) can be solved for the three unknowns Q_{A1}, Q_{A2}, and Q_Z. Assuming linear functional forms for effective areas and the barrier component of the effective distance:[2]

$$g_1 = A_1 - Q_{A10} - Q_{A1} \qquad (42)$$

$$g_2 = A_2 - Q_{A20} - Q_{A2} \qquad (43)$$

$$f_{12} = \left[1 - \frac{Q_{Z0} + Q_Z}{Z}\right] \exp(-\alpha d_{12}) \qquad (44)$$

gives the following marginal effects of development:

$$\frac{\partial g_1}{\partial Q_{A1}} = -1 \qquad (45)$$

$$\frac{\partial g_2}{\partial Q_{A2}} = -1 \qquad (46)$$

$$\frac{\partial f_{12}}{\partial Q_Z} = -\frac{\exp(-\alpha d_{12})}{Z} \qquad (47)$$

Substituting equations (42) through (47) into equations (39) through (41) and solving for the development quantities gives:

$$Q_{A1}^* = A_1 - Q_{A10} - \left[\frac{K_{SMS} Z \zeta}{2 \exp(-\alpha d_{12})}\right]^{\frac{1}{\zeta+1}} \qquad (48)$$

$$Q_{A2}^* = A_2 - Q_{A20} - \left[\frac{K_{SMS} Z \zeta}{2 \exp(-\alpha d_{12})}\right]^{\frac{1}{\zeta+1}} \qquad (49)$$

$$Q_Z^* = Z - Q_{Z0} - \frac{2}{\zeta}\left[\frac{K_{SMS} Z \zeta}{2 \exp(-\alpha d_{12})}\right]^{\frac{1}{\zeta+1}} \qquad (50)$$

The last term in each of the equations above represents the amount of land in the respective patch or landscape management unit that remains undeveloped in order to achieve the ecological objective. The amount of land remaining undeveloped is determined by the strictness of the safe-minimum-standard, the initial size of the landscape management unit, the distance between the two patches, the dispersal ability of the species, and the species area scaling factor. The

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[2] Some species may exhibit a threshold effect associated with increasing development and, therefore, a higher-order polynomial may be a more appropriate functional form. An algebraic solution is not possible with non-linear functional forms, so they are reserved for computer simulations.

amount of land remaining undeveloped is *not* affected by the initial size of the individual patches. In the homogeneous environment, where land quality and habitat quality are the same throughout the landscape, the amount of land remaining in both habitat patches is the same, while the amount of land remaining in the landscape management unit is proportional to the total amount of land remaining in the two patches. Thus, more development occurs in the habitat patch with more developable land under current conditions.

The cost to society of achieving the ecological objective is equal to the net benefits of development without the constraint minus the net benefits of development with the constraint. The net benefits from development without imposing the ecosystem constraint are:

$$V(\mathbf{Q})_{noconstraint} = R^D \left(A_1 - Q_{A10} + A_2 - Q_{A20} + Z - Q_{Z0} \right) \tag{51}$$

while the net benefits from development with the ecosystem constraint binding are:

$$V(\mathbf{Q})_{constraint} = R^D \left(A_1 - Q_{A10} + A_2 - Q_{A20} + Z - Q_{Z0} - \left(2 + \frac{2}{\zeta} \right) \left[\frac{K_{SMS} Z \zeta}{2 \exp(-\alpha d_{12})} \right]^{\frac{1}{\zeta+1}} \right) \tag{52}$$

Therefore, the cost to society of meeting the ecological objective for the two-patch network is:

$$C(\mathbf{Q})_{constraint} = R^D \left(2 + \frac{2}{\zeta} \right) \left[\frac{K_{SMS} Z \zeta}{2 \exp(-\alpha d_{12})} \right]^{\frac{1}{\zeta+1}} \tag{53}$$

Cost increases with increasing Ricardian rent $\left(\frac{\partial C}{\partial R^R} > 0 \right)$, increasing safe minimum standard for metapopulation persistence capacity $\left(\frac{\partial C}{\partial K_{SMS}} > 0 \right)$, increasing area of the landscape management unit $\left(\frac{\partial C}{\partial Z} > 0 \right)$, increasing distance between the two habitat patches $\left(\frac{\partial C}{\partial d_{12}} > 0 \right)$, and decreasing dispersal ability of the focal species $\left(\frac{\partial C}{\partial \left(1/\alpha \right)} < 0 \right)$. The effect of the species-specific scaling parameter on cost is positive $\left(\frac{\partial C}{\partial \zeta} > 0 \right)$ for $0<\zeta<1$ and negative $\left(\frac{\partial C}{\partial \zeta} < 0 \right)$ for $\zeta>1$. Cost is *not* affected by the initial conditions of the habitat patches or the amount of development that has already taken place in the landscape management unit.

Model Extensions
The basic homogeneous model presented in the previous section can be extended to eliminate some of the simplifying assumptions. With each of the following a comparison is made to the basic model.

Heterogeneous Land Quality
Some landscape management units may be better suited for particular land uses. For example, those residential development neighborhoods with a scenic vista would have a higher land rent than otherwise comparable residential development elsewhere. In the heterogeneous land quality

model with still one land use type, D, equations (15), (19), (20), and (21) from the basic homogeneous model are replaced with:

$$\text{Maximize } V(\mathbf{Q}) = \sum_{i=1}^{N} R(L_i) \times Q_{Ai} + \sum_{j=1}^{J} R(L_j) \times Q_{Zj} \tag{54}$$

$$
\begin{aligned}
\mathsf{L} &= \sum_{i=1}^{N} R(L_i) \times Q_{Ai} + \sum_{j=1}^{J} R(L_j) \times Q_{Zj} + \sum_{i=1}^{N} \lambda_{Ai}\left(A_i - Q_{Ai0} - Q_{Ai}\right) \\
&\quad + \sum_{j=1}^{J} \lambda_{Zj}\left(Z_j - Q_{Zj0} - Q_{Zj}\right) + \lambda_K\left(K_{SMS} - K_M(\mathbf{Q})\right)
\end{aligned}
\tag{55}
$$

$$\frac{\partial \mathsf{L}}{\partial Q_{Ai}} = R(L_i) - \lambda_{Ai} - \lambda_K \frac{\partial K_M}{\partial Q_{Ai}} \leq 0 \quad \text{for all i} \tag{56}$$

$$\frac{\partial \mathsf{L}}{\partial Q_{Zj}} = R(L_j) - \lambda_{Zj} - \lambda_K \frac{\partial K_M}{\partial Q_{Zj}} \leq 0 \quad \text{for all j} \tag{57}$$

R(L$_i$) and *R(L$_j$)* are the heterogeneous land quality rents in habitat patch i and landscape management unit j, respectively. The system constraints, associated first-order conditions, and Kuhn-Tucker conditions remain the same.

Case (i): Interior Solution. $0 < Q_{Ai} < A_i - Q_{Ai0}$ and $0 < Q_{Zj} < Z_j - Q_{Zj0}$ for all i and j. The static efficiency conditions for the heterogeneous land quality model are:

$$R(L_i) = \lambda_K \frac{\partial K_M}{\partial Q_{Ai}} \quad \text{for all i} \tag{58}$$

$$R(L_j) = \lambda_K \frac{\partial K_M}{\partial Q_{Zj}} \quad \text{for all j} \tag{59}$$

The marginal benefit of development (the Ricardian land rent) is equal to the marginal cost of damages to ecosystem health in each habitat patch and landscape management unit. But now, the Ricardian land rent is no longer the same everywhere. Solving each of the equations in (58) and (59) for λ_K and setting them equal to each other results in:

$$\frac{\dfrac{\partial K_M}{\partial Q_{Ai}}}{R(L_i)} = \frac{\dfrac{\partial K_M}{\partial Q_{An}}}{R(L_n)} = \frac{\dfrac{\partial K_M}{\partial Q_{Zj}}}{R(L_j)} = \frac{\dfrac{\partial K_M}{\partial Q_{Zm}}}{R(L_m)} \quad \text{for all } i \neq n \text{ and } j \neq m \tag{60}$$

The solution to the heterogeneous land quality problem is determined by both economic and ecological elements, where the per-dollar marginal rates of change in metapopulation persistence capacity are equal between all habitat patches and landscape management units. If *R(L$_i$)>R(L$_n$)*, then $\dfrac{\partial K_M}{\partial Q_{Ai}} > \dfrac{\partial K_M}{\partial Q_{An}}$ at the terminal state. More development occurs in those habitat patches and landscape management units with greater Ricardian land rents.

Cases (ii and iii): Corner Solutions. The existence of corner solutions now depend on per-dollar marginal effects of development on the metapopulation persistence capacity. If the per-dollar damages are so much greater (less) in patch n than elsewhere, then no development (full development) occurs in patch n.

Two-Patch Illustration. Revising equations (39) through (41) for a two-patch network for heterogeneous land quality results is:

$$g_2 = \frac{R(L_1)}{R(L_2)} \frac{\dfrac{\partial g_2}{\partial Q_{A2}}}{\dfrac{\partial g_1}{\partial Q_{A1}}} g_1 \tag{61}$$

$$f_{12} = \frac{2}{\zeta} \frac{R(L_1)}{R(L_Z)} \frac{\dfrac{\partial f_{12}}{\partial Q_Z}}{\dfrac{\partial g_1}{\partial Q_{A1}}} g_1 \tag{62}$$

$$K_{SMS} = g_1^{\frac{\zeta}{2}} g_2^{\frac{\zeta}{2}} f_{12} \tag{63}$$

Maintaining linear functional forms for effective areas and the dispersal barrier, the efficient quantities of development in the heterogeneous land quality model are:

$$Q_{A1}^* = A_1 - Q_{A10} - \left[\frac{K_{SMS} Z \zeta}{2 \exp(-\alpha d_{12})}\right]^{\frac{1}{\zeta+1}} \left[\frac{R(L_Z)(R(L_2))^{\frac{\zeta}{2}}}{(R(L_1))^{\frac{\zeta+2}{2}}}\right]^{\frac{1}{\zeta+1}} \tag{64}$$

$$Q_{A2}^* = A_2 - Q_{A20} - \left[\frac{K_{SMS} Z \zeta}{2 \exp(-\alpha d_{12})}\right]^{\frac{1}{\zeta+1}} \left[\frac{R(L_Z)(R(L_1))^{\frac{\zeta}{2}}}{(R(L_2))^{\frac{\zeta+2}{2}}}\right]^{\frac{1}{\zeta+1}} \tag{65}$$

$$Q_Z^* = Z - Q_{Z0} - \frac{2}{\zeta}\left[\frac{K_{SMS} Z \zeta}{2 \exp(-\alpha d_{12})}\right]^{\frac{1}{\zeta+1}} \left[\frac{(R(L_1)R(L_2))^{\frac{\zeta}{2}}}{(R(L_Z))^{\zeta}}\right]^{\frac{1}{\zeta+1}} \tag{66}$$

The amount of land remaining in each of the habitat patches and the landscape management unit are now functions of all the heterogeneous land quality rents. The ecosystem components are the same, but now the amount of land remaining undeveloped is adjusted by relative land rents. More development occurs in the habitat patch with the greater Ricardian land rent.

The cost to society of meeting the ecological objective for the two-patch network in the heterogeneous land quality model is:

$$C(\mathbf{Q})_{constra\,int} = \left[(R(L_1)R(L_2))^{\frac{\zeta}{2}} R(L_Z)\right]^{\frac{1}{\zeta+1}} \left(2 + \frac{2}{\zeta}\right) \left[\frac{K_{SMS} Z \zeta}{2 \exp(-\alpha d_{12})}\right]^{\frac{1}{\zeta+1}} \tag{67}$$

which is the same as the homogeneous land quality model with the same sensitivity analysis except now:

$$R^D = \left[(R(L_1)R(L_2))^{\frac{\zeta}{2}} R(L_Z)\right]^{\frac{1}{\zeta+1}} \tag{68}$$

such that the marginal effect of land rent on cost depends on the different land rents. Cost is still not affected by the initial conditions in the habitat patches nor the initial level of development in the landscape management unit.

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Heterogeneous Land Use
Land rent in any given habitat patch will be determined by the land use type that the patch is "zoned" for. Thus, land rents may be different for land parcels of homogeneous quality. However, the impact of different land use types on the ecosystem may be different. For example, commercial development results in higher impervious surface coverage than large-lot residential development (Miltner, White, and Yoder 2004). In the heterogeneous land use model with homogeneous land quality, equations (15), (19), (20), and (21) from the basic homogeneous model are replaced with:

$$\text{Maximize } V(\mathbf{Q}) = \sum_w \left[R^w \left(\sum_{i=1}^N Q_{Ai}^w + \sum_{j=1}^J Q_{Zj}^w \right) \right] \tag{69}$$

$$\mathsf{L} = \sum_w \left[R^w \left(\sum_{i=1}^N Q_{Ai}^w + \sum_{j=1}^J Q_{Zj}^w \right) \right] + \sum_{i=1}^N \lambda_{Ai} \left(A_i - Q_{Ai0}^w - Q_{Ai}^w \right)$$

$$+ \sum_{j=1}^J \lambda_{Zj} \left(Z_j - Q_{Zj0}^w - Q_{Zj}^w \right) + \lambda_K \left(K_{SMS} - K_M(\mathbf{Q}) \right) \tag{70}$$

$$\frac{\partial \mathsf{L}}{\partial Q_{Ai}^w} = R^w - \lambda_{Ai} - \lambda_K \frac{\partial K_M}{\partial Q_{Ai}^w} \leq 0 \qquad \text{for all i} \tag{71}$$

$$\frac{\partial \mathsf{L}}{\partial Q_{Zj}^w} = R^w - \lambda_{Zj} - \lambda_K \frac{\partial K_M}{\partial Q_{Zj}^w} \leq 0 \qquad \text{for all j} \tag{72}$$

R^w are the heterogeneous land rents for the various land use types, w. Each habitat patch i and landscape management unit j can be of only one land use type, thus all but one Q^w is zero. The system constraints, associated first-order conditions, and Kuhn-Tucker conditions remain the same.

Case (i): Interior Solution. $0 < Q_{Ai}^w < A_i - Q_{Ai0}^w$ and $0 < Q_{Zj}^w < Z_j - Q_{Zj0}^w$ for all i and j. The static efficiency conditions for the heterogeneous land quality model are:

$$R^w = \lambda_K \frac{\partial K_M}{\partial Q_{Ai}^w} \quad \text{for all i, w} \tag{73}$$

$$R^w = \lambda_K \frac{\partial K_M}{\partial Q_{Zj}^w} \quad \text{for all j, w} \tag{74}$$

The marginal benefit of land use type w is equal to the marginal cost of damages to ecosystem health in each habitat patch and landscape management unit of land use type w. The land rent, R^w, is not the same everywhere. Solving each of the equations in (73) and (74) for λ_K and setting them equal to each other results in:

$$\frac{\frac{\partial K_M}{\partial Q_{Ai}^w}}{R^w} = \frac{\frac{\partial K_M}{\partial Q_{An}^w}}{R^w} = \frac{\frac{\partial K_M}{\partial Q_{Zj}^w}}{R^w} = \frac{\frac{\partial K_M}{\partial Q_{Zm}^w}}{R^w} \qquad \text{for all i≠n, j≠m, and w} \tag{75}$$

The static efficiency solution to the heterogeneous land use problem is also determined by both economic and ecological elements, where the per-dollar marginal rates of change in metapopulation persistence capacity are equal between all habitat patches and landscape management units.

Cases (ii and iii): Corner Solutions. The existence of corner solutions again depend on per-dollar marginal effects of development on the metapopulation persistence capacity. If the per-dollar damages are so much greater (less) in patch n than elsewhere, then no development (full development) occurs in patch n.

Two-Patch Illustration. Equations (39) through (41) for the homogeneous two-patch network revised for heterogeneous land use become:

$$g_2 = \frac{R^{D1}}{R^{D2}} \frac{\dfrac{\partial g_2}{\partial Q_{A2}}}{\dfrac{\partial g_1}{\partial Q_{A1}}} g_1 \tag{76}$$

$$f_{12} = \frac{2}{\zeta} \frac{R^{D1}}{R^{DZ}} \frac{\dfrac{\partial f_{12}}{\partial Q_Z}}{\dfrac{\partial g_1}{\partial Q_{A1}}} g_1 \tag{77}$$

$$K_{SMS} = g_1^{\frac{\zeta}{2}} g_2^{\frac{\zeta}{2}} f_{12} \tag{78}$$

where R^{D1}, R^{D2}, and R^{DZ} are the land rents associated with land use types D1, D2, and DZ, respectively. With heterogeneous land use, the effects of development on effective areas and dispersal barriers will vary by land use type. Thus, equations (42) through (47) from the basic homogeneous model need to be modified with additional parameters (a_i and b_j) that indicate the intensity of the land use type:

$$g_1 = A_1 - a_1 Q_{A10} - a_1 Q_{A1} \tag{79}$$

$$g_2 = A_2 - a_2 Q_{A20} - a_2 Q_{A2} \tag{80}$$

$$f_{12} = \left[1 - \frac{b_Z(Q_{Z0} + Q_Z)}{Z} \right] \exp(-\alpha d_{12}) \tag{81}$$

which gives the following marginal effects of development:

$$\frac{\partial g_1}{\partial Q_{A1}} = -a_1 \tag{82}$$

$$\frac{\partial g_2}{\partial Q_{A2}} = -a_2 \tag{83}$$

$$\frac{\partial f_{12}}{\partial Q_Z} = -\frac{b_Z}{Z} \exp(-\alpha d_{12}) \tag{84}$$

Solving equations (76) through (78) using equations (79) through (84) gives the efficient quantities of development in the heterogeneous land use model:

$$Q_{A1}^* = \frac{A_1}{a_1} - Q_{A10} - \frac{1}{a_1} \left[\frac{K_{SMS} Z \zeta}{2 b_Z \exp(-\alpha d_{12})} \right]^{\frac{1}{\zeta+1}} \left[\frac{R^{DZ}}{b_Z} \left(\frac{R^{D2}}{a_2} \right)^{\frac{\zeta}{2}} \left(\frac{R^{D1}}{a_1} \right)^{-\left(\frac{\zeta+2}{2}\right)} \right]^{\frac{1}{\zeta+1}} \tag{85}$$

$$Q_{A2}^* = \frac{A_2}{a_2} - Q_{A20} - \frac{1}{a_2}\left[\frac{K_{SMS}Z\zeta}{2b_Z\exp(-\alpha d_{12})}\right]^{\frac{1}{\zeta+1}}\left[\frac{R^{DZ}}{b_Z}\left(\frac{R^{D1}}{a_1}\right)^{\frac{\zeta}{2}}\left(\frac{R^{D2}}{a_2}\right)^{-\left(\frac{\zeta+2}{2}\right)}\right]^{\frac{1}{\zeta+1}} \tag{86}$$

$$Q_Z^* = \frac{Z}{b_Z} - Q_{Z0} - \frac{2}{\zeta}\left[\frac{K_{SMS}Z\zeta}{2b_Z\exp(-\alpha d_{12})}\right]^{\frac{1}{\zeta+1}}\left[\left(\frac{R^{DZ}}{b_Z}\right)^{-\zeta}\left(\frac{R^{D1}}{a_1}\right)^{\frac{\zeta}{2}}\left(\frac{R^{D2}}{a_2}\right)^{\frac{\zeta}{2}}\right]^{\frac{1}{\zeta+1}} \tag{87}$$

The amount of land remaining in each of the habitat patches and the landscape management unit are now functions of the heterogeneous land rents and the land use intensity parameters. If the land rents are all the same ($R^{D1}=R^{D2}=R^{DZ}$) but the development intensity of land use type D1 is greater than the development intensity of land use type D2 ($a_1>a_2$), then more land will be left undeveloped in patch 1.

The cost to society of meeting the ecological objective for the two-patch network in the heterogeneous land use model is:

$$C(\mathbf{Q}) = R^{D1}\left(A_1 - \frac{A_1}{a_1} + \frac{1}{a_1}\left[\frac{K_{SMS}Z\zeta}{2b_Z\exp(-\alpha d_{12})}\right]^{\frac{1}{\zeta+1}}\left[\frac{R^{DZ}}{b_Z}\left(\frac{R^{D2}}{a_2}\right)^{\frac{\zeta}{2}}\left(\frac{R^{D1}}{a_1}\right)^{-\left(\frac{\zeta+2}{2}\right)}\right]^{\frac{1}{\zeta+1}}\right)$$

$$+ R^{D2}\left(A_2 - \frac{A_2}{a_2} + \frac{1}{a_2}\left[\frac{K_{SMS}Z\zeta}{2b_Z\exp(-\alpha d_{12})}\right]^{\frac{1}{\zeta+1}}\left[\frac{R^{DZ}}{b_Z}\left(\frac{R^{D1}}{a_1}\right)^{\frac{\zeta}{2}}\left(\frac{R^{D2}}{a_2}\right)^{-\left(\frac{\zeta+2}{2}\right)}\right]^{\frac{1}{\zeta+1}}\right)$$

$$+ R^{D1}\left(Z - \frac{Z}{b_Z} + \frac{2}{\zeta}\left[\frac{K_{SMS}Z\zeta}{2b_Z\exp(-\alpha d_{12})}\right]^{\frac{1}{\zeta+1}}\left[\left(\frac{R^{DZ}}{b_Z}\right)^{-\zeta}\left(\frac{R^{D2}}{a_2}\right)^{\frac{\zeta}{2}}\left(\frac{R^{D1}}{a_1}\right)^{\frac{\zeta}{2}}\right]^{\frac{1}{\zeta+1}}\right)$$

which simplifies to:

$$C(\mathbf{Q}) = R^{D1}\left(A_1 - \frac{A_1}{a_1}\right) + R^{D2}\left(A_2 - \frac{A_2}{a_2}\right) + R^{D1}\left(Z - \frac{Z}{b_Z}\right)$$

$$+ \left(\frac{1}{a_1} + \frac{1}{a_2} + \frac{2}{\zeta}\right)\left[\frac{K_{SMS}Z\zeta}{2b_Z\exp(-\alpha d_{12})}\right]^{\frac{1}{\zeta+1}}\left[\frac{R^{DZ}}{b_Z}\left(\frac{R^{D2}}{a_2}\right)^{\frac{\zeta}{2}}\left(\frac{R^{D1}}{a_1}\right)^{\frac{\zeta}{2}}\right]^{\frac{1}{\zeta+1}} \tag{88}$$

The initial size of the habitat patches now matter in determining the cost to society of achieving the ecological objective, even if all the land rents are the same. Cost also now depends on the development intensity parameters.

"Neighborhood" Stock Effect
The Ricardian rent associated with some types of development is a function of the amount of undeveloped land remaining after the ecosystem constraint becomes binding. The larger the amount of undeveloped land the higher the rent. Commercial and industrial development may have no stock effect while different types of residential development have different stock effects. With "neighborhood" stock effects, it is assumed that land rents are a function of the amount of undeveloped land *within* a given habitat patch or landscape management unit. Assuming homogeneous land quality and land use, equations (15), (19), (20), and (21) from the basic homogeneous model are replaced with:

$$\text{Maximize } V(\mathbf{Q}) = \sum_{i=1}^{N} R(Q_{Ai}) \times Q_{Ai} + \sum_{j=1}^{J} R(Q_{Zj}) \times Q_{Zj} \tag{89}$$

$$\begin{aligned}
\mathsf{L} = & \sum_{i=1}^{N} R(Q_{Ai}) \times Q_{Ai} + \sum_{j=1}^{J} R(Q_{Zj}) \times Q_{Zj} + \sum_{i=1}^{N} \lambda_{Ai}\left(A_i - Q_{Ai0} - Q_{Ai}\right) \\
& + \sum_{j=1}^{J} \lambda_{Zj}\left(Z_j - Q_{Zj0} - Q_{Zj}\right) + \lambda_K\left(K_{SMS} - K_M(\mathbf{Q})\right)
\end{aligned} \tag{90}$$

$$\frac{\partial \mathsf{L}}{\partial Q_{Ai}} = R(Q_{Ai}) + Q_{Ai}\frac{\partial R}{\partial Q_{Ai}} - \lambda_{Ai} - \lambda_K \frac{\partial K_M}{\partial Q_{Ai}} \le 0 \qquad \text{for all i} \tag{91}$$

$$\frac{\partial \mathsf{L}}{\partial Q_{Zj}} = R(Q_{Zj}) + Q_{Zj}\frac{\partial R}{\partial Q_{Zj}} - \lambda_{Zj} - \lambda_K \frac{\partial K_M}{\partial Q_{Zj}} \le 0 \qquad \text{for all j} \tag{92}$$

Land rents, $R(Q_{Ai})$ and $R(Q_{Zj})$, are decreasing functions of the quantity of land developed in habitat patch i and landscape management unit j, respectively. That is, $\frac{\partial R}{\partial Q} < 0$ and $\frac{\partial^2 R}{\partial Q^2} > 0$.

The rental value of land decreases as the amount of development increases and as the corresponding amount of open space decreases. This can be viewed as a congestion effect that is merely the opposite of an open space effect. The system constraints, associated first-order conditions, and Kuhn-Tucker conditions remain the same.

Case (i): Interior Solution. $0 < Q_{Ai} < A_i - Q_{Ai0}$ and $0 < Q_{Zj} < Z_j - Q_{Zj0}$ for all i and j. The static efficiency conditions for the homogeneous model with neighborhood stock effects are:

$$R(Q_{Ai}) = \lambda_K \frac{\partial K_M}{\partial Q_{Ai}} - Q_{Ai}\frac{\partial R}{\partial Q_{Ai}} \quad \text{for all i} \tag{93}$$

$$R(Q_{Zj}) = \lambda_K \frac{\partial K_M}{\partial Q_{Zj}} - Q_{Zj}\frac{\partial R}{\partial Q_{Zj}} \quad \text{for all j} \tag{94}$$

The marginal benefit of development is equal to the marginal cost of ecosystem damages plus the marginal cost of lost open space amenities in each habitat patch and landscape management unit. Solving each of the equations in (93) and (94) for λ_K and setting them equal to each other

results in:

$$\frac{\dfrac{\partial K_M}{\partial Q_{Ai}}}{R(Q_{Ai}) + Q_{Ai}\dfrac{\partial R}{\partial Q_{Ai}}} = \frac{\dfrac{\partial K_M}{\partial Q_{An}}}{R(Q_{An}) + Q_{An}\dfrac{\partial R}{\partial Q_{An}}} = \frac{\dfrac{\partial K_M}{\partial Q_{Zj}}}{R(Q_{Zj}) + Q_{Zj}\dfrac{\partial R}{\partial Q_{Zj}}} = \frac{\dfrac{\partial K_M}{\partial Q_{Zm}}}{R(Q_{Zm}) + Q_{Zm}\dfrac{\partial R}{\partial Q_{Zm}}} \qquad (95)$$

Once again, the static efficiency solution is determined by both economic and ecological elements.

Cases (ii and iii): Corner Solutions. With a strong neighborhood stock effect, it will be less (more) likely to reach a full development (no development) corner solution.

Two-Patch Illustration. It is not possible to solve this system of equations algebraically for quantities of development in the two patches and the landscape management unit.

SUMMARY AND CONCLUSIONS

This paper developed a model that combines ecological and economic constructs to determine the optimal allocation of development across a spatially-realistic landscape. It was shown that in an economically homogeneous environment, such as would be considered by the von Thunen locational rent model, the allocation of land to developed uses is determined solely by ecological elements (landscape and species parameters). In the homogeneous case, the amount of land remaining in each habitat patch is the same regardless of their initial sizes or initial levels of development. The cost to society of meeting the ecological objective for metapopulation persistence depends on the Ricardian land rent, the level of the safe-minimum-standard, the area of the landscape management unit, the distance between habitat patches, the dispersal ability of the focal species, and the species-specific area scaling parameter. Cost is not affected by the initial conditions of the habitat patches or the amount of development that has already taken place in the landscape management unit.

Heterogeneity was introduced into the land allocation model in three ways: (*i*) heterogeneous land quality, (*ii*) heterogeneous land use, and (*iii*) neighborhood stock effects. In addition to the ecological elements that were important in the homogeneous case, the allocation of land in the heterogeneous case is also determined by the differential land rents. More development occurs in habitat patches and landscape management units with higher land rents compared with the homogeneous case. In the heterogeneous land use case, where different land uses have different intensities of damages, the development intensity parameters are factors in the solution with more development occurring in areas zoned for less intensive land uses. The cost to society of achieving the ecological objective in the heterogeneous land use case is now a function of initial habitat patch sizes. Therefore, it is important to consider the heterogeneity of the landscape from both an ecological and economic perspective when making land allocation decisions.

The "optimality" of this analysis is based on society's ability to optimally set the safe-minimum-standard. This may or may not be possible with currently available ecological data. In addition, setting a safe-minimum-standard determines the minimum cost that society is willing to pay for

long-term species persistence. It is possible that society would be willing to pay more to achieve the ecological objective. Thus, this analysis results in a cost-effective solution rather than a socially-optimal solution.

Three potential scenarios exist where a dynamic analysis would be more appropriate. First, the development process itself (e.g., development rate and intensity) may adversely affect species living outside the area of development pushing the entire metapopulation beyond an extinction threshold. Second, a dynamic analysis would also be more appropriate (in fact, necessary) if the geographic region of concern were dominated by agriculture and forestry (renewable resource industries) land uses with parcels continually entering into and falling out of production. Third, the choice of policy instrument may involve the gradual purchase of land over time.   This would result in changing land rents over time.

The research presented in this paper used a static model for analysis that assumed all land required to remain undeveloped was purchased outright. Several factors contribute to the reasonableness of this assumption. First, what are the current conditions of the landscape. If the initial conditions include lots of already preserved lands, then the quantity of additional lands needed to meet the ecological objective may be small. Second, what are the costs per person in the community or region of concern? If the cost of land purchase is low relative to the number of members in the society, there may be little opposition to a minor increase in taxes in the current year. Third, what are the transaction costs of alternative land use/open space preservation policies? Are the costs of borrowing (i.e., the current interest rate) high or low? And fourth, are there equity issues that make some policies more appealing than others? Who incurs the benefits and who incurs the costs of policy alternatives.

If the current regulatory structure proves to be inadequate for achieving the ecological objective, a follow-up question of *how* to reach the desired end state emerges. This is a policy decision entailing how to distribute the costs across members of society and, potentially, across time. Multiple policy mechanisms are available to achieve the desired land allocation at full buildout. Each mechanism has associated advantages and disadvantages including the distribution of costs and benefits among members of society. Purchasing land over time rather than in one lump-sum transaction results in greater net present value of total costs because of the lost flexibility/options available in the choice set. Plus, there may be additional transactions costs associated with "updating" local tax rates or impact fees each year to accommodate the changing conditions.

Several areas exist for future research. First, the existence of a development threshold effect on species persistence would indicate the need to replace the linear functional forms for effective area and dispersal barrier with a higher-order polynomial. In addition, the choice of functional form and land use intensity parameters may be species-specific. Second, development in neighboring land units may impact effective area and/or effective distance. These indirect development damages may depend on the scale of habitat patches and landscape management units as well as the target species. Third, many applications require the protection of multiple species that may or may not share habitat patches. An examination of multiple ecosystem constraints would be appropriate.

APPENDIX: TWO-PATCH METAPOPULATION PERSISTENCE

A two-patch metapopulation is represented by a system of two differential equations. For the purposes of this two-patch illustration, assume that habitat quality is homogeneous ($H_1 = H_2 = 1$) and that there are no dispersal barriers other than distance ($B_{12} = B_{21} = 1$ and $d_{12} = d_{21}$). Thus, from equations (1), (4) and (5), a two-patch metapopulation is given by:

$$\frac{dP_1}{dt} = cA_1^{\zeta_{im}} A_2^{\zeta_{em}} \exp(-\alpha d_{12}) P_2 (1 - P_1) - \frac{e}{A_1^{\zeta_{ex}}} P_1 \tag{A.1a}$$

$$\frac{dP_2}{dt} = cA_2^{\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) P_1 (1 - P_2) - \frac{e}{A_2^{\zeta_{ex}}} P_2. \tag{A.1b}$$

The landscape structure matrix associated with this two-patch environment is given by:

$$M = \begin{bmatrix} 0 & A_1^{\zeta_{ex} + \zeta_{im}} A_2^{\zeta_{em}} \exp(-\alpha d_{12}) \\ A_2^{\zeta_{ex} + \zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) & 0 \end{bmatrix}. \tag{A.2}$$

Using equation (A2.2), the characteristic polynomial for this landscape matrix is:

$$\lambda^2 - A_1^{\zeta_{ex} + \zeta_{im} + \zeta_{em}} A_2^{\zeta_{ex} + \zeta_{im} + \zeta_{em}} \exp(-2\alpha d_{12}) = 0. \tag{A.3}$$

The solution to equation (A3) gives the following two eigenvalues:

$$\lambda = \pm A_1^{\frac{\zeta_{ex} + \zeta_{im} + \zeta_{em}}{2}} A_2^{\frac{\zeta_{ex} + \zeta_{im} + \zeta_{em}}{2}} \exp(-\alpha d_{12}). \tag{A.4}$$

The metapopulation persistence capacity K_M for a two-patch network is equal to the leading eigenvalue of the landscape matrix, which from equation (A.4) is:

$$K_M = A_1^{\frac{\zeta_{ex} + \zeta_{im} + \zeta_{em}}{2}} A_2^{\frac{\zeta_{ex} + \zeta_{im} + \zeta_{em}}{2}} \exp(-\alpha d_{12}). \tag{A.5}$$

Long-Term Metapopulation Persistence Threshold Condition

In order to determine the threshold condition for metapopulation persistence, it is necessary to first find equilibrium values for the probability of persistence in each of the patches, $\mathbf{P}^*$.

Equilibrium occurs when equations (A.1a) and (A.1b) are both equal to zero $\left(\frac{dP_1}{dt} = \frac{dP_2}{dt} = 0 \right)$.

Setting equation (A.1a) equal to zero and solving for P_2:

$$cA_1^{\zeta_{im}} A_2^{\zeta_{em}} \exp(-\alpha d_{12}) P_2 (1 - P_1) - \frac{e}{A_1^{\zeta_{ex}}} P_1 = 0 \quad cA_1^{\zeta_{im}} A_2^{\zeta_{em}} \exp(-\alpha d_{12}) P_2 (1 - P_1) = \frac{e}{A_1^{\zeta_{ex}}} P_1$$

$$P_2 = \frac{eP_1}{c(1 - P_1) A_1^{\zeta_{ex} + \zeta_{im}} A_2^{\zeta_{em}} \exp(-\alpha d_{12})} \tag{A.6}$$

Similarly, setting equation (A.1b) equal to zero and solving for P_2:

$$cA_2^{\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) P_1 (1 - P_2) - \frac{e}{A_2^{\zeta_{ex}}} P_2 = 0$$

$$cA_2^{\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) P_1 (1 - P_2) = \frac{e}{A_2^{\zeta_{ex}}} P_2$$

$$cA_2^{\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) P_1 = P_2 \left[\frac{e}{A_2^{\zeta_{ex}}} + cA_2^{\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) P_1 \right]$$

$$P_2 = \frac{cA_2^{\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) P_1}{\dfrac{e}{A_2^{\zeta_{ex}}} + cA_2^{\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) P_1}$$

$$P_2 = \frac{cA_2^{\zeta_{ex}+\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) P_1}{e + cA_2^{\zeta_{ex}+\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) P_1} \tag{A.7}$$

Setting equations (A.6) and (A.7) equal to each other and solving for P_1:

$$\frac{eP_1}{c(1-P_1)A_1^{\zeta_{ex}+\zeta_{im}} A_2^{\zeta_{em}} \exp(-\alpha d_{12})} = \frac{cA_2^{\zeta_{ex}+\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) P_1}{e + cA_2^{\zeta_{ex}+\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) P_1}$$

$$\frac{e}{c(1-P_1)A_1^{\zeta_{ex}+\zeta_{im}} A_2^{\zeta_{em}} \exp(-\alpha d_{12})} = \frac{cA_2^{\zeta_{ex}+\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12})}{e + cA_2^{\zeta_{ex}+\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) P_1}$$

$$e^2 + ecA_2^{\zeta_{ex}+\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) P_1 = c^2 A_1^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} A_2^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} \exp(-2\alpha d_{12})(1-P_1)$$

$$\left(ecA_2^{\zeta_{ex}+\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) + c^2 A_1^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} A_2^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} \exp(-2\alpha d_{12}) \right) P_1$$

$$= c^2 A_1^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} A_2^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} \exp(-2\alpha d_{12}) - e^2$$

$$P_1^* = \frac{c^2 A_1^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} A_2^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} \exp(-2\alpha d_{12}) - e^2}{ecA_2^{\zeta_{ex}+\zeta_{im}} A_1^{\zeta_{em}} \exp(-\alpha d_{12}) + c^2 A_1^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} A_2^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} \exp(-2\alpha d_{12})} \tag{A.8}$$

A similar set of calculations solving for P_2 results in:

$$P_2^* = \frac{c^2 A_1^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} A_2^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} \exp(-2\alpha d_{12}) - e^2}{ecA_1^{\zeta_{ex}+\zeta_{im}} A_2^{\zeta_{em}} \exp(-\alpha d_{12}) + c^2 A_1^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} A_2^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} \exp(-2\alpha d_{12})} \tag{A.9}$$

Equations (A.8) and (A.9) give the equilibrium probability of occupancy for patches 1 and 2, respectively. The denominator is positive in both equations, thus, the numerator determines whether or not the local population goes extinct $(P_i^* > 0)$. If the numerator is less than or equal to zero, then the local population is extinct at equilibrium. Because the numerator is the same in both equations, the metapopulation avoids extinction ($\mathbf{P}^* > 0$) when:

$$c^2 A_1^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} A_2^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} \exp(-2\alpha d_{12}) - e^2 > 0 . \tag{A.10}$$

Rearranging the terms in equation (A3.10) to bring the species-specific parameters, c and e, to the right-hand side and solving for the threshold condition $\dfrac{e}{c}$:

$$c^2 A_1^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} A_2^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} \exp(-2\alpha d_{12}) < e^2$$

$$A_1^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} A_2^{\zeta_{ex}+\zeta_{im}+\zeta_{em}} \exp(-2\alpha d_{12}) < \frac{e^2}{c^2}$$

$$A_1^{\frac{\zeta_{ex}+\zeta_{im}+\zeta_{em}}{2}} A_2^{\frac{\zeta_{ex}+\zeta_{im}+\zeta_{em}}{2}} \exp(-\alpha d_{12}) < \frac{e}{c} \tag{A.11}$$

The left-hand side of equation (A.11) is equal to the metapopulation capacity given by equation (A.5). Thus, equation (A.11) is the metapopulation threshold condition given in equation (8) for a two-patch network.

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