

ECOLOGICALLY SCALED RECOGNITION OF PATCHES WITHIN A GIS ENVIRONMENT

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CHAPTER OVERVIEW

A landscape is composed of multiple elements, including habitat patches, corridors, and matrix. Wildlife species often use different types of landscape elements for different parts of their life history or, differentially according to their ability, to fulfill certain life-history requirements. The relationship between types of landscape elements and life-history requirements also depends on the spatial scale at which a species interacts with its environment. Metapopulation models typically characterize components of landscapes as either usable (i.e., habitat) or unusable (not habitat, often used synonymously with matrix), although gradients in habitat quality and matrix permeability often exist. We present a general methodology for translating a landscape map composed of multiple types of elements into a dichotomous habitat map that considers both species-specific life histories, the spatial scale at which a species interacts with its environment, and a species' ability to move through the matrix. We illustrate the methodology for a suite of hypothetical species with different levels of niche breadth, spatial scale, and movement ability occupying an agricultural landscape in Indiana, United States. We conclude by discussing applications of the technique for models requiring spatially explicit habitat maps as input and areas in which improvements to the approach are needed.

KEY WORDS—Animal movements, agriculture, connectivity, dispersal, geographic information system, habitat fragmentation, home range, landscape elements, metapopulation, spatial scale

INTRODUCTION

Rationale and Terminology

An understanding of the relationship between wildlife and habitat is essential for the management and conservation of species. Forecasting models linking wildlife distribution or abundance to habitat surrogates derived from remotely sensed land-cover data provide an opportunity to assess the effect of alternative land-use scenarios on species (Hepinstall and Sader 1997; Tucker *et al.* 1997; Roseberry and Sudkamp 1998). Unfortunately, the concept of habitat has suffered from imprecise terminology and a general failure by researchers to recognize the scale-dependent nature of wildlife-habitat relationships (Hall *et al.* 1997). For clarity, we provide a brief definition of terms used in this chapter. *Habitat* refers to an area providing the resources and other conditions needed for occupancy during at least some portion of a species' life history (Hall *et al.* 1997). Landscape elements are the fundamental structural components of a landscape (Forman 1995). An element is a spatially contiguous area that often is categorized into three types. Note that we will deviate from the usual notion of an element by defining spatial contiguity from a species' perspective, resulting in elements that are scaled ecologically to account for differences among species. Elements can include *patches* in which individuals or populations can reside, *corridors* which facilitate movement between patches, and *matrix* which generally is perceived as a sterile component bereft of resources and posing an impediment to movement of organisms. Thus, areas qualifying as patches or corridors for a species also are habitat for that species. Matrix, in the traditional sense, is not habitat, a point to which we will return later. *Movement*, unless specified otherwise, refers to travel between patches, either along a corridor or across the intervening matrix. Depending on the mobility of a species and the degree of spatial separation between patches, movements by an individual may occur frequently (e.g., daily during foraging) or once in a lifetime (e.g., natal dispersal from a patch).

Metapopulation Ecology

Metapopulation ecology provides a firm conceptual foundation for examining issues of scale related to habitat fragmentation, because it occupies a middle ground between the overly simplistic assumptions associated with theoretical models of population dynamics and the structural emphasis of landscape ecology (Hanski 1998). Consider a landscape classified dichotomously into patch and matrix elements. Patches can vary in quality, size, and degree of isolation (Moilanen and Hanski 1998). A *metapopulation* is defined, within the context of a network of patches, as a set of local popula-

tions (i.e., populations associated with specific patches) linked by dispersal between patches. At any given time, some patches in the network are occupied and others are not, with the equilibrium proportion of occupied patches determined by local extinction and colonization events. Importantly, patches are embedded within a matrix that provides no resources for the focal species (Hanski 1998).

The metapopulation concept is especially appropriate for human-dominated landscapes where fragmentation is severe, because habitat often occurs in discrete units and matrix (e.g., crop fields, urban areas) cannot support the ecological requirements of many of the native species. Models based on metapopulation ecology, such as the incidence function model (Hanski 1994; Gu and Verboom—Chapter 5), can provide useful estimates of a species' viability in a landscape. Indices based on metapopulation ecology, such as ecologically scaled landscape indices, provide an alternative means of assessing the suitability of a landscape for a species (Vos *et al.* 2001; Swihart and Verboom—Chapter 6). Finally, these methods can be combined to provide a robust assessment of landscape suitability (Verboom *et al.* 2001). In short, the metapopulation concept provides a fruitful means of quantitatively comparing the effect of alternative land-use scenarios in agricultural landscapes on species well-being.

THE CONCEPT OF ECOLOGICALLY SCALED PATCHES

The “Patchiness” Continuum

Habitat fragmentation can affect wildlife at a variety of levels. Metapopulation ecology deals with fragmentation at the population level, where each patch of habitat contains a population of individuals. Fragmentation also may occur at a spatial scale smaller than the individual area requirements of a species. In the field of landscape ecology, the scale of interest is usually (but not always!) the scale at which human-dominated land use occurs. This is the scale at which humans have the largest impact and also the greatest ability to manage over large geographic areas. In agricultural landscapes of the midwestern United States, the magnitude of this scale typically coincides with average crop-field sizes (i.e., 10–30 ha). At this scale, passerine birds, small mammals, and herpetofauna generally will experience habitat fragmentation at the population level, whereas raptors, larger mammals, and possibly more mobile reptiles will experience fragmentation at the individual level.

The effects of habitat loss on a species will be dependent on the ratio of patch size to individual area requirements. Assume that all habitat patches are identical in quality but vary in size. Define A_{patch} to be the mean patch area, A_{ind} to be the individual area requirements, and m to be the ratio of mean patch area to individual area requirements ($m = A_{\text{patch}}/A_{\text{ind}}$). The term m is thus the number of individuals an average patch could support. For each species there is some population level that represents the minimum viable population size for a patch (N_{mvp}). When $m > N_{\text{mvp}}$, fragmentation effects are minimal and abundance of a resource-limited population is proportional to the amount of habitat in the landscape. As habitat loss occurs and patches become smaller, m becomes less than N_{mvp} and fragmentation effects related to small population size occur. A landscape with highly variable patch sizes begins to exhibit fragmentation effects prior to $m = N_{\text{mvp}}$ as populations occupying smaller patches experience extinction events. When $m < 1$, more than one patch is required to satisfy an individual's area requirements. A species occurring in a landscape where $m < 1$ needs to have relatively high mobility in order to move between patches. The species also has to increase its movements and home-range size to account for the increased proportion of matrix habitat. Consequently, a realized home-range size (A_{real}) exceeds A_{ind} by an amount that is a function of p , the proportion of suitable habitat within a landscape. Effects of fragmentation under this scenario are experienced at the individual level through increased risk while traveling through the matrix and the energetic costs of maintaining a larger home-range size. Most theoretical work to date has dealt with population-level fragmentation, but processes operating at the population level have analogs at the individual level. For instance, patch isolation at the population level influences colonization and extinction rates (via the rescue effect). At the individual level, isolated patches may be visited less often, but patch residency may be longer due to a reluctance to cross large expanses of matrix.

Single-species assessments seldom are adequate in a planning context, raising the question: How generally applicable is metapopulation ecology, as defined above, to a wide range of species? In our opinion, the answer to this question is dependent largely on two factors: (1) the ability to quantify habitat patchiness in an ecologically meaningful way and (2) the degree to which matrix elements are unusable. Implicit in this thesis is the notion that ecological characteristics of species interact with landscape structure to produce varying levels of habitat heterogeneity, or patchiness. If the landscape resulting from such an interaction maintains a dichotomy of discrete patches interspersed with matrix, then methods developed for metapopulations can be applied. However, for some species it is likely that ecological characteristics will interact with landscape structure to produce a single, spatially structured population rather than a metapopulation. Or in the

most extreme case, the interaction will yield an ecologically scaled landscape map that is essentially homogeneous. A first step, then, is to scale landscape structure in an ecologically meaningful manner.

Ecological Scaling of Patches: Inhospitable Matrix

Each species requires areas with specific environmental characteristics (abiotic and biotic) to fulfill its life-history requirements, and many species use areas differing in vegetative structure or composition to fulfill different requirements. For instance, foraging, breeding, thermal regulation, and resting are activities that can require different vegetative associations. To the extent that vegetative associations occur as discrete spatial units interspersed among a matrix, an individual (or local population) may require a collection of these units. But previously we defined a landscape element as a spatially contiguous area. How, then, do we reconcile the notion of physical separation of vegetative associations, which are collectively required for the occurrence of a local population, with the constraint of spatial contiguity imposed by our definition of a patch? We propose to define spatial contiguity and area using as our units the mobility and energetic requirements of organisms. In this way, patches are defined operationally and scaled to a species' ecological characteristics.

The rationale for an organism-centered definition of patch is intuitive and based on two attributes: area requirements and mobility. Given that a patch is defined as a spatially distinct area either containing or able to support a population, there is a threshold area below which even high-quality habitat will not constitute a patch. This threshold area should be related to the individual area requirements of the focal species. Although the exact relationship is arbitrary and could vary with management objectives (e.g., occupancy versus long-term local viability), an absolute minimum would appear to be the area required by one individual of the focal species.

For two patches to be considered spatially distinct in the metapopulation context, the rate of movement between patches should occur slowly relative to the rate of change in the local populations' dynamics (Feng and DeWoody—Chapter 4). Habitats that are physically separated may still be indistinguishable in terms of population processes if the distance between them is small relative to the movement ability of the focal species. For example, forested habitat separated by 50 meters would almost certainly comprise the same patch for a highly mobile species such as white-tailed deer (*Odocoileus virginianus*), but the same habitat might well function as separate patches for a species that is poorly equipped to move through the intervening matrix, such as southern flying squirrels (*Glaucomys volans*).

Ecological Scaling of Patches: Variation in Matrix Elements

At this point, we revisit our concept of matrix as a landscape element that essentially is an unusable filter through which organisms must pass as they move between patches. For many organisms in human-dominated landscapes, particularly species that have persisted for long periods following habitat loss and fragmentation, matrix elements are more appropriately viewed along a continuum dictated by the ease with which species can travel through them. Where a matrix element resides on the continuum will depend on ecological characteristics of species and matrix composition (Laurance *et al.* 2002). Thus, the narrow definition of a metapopulation (*see* page 104–105) no longer applies, because organisms may view the matrix itself as a heterogeneous entity. In this context, it is more appropriate to think of the landscape as a spatially structured mosaic of habitat of varying quality and matrix of varying permeability (Figure 7-1).

In summary, ecological characteristics of species interact with landscape structure to determine the scale at which patchiness operates. Creating habitat maps using such an ecologically based definition of patchiness has great potential for assessing the position of a species-landscape combination along a continuum of spatial structure. For any given landscape, identifying the location of a species along this continuum also provides guidance in selecting metrics for measuring a landscape's suitability to the species (Figure 1-3 of Swihart and Slade—Chapter 1).

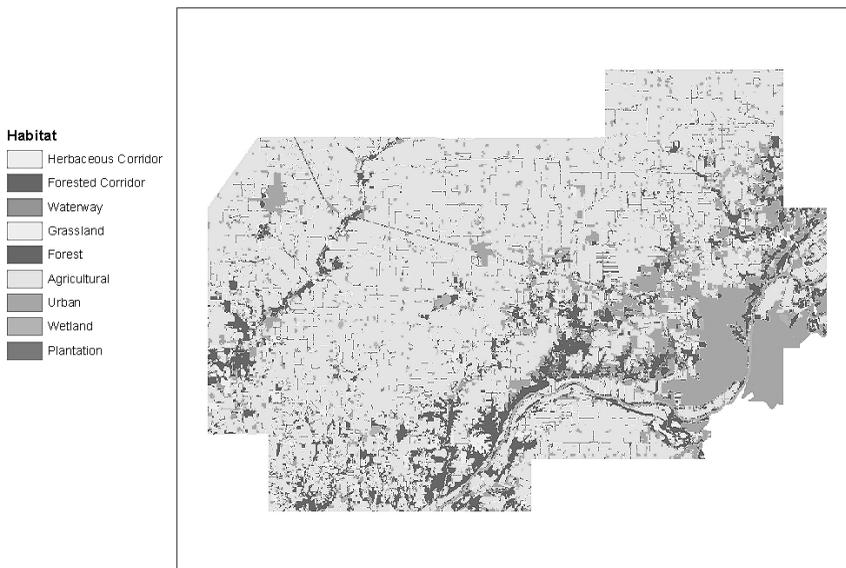


Figure 7-1. Land-cover map of Indian Pine, west-central Indiana. A color version of this figure is provided in the insert.

CREATING ECOLOGICALLY SCALED HABITAT MAPS: AN ALGORITHM

Here, we present a general methodology for translating a land-use map to a dichotomous habitat map relevant to the focal species. The translation to a habitat map considers niche breadth, spatial scale, and movement ability as a means of determining which landscape elements should be combined into patches. Results can then be examined visually or statistically to determine whether assessment methods for metapopulations *sensu stricto*, spatially structured populations, or single well-mixed populations are more appropriate.

The approach assumes that an existing land-cover map is available, from which habitat categories can be determined (Figure 7-1). In general terms, the algorithm proceeds as follows: A species-specific habitat map is created by reclassifying the land-cover map using habitat weights for the focal species. Habitat weights are used to approximate differences in quality among habitats. Next, the species-specific habitat map is reclassified into a map of habitat patches using a moving-window average that incorporates neighborhood effects. An ecologically relevant spatial scale is obtained by making the minimum patch size proportional to the individual area requirements of the focal species and the size of the moving window proportional to the species' dispersal ability. We discuss each step of the algorithm in more detail in the following sections.

Inferring Habitat Quality from Habitat Weights

Ideally, data on survival and reproduction for specific habitats should be used to assess habitat quality for a species, based on the premise that individuals in higher-quality habitat will exhibit greater fitness than individuals in poorer habitats (Van Horne 2002). In practice, however, these sorts of demographic data seldom are available, leading to use of other, indirect indicators of habitat quality. Ecologists and wildlife professionals have relied on expert opinion, estimates of density, and estimates of intensity of use as surrogates for habitat quality. Van Horne (2002) termed these approaches to linking habitat quality and organisms as knowledge-based, population, and individual-based, respectively. In the absence of data or as an adjunct to data, the knowledge-based approach can be used. If data on habitat-specific estimates of density are available, these may be useful in some instances. However, caution should be exercised, because density-dependent or socially mediated habitat selection may actually lead to erroneous inferences regarding habitat quality when the overall abundance of the species is high (Van Horne 1983). In general, use of density to infer hab-

itat quality probably should be restricted to periods following population bottlenecks, when only habitat of high quality remains occupied. Herein, we emphasize an individual-based approach to assessing habitat quality, in which behavioral decisions determine the relative intensity with which habitats are used. To the extent that behavioral decisions reflect optimal choices by individuals, inferences regarding habitat quality will be worthwhile. We recognize that the same factors that can cause density to be a misleading indicator of habitat quality also may influence behavioral choices of individuals. Moreover, inferring habitat quality from studies of habitat selection is dependent upon determining availability from an organism's perspective (Hall *et al.* 1997) and the ability to recognize important habitats that are used rarely.

Despite these caveats, we believe that the individual-based approach has merit as a pragmatic alternative to habitat-specific demographic data on multiple species because conditional inferences regarding habitat selection are possible. An individual may be forced to occupy a home range containing a large proportion of suboptimal habitat. However, analyses of individual choices within a home range still provide information regarding the relative value of the habitats that occur there, i.e., habitat quality can be measured conditionally within each home range. Resolving the problem of identifying important but rarely used habitat is dependent upon adequate sample size (of individuals, and of observations per individual) and an appropriate sampling design, as discussed below.

Methodologically, we first must assign weights to each habitat. A weight of 0 indicates habitat that is average in quality to the focal organism, positive values indicate greater quality, and negative values indicate lower quality. If no data are available for the population and landscape in question, expert opinion or data extracted from other studies can be used to assign weights. Whenever possible, though, data from the focal landscape should be used, as conditions and behaviors can vary regionally (Morrison and Hall 2002; Stauffer 2002). If locational data of habitat use are available from uniquely identifiable individuals (e.g., radiotelemetry studies), habitat weights may be estimated directly. A reasonable first approximation for habitat weights is the selection ratio, w , transformed to yield weights that are symmetric and centered on 0:

$$\log(\bar{w}_i) = \log\left(\frac{\pi_i}{o_i}\right),$$

where o_i = the proportion of habitat i available in the home range of the animal and π_i = the proportion of observations occurring in habitat i . Data of this type should be collected using a sampling design in which habitat use and availability are determined for each animal within its home

range based on a sample or a census (Thomas and Taylor 1990; Manly *et al.* 1993). Technological advances enabling automated telemetry and geographic positioning systems to be used for obtaining locational data at frequent intervals permit estimates of travel distances to be computed from trajectory data. In this case, the proportion of the total distance traveled in habitat i would be substituted for the proportion of observations in the above equation. Using $\log(w_i)$ as habitat weights has the advantage of being empirically based and readily available from either field studies or literature review. Another important advantage is that standard errors of $\log(w_i)$ can be readily computed. Because individuals are the sampling units, each individual's $\log(w_i)$ represents a replicate that can be used to compute a sample mean and variance for each habitat based on the data from n individuals:

$$\overline{\log(w_i)} = \sum_{j=1}^n \log(w_{ji})/n$$

$$\text{var}[\log(w_i)] = \frac{1}{n-1} \sum_{j=1}^n (\log(w_{ji}))^2 - \frac{\left(\sum_{j=1}^n \log(w_{ji})\right)^2}{n}.$$

Together, these statistics are useful in pairwise comparisons of habitats and in sensitivity analysis. Aebischer *et al.* (1993) and Pendleton *et al.* (1998) provide details on the use of $\log(w_i)$, including suggestions for dealing with situations in which a habitat is available but unused by an animal during the period of study (natural zero) and situations in which a habitat is unavailable to an individual (structural zero).

Ecologically Scaled Habitat Maps Using GIS

The initial step in implementing this algorithm is to reclassify a raster habitat map with the habitat weight associated with each habitat type. The resolution of this map is dependent on data availability and unrelated to ecological scale. A moving-window approach is used to create a new raster map which is scaled appropriately to the species' individual area requirements and mobility. The moving-window approach calculates the cell values for the new map as the average of the habitat weights within the area encompassed by the moving window.

Spatial scale is addressed by specifying the output cell size. An appropriate cell size should correlate to the spatial requirements of the animal (i.e., home-range size). Changes in spatial scale affect the resolution of the output map and preclude the inclusion of small isolated areas of suitable

habitat. These areas do not constitute a population-level patch, but they may be important as stepping stones to facilitate movement between patches (*see* Miller and Russell–Chapter 8).

Habitat weights are centered on 0 and classified dichotomously; thus, a cell value greater than 0 indicates suitable habitat, whereas a cell value less than 0 indicates unsuitable habitat. For some types of analysis it may be useful to classify neutral habitats centered around 0, although the critical values forming the boundary between suitable, neutral, and unsuitable habitats are likely to be subjective and dependent on the question being addressed.

Mobility is accounted for in this algorithm by specifying the size of the moving window. As window size increases, small areas of unsuitable habitat become less important. This is analogous to small areas of unsuitable habitat having less of an impact on species with high mobility. In general the ratio of window size to output cell size should be proportional to the ratio of movement capacity (such as mean dispersal distance) to individual area requirements. One potential method for determining this distance would be to use a quantile from the distribution of dispersal distances. The exact quantile would be dependent on the questions being addressed; however, it should be sufficiently large to ensure that population dynamics within a patch are distinct from neighboring patches. It may also be useful to use a weighted average of habitat weights, with the weights coming from the cumulative density function of either an empirical distribution of dispersal distances or from a theoretical model (geometric, exponential) fit to the empirical data.

CREATING ECOLOGICALLY SCALED HABITAT MAPS: AN EXAMPLE

From Land Cover . . .

To illustrate the method for constructing ecologically scaled habitat maps, we use a land-cover map of the Indian Pine Natural Resources Area (IPNRA) as an input (Figure 7-1). The area is intensively agricultural and is part of the upper Wabash River basin. Its structure has been described in detail previously (Gehring 2000). The land-cover map was digitized from digital orthophoto quad images at 1-m resolution and converted to a 5-m resolution raster image. We translated this map into a dichotomous patch map for a suite of hypothetical species (Table 7-1) covering a range of niche breadths (specialist, generalist), individual area requirements (small, medium, and large), and dispersal abilities (low, medium, and high). The patch map was implemented on the IPNRA landscape as follows.

TABLE 7-1.
Habitat weights used in the hypothetical example.

<i>Habitat</i>	<i>Weight</i>			
	<i>Specialist</i>	<i>Generalist</i>		
Herbaceous corridor	-1	2		
Wooded corridor	6	4		
Waterway	0	2		
Grassland	-1	1		
Forest	3	2		
Agriculture	-4	-2		
Urban	-5	1		
Wetland	1	1		
Plantation	0	1		
		<i>Small</i>	<i>Medium</i>	<i>Large</i>
Individual Area Requirements (ha)	0.25	4	100	

Nine land-cover categories were classified and assigned weights so that our hypothetical habitat specialists showed a strong preference for natural woodlands and a strong avoidance of human-dominated areas, i.e., agricultural and urban areas (Table 7-1). Habitat generalists preferred natural habitats but demonstrated true avoidance only of areas in agriculture (Table 7-1). The magnitude of the habitat weights also was less for generalists compared to specialists (Table 7-1), accentuating the typically strong reliance of specialists on some habitats and strong avoidance of others. In contrast, generalists tend more towards neutrality with respect to most habitats.

An ecologically appropriate spatial scale was incorporated when setting the resolution of the output grid (Table 7-1). For the hypothetical species with small individual area requirements, we assigned an output grid with a resolution of 50 m × 50 m. Terrestrial species in this landscape with home ranges of approximately this magnitude (0.25 ha) include white-footed mice (*Peromyscus leucopus*) and prairie voles (*Microtus ochrogaster*). For the hypothetical species with medium individual area requirements, we assigned an output-grid resolution of 200 m × 200 m. Occupants of this landscape with home ranges of approximately this magnitude (4 ha) include fox squirrels (*Sciurus niger*), eastern cottontails (*Sylvilagus floridanus*), and woodchucks (*Marmota monax*). Finally, for the hypothetical species with large individual area requirements, we assigned an output-grid resolution of 1000 m × 1000 m. Vertebrate species with home ranges of this size (100 ha) include white-tailed deer and raccoon (*Procyon lotor*).

Dispersal ability was considered in this procedure by averaging weights of habitats over areas equal to or larger than the size of the output cell (Table 7-2). For poor dispersers, only the habitat weights within the focal output-grid cell were included in the average value. Thus, if a poor disperser had a medium

TABLE 7-2.
Diameter of moving window (m) used to characterize habitat patches for hypothetical species of varying dispersal ability and individual area requirements.

<i>Dispersal ability</i>	<i>Individual Area Requirements (ha)</i>		
	<i>Small (0.25 ha)</i>	<i>Medium (4 ha)</i>	<i>Large (100 ha)</i>
Poor	50 m	200 m	1,000 m
Moderate	150 m	600 m	3,000 m
Good	450 m	1,800 m	9,000 m

individual area requirement (4 ha), averaging of habitat weights would be conducted over a 4-ha moving window. The value assigned to moderate dispersers was averaged over a window with a diameter of three output-grid cells, and the value assigned to good dispersers was averaged over an area with a diameter of nine output-grid cells (Table 7-2).

... To Habitat Maps

Habitat maps created using the land-cover map of Figure 7-1 were influenced strongly by ecological characteristics (Figures 7-2 through 7-7). For a given

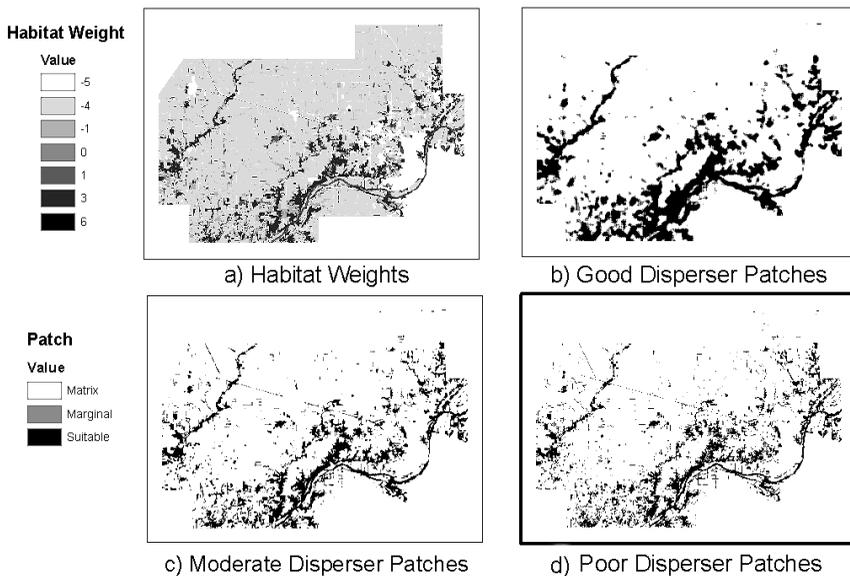


Figure 7-2. Ecologically scaled habitat maps of Indian Pine for hypothetical habitat specialists (weights depicted in panel a) with small individual area requirements (0.25 ha). Panels b, c, and d represent the effects of good, moderate, and poor dispersal abilities, respectively, on perceptions of landscape patchiness.

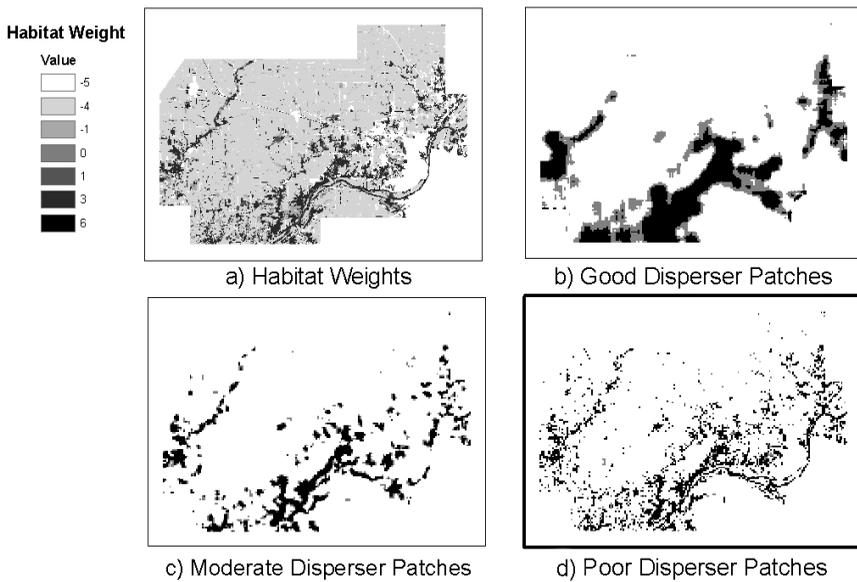


Figure 7-3. Ecologically scaled habitat maps of Indian Pine for hypothetical habitat specialists (weights depicted in panel a) with moderate individual area requirements (4 ha). Panels b, c, and d represent the effects of good, moderate, and poor dispersal abilities, respectively, on perceptions of landscape patchiness.

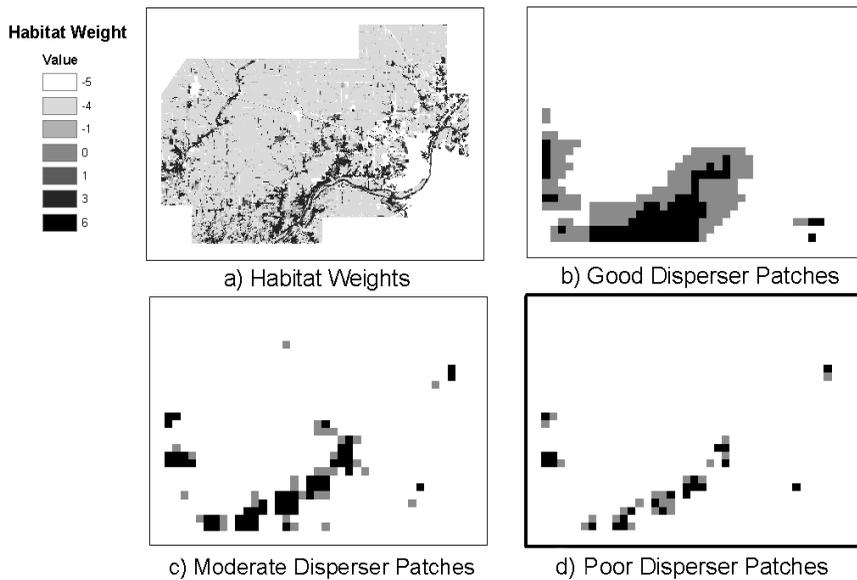


Figure 7-4. Ecologically scaled habitat maps of Indian Pine for hypothetical habitat specialists (weights depicted in panel a) with large individual area requirements (100 ha). Panels b, c, and d represent the effects of good, moderate, and poor dispersal abilities, respectively, on perceptions of landscape patchiness.

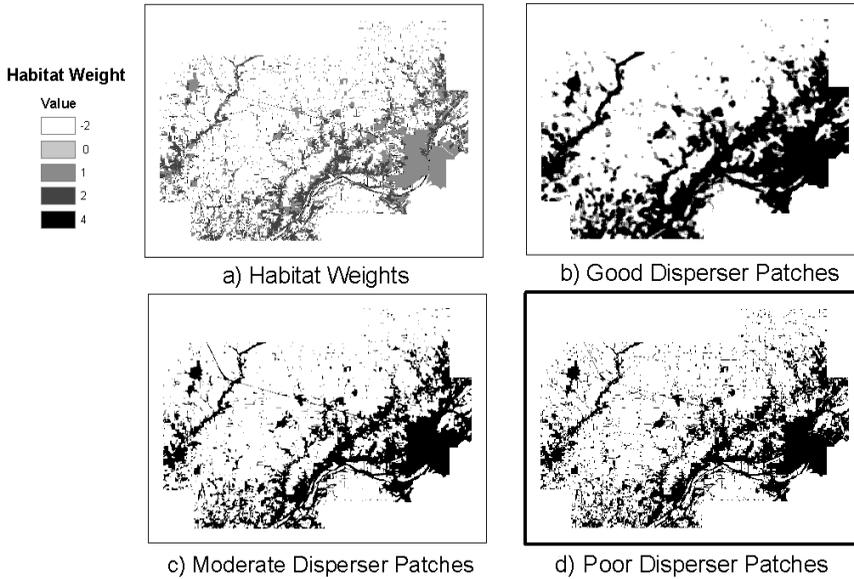


Figure 7-5. Same as Figure 7-2, except for hypothetical habitat generalists.

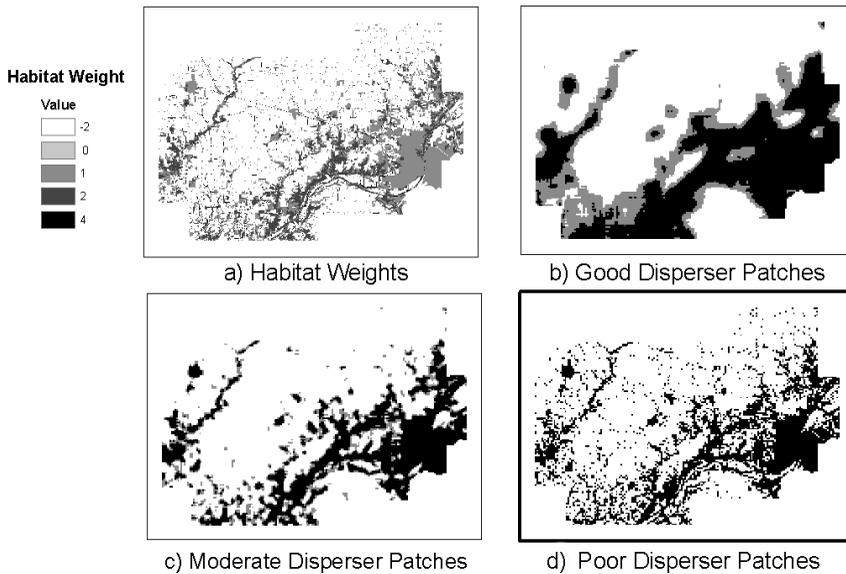


Figure 7-6. Same as Figure 7-3, except for hypothetical habitat specialists.

level of home-range size and mobility (i.e., dispersal), species with broad habitat tolerances perceived the landscape as more productive and better connected than woodland specialists (compare Figure 7-2 with 7-5, 7-3 with 7-6, and 7-4 with 7-7). Effects of habitat breadth on the landscape's carrying capacity were more pronounced for species with large area requirements and large dispersal abilities, because these attributes served to homogenize the

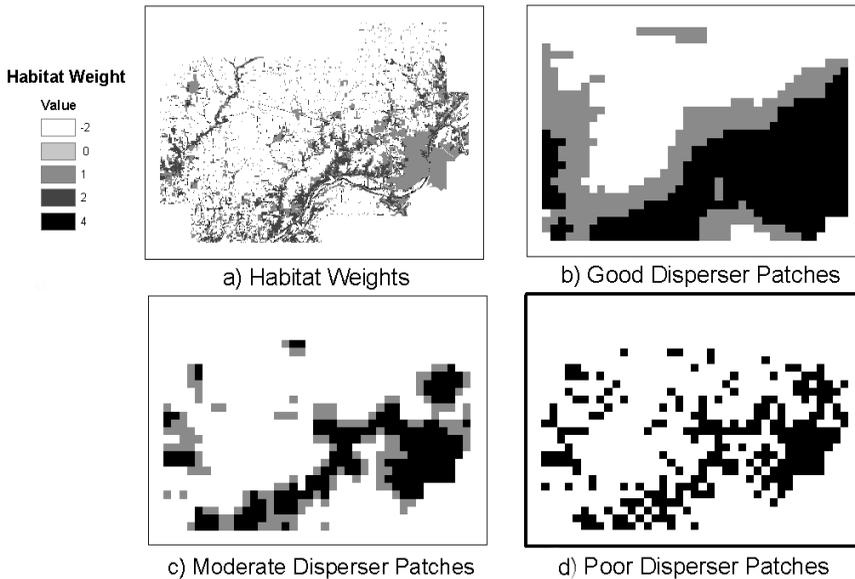


Figure 7-7. Same as Figure 7-4, except for hypothetical habitat generalists.

landscape from a habitat perspective (e.g., compare Figure 7-4b with 7-7b). Similarly, effects of habitat breadth on landscape connectivity were most notable for species with large area requirements (compare Figure 7-4 with 7-7), because patches of sufficient quality were more plentiful for the species capable of using nonwooded habitat.

Dispersal ability and energetic requirements appeared to have interactive effects in terms of patchiness of landscapes. As expected, enhanced dispersal ability produced landscapes that were more well connected (e.g., Figure 7-3b versus 7-3d). However, the effect of dispersal on connectivity was lessened for individuals with smaller area requirements, as home-range size became the limiting factor dictating landscape patchiness (e.g., compare Figure 7-2 and 7-4).

DISCUSSION

Applications

The method described in this chapter is useful for converting a land-use/land-cover map into a species-specific habitat map that discerns between suitable and unsuitable habitat. This dichotomous patch network can then be used as input into spatially explicit ecological models, such as incidence function models (Hanski 1994), ecologically scaled landscape indices (Vos *et*

al. 2001), graph-theoretic networks (Urban and Keitt 2001), and the hybrid ESLI-graph theory model described by Miller and Russell (Chapter 8).

Incidence function models provide a mathematically tractable method for exploring the effects of patch size and isolation on patch occupancy, population persistence, and carrying capacity. Required inputs are a dichotomous habitat map and presence/absence of the focal species in each patch at one or more points in time (Hanski 1994; ter Braak *et al.* 1998). From these data, estimates of colonization rates, extinction rates, and two scaling parameters are derived. Recent extensions to this basic model allow estimation of metapopulation persistence and carrying capacity (Hanski and Ovaskainen 2000; Feng and DeWoody—Chapter 4).

Ecologically scaled landscape indices provide estimates of carrying capacity and connectivity that are scaled according to the individual area requirements and dispersal abilities of a species (reviewed by Swihart and Verboom—Chapter 6). Required inputs are a dichotomous habitat map, an estimate of individual area requirements, and an estimate of mean dispersal distance. Evaluation of the contribution of each patch can be performed by removing the focal patch and recalculating the landscape indices without them (Vos *et al.* 2001; Opdam *et al.* 2003).

Graph theory has been proposed as an alternative measure of landscape connectivity, in which patches are nodes in a mathematical network. Operations based on the minimum-spanning tree have been developed for use in computer networking, utility, and transportation applications. Many of these operations are directly applicable to ecological patch networks (Urban and Keitt 2001). Miller and Russell (Chapter 8) present an approach that incorporates stepping-stone patches and linear barriers to provide more realistic measures of connectivity in landscapes with complex matrix habitat. Their method also accounts for multiple routes between patches and variable matrix habitat.

Relation to Other Approaches

Statistically based approaches to assessing landscape suitability have been used by wildlife biologists for over 2 decades. Logistic regression, neural networks, and fuzzy logic are some of the more recent applications of statistical-modeling applications that attempt to estimate the probability of a species' occurrence or abundance at a site as a function of environmental covariates (reviewed by Stauffer 2002). Williams *et al.* (1978) developed a procedure (PATREC, for pattern recognition) for assessing habitat suitability using Bayes' theorem, with conditional probabilities of suitable and unsuitable sites tied to environmental characters. Recent applications of PATREC have used GIS layers and knowledge of a species' habitat associations to guide the assignment of conditional probabilities (e.g., Roseberry and Sudkamp 1998;

Swimley *et al.* 1998). An advantage of PATREC and related approaches is the ability to predict the probability of occurrence of a species without the time-consuming process of creating a habitat map (Hepinstall and Sader 1997; Tucker *et al.* 1997). A singular disadvantage of these statistical tools is their reliance on patch occupancy as a surrogate for habitat quality, even though stochastic variation in equilibrial metapopulations can produce markedly different patterns of occupancy when viewed at different points in time (ter Braak *et al.* 1998). A feature shared by all of these statistical approaches is their focus on patterns, without regard for the processes generating these patterns. In contrast, the methods described in the preceding section are based on the movement potential and spatial requirements of organisms, which translate into the currency of metapopulation dynamics, colonization, and extinction (Hanski 1998). Statistical approaches to assessing patch or landscape suitability can be useful if the data needed for more process-oriented models are lacking. However, the development of our GIS-based method largely removes time and cost as significant obstacles to the creation and use of habitat maps when such data are available.

Caveats

Incidence function models, ecologically scaled landscape indices, and graph-theoretic measures all require as input a habitat map. We have argued that these process-based approaches are preferable to statistical approaches (*see also* Swihart and Verboom—Chapter 6). The success of these approaches is dependent on the extent to which the habitat map is a suitable representation of the habitat requirements of the species. Of course our method of defining patches based on a species' ecology is subject to constraints of data availability and resolution. Ideally, habitat maps should be created that are specific to the environmental characteristics driving the population dynamics of the focal species. Such maps might incorporate forage density and availability, predator density and detectability, interspecific competition, thermal and resting cover, etc. In reality, though, the characteristics driving population dynamics rarely are known. Even if these characteristics were known, they would be extremely difficult to map over large spatial scales. Moreover, the available data often are limited to relatively coarse habitat classifications (e.g., forest/grassland/urban/water) or collected for an unrelated purpose, such as land-use planning. For a predictive model relating land-use planning to ecological effects on wildlife populations, the base habitat map is constrained by the methods, resolution, and accuracy of the land-use model (*see* Craig *et al.*—Chapter 9).

Our method should be viewed as a starting point for considering the role of habitat requirements, spatial scale, and mobility in defining the patch network for a species. Several technical issues still need to be addressed.

The use of an average habitat weight in the moving window results in some edge effects at the patch boundary, particularly when the habitat weights of cells on opposite sides of the boundary are asymmetrical. If, for instance, the magnitude of the negative weight in unsuitable habitat is greater than the magnitude of the positive weight in suitable habitat, the patch area will be biased low and vice versa. Alternatives to a moving average, such as edge recognition or geostatistical methods such as kriging (Cressie 1993), might improve upon the algorithm described here. However, the basic considerations of weighting habitat quality, spatial scale, and mobility will still need to be explicitly addressed.

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