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PATCH: A spatially explicit life history simulator for terrestrial vertebrates

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to directly examine the cost, in terms of species' viability, of rates and patterns of habitat alteration.

This chapter is devoted to a description of the PATCH model, but it includes a case study reminiscent of the analysis of habitat alteration conducted by Wallin et. al. (1994). The model is presented in considerable detail in hopes of introducing the reader to some of the complications involved in merging realistic spatial detail with an otherwise simple demographic model. The case study is intended to serve as an example of the types of questions that can only be addressed using a model that conducts viability analysis within the confines imposed by landscape pattern.

MODEL DESCRIPTION

History

I first started working on the predecessor to the PATCH model while attending a summer school on Patch Dynamics organized by S. A. Levin, T. M. Powell, and J. H. Steele, and held at Cornell University in 1991. The first study to emerge from this modeling effort examined pattern formation generated from a spatially explicit version of a simple Nicholson-Bailey predator-prey model (Deutschman et. al. 1993). I continued the development of the model over the period from 1991 to 1995 at the University of Washington. During this period, I used the model to explore issues of habitat connectivity (Schumaker 1996), and I modified it to create a life history simulator for the Northern Spotted Owl (Schumaker 1995). An additional two years of work, from 1995 to 1997, saw the transformation of the spotted owl simulator into the present PATCH model. The PATCH model will be available, free of charge, from the US EPA beginning either in late 1997, or early 1998.

INTRODUCTION

The consequences of habitat alteration for wildlife species include the direct effects of habitat loss plus a host of indirect effects such as reduced inter-patch dispersal (Thomas et al. 1990, McKelvey et al. 1993, Schumaker 1995), increased edge effects (Chen et al. 1992), and conversion of source habitats to sinks (Pulliam et al. 1992, Dunning et al. 1992). Such indirect effects are difficult to detect, but they can strongly influence a landscape's ability to support the species that inhabit it (Reid and Miller 1989, Jensen et al. 1993, Lawton 1993, Schumaker 1995, Schumaker 1996). Complications such as these dictate that management efforts aimed at preserving wildlife diversity must consider how different species' habitat requirements and behaviors couple with landscape pattern, and to what extent landscape pattern limits species' viability.

Unfortunately, few meaningful generalizations exist with which to estimate the consequences of habitat alteration for wildlife species (Fahrig 1991, Doak and Mills 1994, Schumaker 1996). The research described here attempts to overcome such shortcomings by making use of a new spatially explicit life history simulator called PATCH. This model has been recently completed, but was derived from an existing spotted owl simulator (Schumaker 1995) that has undergone extensive peer review. PATCH reads Geographical Information System (GIS) imagery directly, and it uses these data to link every attribute of a species' life cycle to the quality and distribution of habitat throughout a landscape. The model tracks an entire population of organisms comprised of individuals that each are born, disperse, breed, and then die. PATCH is designed specifically to work with a complex landscape composed of habitats of various shapes, sizes, and qualities. Further, these landscapes can change continuously through time, and in this way the model is able

Overview

PATCH (figure 1) is a Spatially Explicit Population Model, or SEPM (Dunning et al. 1995). PATCH stands for *a Program to Assist Tracking Critical Habitat* (its focus on critical habitat will become apparent later). The model is distinguished by the attention it pays to landscape pattern, and by its ability to work with an entire spectrum of terrestrial vertebrates. PATCH directly imports GIS habitat coverages, and is parameterized with habitat utility indices, territory size, survival and fecundity information in the form of a population projection matrix (Leslie 1945, Lefkovitch 1965, Caswell 1989, Gotelli 1995), and estimates of movement ability and behavior. PATCH is females-only model, is highly parsimonious, and is designed to accommodate a range of data availability and quality. The outputs generated by the PATCH model include population size as a function of time, effective survival and fecundity rates (rates that reflect the effect of habitat quality on the population), and estimates of the importance of each territory-sized parcel of habitat for the modeled population. These features permit the user to quantify the consequences of landscape change for population viability, to estimate changes in vital rates corresponding to habitat loss or fragmentation, and to identify source and sink habitats within a landscape.

PATCH was designed specifically to address the contribution of spatial pattern to the viability of a wildlife species. A typical use of the model would include establishing a baseline viability analysis under current landscape conditions. The investigation might stop here, or the model landscape could be modified, and the consequences of this change for the viability of the organism would then be assessed by repeating the demographic analysis.

Patch identification

It is often desirable to identify aggregate features of landscape pattern that correlate with measures of ecological quality such as population viability, or habitat connectivity (Schumaker 1996). PATCH facilitates this type of analysis because it includes a module devoted specifically to quantifying landscape pattern. Many different metrics can be developed from measures of landscape pattern. PATCH's approach to providing such information is to break a landscape up into a collection of individual fragments of habitat, and then to provide a limited amount of information about each one. Indices of landscape pattern, can subsequently be constructed from this information.

For the purposes of patch identification, PATCH allows each habitat type to be assigned a weighting value (i.e. species' habitat preferences), which takes the form of an integer between 0 and 99. Any pixel that has been assigned a non-zero weight is treated as habitat, whereas the rest are considered non-habitat. PATCH then locates individual patches in the imagery using one of two rules for defining connectivity. One rule specifies that each pixel has only four neighbors that touch it, while the other implies that each pixel has a total of eight touching neighbors. Based on the rule that is applied, PATCH then assigns every habitat pixel to one, and only one, patch. The area, weighted area, interior area, and perimeter are then computed for each patch. Area is measured as the number of pixels of habitat present. Weighted area is measured as the sum, taken over every pixel in a patch, of the weighting values assigned to each pixel. Interior area is computed based on a user defined edge width, which is specified as a number of pixels. A patch's interior area is defined as the number of pixels that are at separated from the patch's perimeter by a distance equal to at least one edge width.

Many well known indices of habitat pattern can be built up from the measures described above. Examples include perimeter-area ratio, shape index (Patton 1975, Forman and Godron 1986), estimates of fractal dimension (Milne 1988, Milne 1991), and patch cohesion (Schumaker 1996). More importantly, this analysis provides the raw data necessary to construct yet undescribed measures of landscape pattern that might serve as effective indicators of ecological quality.

Territory allocation

Before PATCH's demographic analysis can be conducted, it is necessary to break the landscape being used into an array of territory-sized units. This process, termed territory allocation, is accomplished by intersecting the GIS image with an array of hexagonal cells. PATCH was designed with the intent that each hexagon's area would equal the size of a typical territory for an individual of the species being modeled. In addition to setting the hexagon size, the user also provides a minimum and a maximum territory size. The minimum size corresponds to the size of a territory in optimal habitat, while the maximum size would be assumed to occur in the most marginal habitats. Each individual hexagon within the territory map has two attributes: its score, and its breeding status. A hexagon's score is computed as the arithmetic average of the weighting values assigned to each of the data pixels contained within it. Thus the scores are real numbers between zero and the maximum weighting value assigned to any of the habitat categories present in the GIS imagery. A hexagon's breeding status is a binary attribute that determines whether or not breeding is allowed at the site. Breeding status is determined based on the minimum and maximum territory sizes, as described below.

The territory minimum and maximum sizes do not affect the hexagon areas. Instead, these parameters govern the degree to which habitat can be shared across hexagon boundaries in an attempt to allocate the maximum number of breeding sites throughout the landscape. The territory allocation algorithm proceeds in several steps. Initially, PATCH computes a threshold score using the equation

$$\text{threshold score} = \text{maximum weighting value} \times \frac{\text{minimum territory size}}{\text{hexagon size}}.$$

This relationship defines the threshold score to be that which would be assigned to a hexagon containing only the minimum territory size worth of optimal habitat. Any hexagon with a score of at least this threshold value is automatically labeled suitable for breeding. Hexagons that do not meet this threshold value still have a chance to be classified as breeding sites, and this depends on the maximum territory size parameter.

PATCH determines the extent to which habitat can be shared across the hexagon boundaries using the expression

$$\text{expansion} = \frac{\text{maximum territory size}}{\text{hexagon size}} - 1.$$

The expansion parameter defines the maximum amount of habitat, expressed in fractions of a hexagon, that one cell can borrow from its six immediate neighbors. The maximum territory size is never allowed to exceed seven times the size of a single hexagon, and thus the expansion parameter can never exceed the area of a hexagon's six neighbors. After identifying every hexagon that contains enough high quality habitat to qualify as a breeding site, PATCH builds a

list of all of the remaining sites that have any habitat at all. These hexagons are sorted by score, in decreasing order. The hexagons are then allowed, in turn, to borrow habitat from their neighbors up to the limit set by the expansion parameter. Borrowing continues until a hexagon either meet the suitability threshold, or exhaust its license to infringe on its neighbors. Habitat can only be lent once, but hexagons that are unable to meet the suitability threshold return any habitat they have borrowed in the process.

The amount of habitat that can be borrowed depends on whether the lending hexagon is suitable for breeding. Suitable hexagons are allowed to lend only what they hold in excess of the threshold score, while unsuitable hexagons can lend all of their habitat. Borrowing begins with the neighbor having the largest amount of habitat to lend, and concludes with the neighbor having the least. This process, coupled with the initial sorting of the borrowing hexagons by score, approximately maximizes the allocation of suitable breeding sites across the landscape. What borrowing really entails is one hexagon laying claim to a fraction of the total quality of some (or all) of its neighbors habitat. If the expansion parameter has a value of 2.5, that implies that portions of each neighbor can be borrowed until a total of 1.5 hexagons worth of the neighboring habitat has been claimed. The borrowing process is conducted under the assumption that each lending hexagons habitat is distributed uniformly throughout its area. It is important to note that the process of borrowing habitat does not change any features of the territory map other than the determination of which hexagonal sites are deemed suitable for breeding. The additional energetic costs of defending a larger territory are approximated through the borrowing process since hexagons that are labeled suitable for breeding by virtue of having borrowed habitat will have lower scores than those that had sufficient habitat on their own. These lower scores can then translate into higher mortality rates and lower reproductive output later in the demographic analysis.

The construction of a territory map from the initial GIS imagery adds a number of desirable features to the PATCH model. The structure of a territory map is simple compared to the GIS imagery from which it was derived. For the purposes of demographic modeling, PATCH is only concerned only with each hexagon's score, whether or not it is suitable for breeding, and who its neighbors are. The details of habitat patterning within each hexagon are not important at this level of analysis, and they are therefore ignored. The hexagon map may sometimes constitute the final product of the analysis, or it may serve as an intermediate product that can be peer reviewed. The PATCH model also contains an editor that allows the user to alter the territory map. Using this tool, alternative future landscapes can quickly be developed, or "what if" questions addressing the consequences of specific habitat modifications can be easily pursued. PATCH also makes it possible to randomize the placement of hexagons within a territory map, and this feature can be used to test hypotheses about the importance of particular orientation of habitat across a landscape.

Demographic simulations

PATCH conducts demographic simulations within the territory maps described in the previous section. The life cycle is modeled as a series of discrete events that take place on a yearly basis. The model year begins in the summer with a breeding pulse, which is followed in the autumn by the mandatory dispersal of the young-of-the-year (hence referred to as "juveniles"). Next comes over-winter survival, which is followed by the optional movements of adult animals in the spring, and finally a census it taken. The process then begins again with the summer of the following year. For simplicity, all mortality is collapsed into the single evaluation that takes place in the winter. There is no additional mortality associated with the movement process. The model also allows the

landscape to change in time. The user activates this feature by instructing the model to load new territory maps at different points during a simulation. A new territory map can be installed at the start of any given year, and this function can be used even if multiple replicate simulations are being conducted.

Survival and reproductive information is entered into the PATCH model in the form of a population projection matrix, and its demographic simulations can be thought of as an extension of the analysis that would be performed using a matrix model. If an entire landscape consists of optimal habitat, and if breeding sites are unlimited, then PATCH will generate results essentially identical to those that would be obtained using a projection matrix. However, to the extent that high quality habitat is limiting, the model results will differ from those of a projection matrix. PATCH also differs from a matrix model in that it is individual based, and because its survival, reproduction, and movement modules all incorporate an element of stochasticity. Decisions regarding survival probability, reproductive output, and movement behavior, are all made on an individual basis, and they can be significantly influenced by the quality of the habitat contained within the hexagonal cells that the organisms occupy.

PATCH does not automatically make the assumption that survival and reproductive output scale linearly with habitat quality. Instead, the user is provided with a set of six generic interpolation functions that can be used to describe the manner in which habitat quality affects these vital rates. These functions are linear, logistic, concave, convex, constant, and piecewise constant (see figure 1). The user is required to provide survivals and fecundities (number of females per female that survive to the following year) in the form of a projection matrix. It is also necessary to specify what quality of habitat these vital rates should be associated with. That is,

PATCH needs to know if these survivals and fecundities that are supplied to the model will be realized in the best habitat, or the worst, etc. The user then specifies an interpolation function for survival, and one for fecundity, and then this portion of the model parameterization is complete.

Other than specifying the model organism's movement behavior (discussed below), there are only a few remaining parameters for the user to define. It is necessary to specify the duration in years of each simulation, and the number of replicate simulations that will be conducted. PATCH must also be told where within the territory map to locate the initial population of organisms, and what age or stage class they are to be assigned to. It is also necessary to specify whether any of the hexagons (other than at the edges of the GIS imagery) should be treated as reflecting boundaries. Lastly, a transient period can be specified before which information about the emigration and immigration into breeding sites will not be tallied (see below).

The movement module

Three different movement routines are available within the PATCH model. In addition, three distinct rules can be used to specify a level of site fidelity (the likelihood of remaining on an occupied breeding site from one year to the next). The options for simulating movement include a directed random walk, selection of the best available site within a search radius, and selection of the closest available site within a search radius. These movement routines require that the user specify a minimum and a maximum movement ability in terms of the total number of steps that can be taken from a hexagon to one of its six neighbors. It is also necessary to place bounds on how random vs. directed the movement will be when a random walk is taken. This is done through the specification of a minimum and a maximum turning rate. The options for site fidelity are termed high, medium, and low. High site fidelity implies that organisms possessing a territory

will never relinquish it. Low site fidelity implies that every territorial individual will search yearly for a new site. If site fidelity is set to medium, then the decision regarding whether to remain on a territory, or to leave it in search for a superior site, is made based upon the quality of the habitat at the current location. All of these features of the movement module are discussed in detail below.

The movement routine is called twice per year. It is used to drive the movements of adult organisms prior to the breeding pulse, and is used later to control the dispersal of the year's new juveniles (the young-of-the-year). The implementation of the movement routine is slightly different depending on whether juveniles or adults are moving. Every juvenile is obliged to disperse away from its natal site, whereas adults may or may not elect to move. Decisions regarding adult movement are based upon the individual's status (territorial vs. floater), the quality of habitat currently being occupied (for territorial individuals), and the site fidelity parameter. Juveniles are not allowed to settle until they have moved at least the minimum distance specified by the user. In addition, until this minimum distance has been traversed, juveniles travel with the minimum turning rate (i.e. these movements are made as linear as possible, forcing the juveniles to move away from the natal site). Adults, on the other hand, are not subject to a minimum movement distance or the restrictions on turning rate imposed on the juveniles. As a whole, this scheme provides the user with the flexibility necessary to apply the model to a variety of organisms using only a small number of parameters.

When a random walk is used for the movement routine, individual organisms take a series of steps from a the hexagon currently occupied to one of its six neighbors. The direction of the walk is influenced by the quality of the habitat within which the movement is taking place, the minimum and maximum turning rate, and the direction previously moved. Individuals taking a

random walk first look to see if any of their neighboring hexagons are suitable for breeding and available. If so, then they elect whether or not to settle in that site. This determination is based upon the site's quality, and upon the site fidelity parameter. The better the quality of the site, the more likely an individual is to settle in it. Given this, individuals are more selective when site fidelity is high (they will not get another chance to move) and are less selective when site fidelity is low (they will always get another chance to move). In addition, individuals become less selective as their ability to continue searching diminishes. If a suitable, available, neighbor does not exist, then individuals will select a neighbor to move into with a degree of randomness that is governed by a general tendency to move towards (but not necessarily to remain in) higher quality habitats, and by the influence of the turning rate parameter.

The turning rate parameter takes on values between 0 and 100%. When the turning rate is 100 percent, the choice of which of a hexagon's six neighbors to move into will be made randomly (in the absence of decisions to move specifically to a higher quality site). When the turning rate is zero, an individual will always move in the direction of the previous step, thus producing linear motion. The user sets the bounds on the turning rate parameter by setting its minimum and maximum values. However, at any given location in the landscape, the turning rate that is actually used is derived from the relationship

$$\text{turning rate} = \frac{\text{hexagon score}}{\text{maximum score}} \times (\text{max turning rate} - \text{min turning rate}) + \text{min turning rate}.$$

This ensures that the turning rate used in any movement decision falls in the range spanned by the minimum and maximum turning rates, and that this value increases linearly with the quality of the hexagon presently occupied. The value obtained for the turning rate is then used in the process of

selecting the next hexagon to move to. The result of this scheme is that movements are generally more linear in poorer habitats, and they become more random in higher quality habitats. Thus, the organisms tend to travel quickly through sparse regions of the landscape, and they perform a more exhaustive search for available breeding sites when they arrive at clusters of suitable habitat. This behavior is accentuated by the individuals tendency to move into, but not necessarily to remain in, high quality habitats.

When individuals searching for breeding sites are instructed to select the best, or closest, available site within a search radius, the movement process takes on a very different set of characteristics. For juveniles, the search radius becomes the annulus, centered on the current site, defined by the minimum and maximum movement abilities. For adults, the search radius becomes the disk with a radius equal to the maximum movement ability. The quality and availability of every hexagon within the search radius is examined if the best site is to be selected. If the closest available site is to be selected, then the search radius is expanded iteratively from the minimum to the maximum until a suitable hexagon is located. In either case, if the searching individual is unable to locate a suitable site, a random walk is taken.

The behavior of PATCH's movement algorithm is also controlled by the site fidelity parameter. Site fidelity governs the probability that a territorial adult will elect to abandon its territory in search of one of higher quality. In the spring, just before floaters begin searching for breeding sites, the territorial adults decide whether or not to venture out in search of a better site. If the site fidelity parameter is low, then every adult will abandon its territory (if one is held) and search for another site. If site fidelity is high, individuals holding territories remain on them indefinitely. When the site fidelity parameter is set to medium, individuals will elect to move if the

site is expected to behave as a demographic sink. The analysis involved in making this decision is explained in greater detail in the section on model outputs, below.

Individuals in motion will reflect off of the edges of the GIS image. In addition, the user can force any hexagon to behave like a reflecting boundary as long as it is not suitable for breeding. This feature is designed to allow the user to prohibit movement beyond a coastline, or over a mountain range, etc.

Model outputs

The PATCH model produces an array of output information. PATCH provides the user with a histogram showing the number of data pixels of each habitat type present in the GIS imagery. In addition, the patch counting algorithm produces a table that displays the area, weighted area, interior area, and perimeter of each patch in the landscape. The territory allocation algorithm produces a table that displays the score, area, weighted area, and breeding status of each hexagon. This table also provides the interior area and perimeter, computed on a patch by patch basis, that happen to fall within each hexagon. These outputs allow the user to build up a broad range of pattern-based indices of landscape quality, from the simplest measures of habitat area up to sophisticated estimates of the range of breeding site qualities present in a landscape.

The demographic model produces five additional outputs. The principal output file contains the input parameters used, and an array of information for every replicate run and year. The array of information includes the mean dispersal distance (juveniles only) reported as both the total distance moved, and as the net displacement from the starting point. Also included are the sizes of the floater and breeder populations, and the number of individuals in each age/stage class. A

second demographic output file contains the means and standard deviations, taken over each replicate run, of the total population size, the number of floaters, breeders, and the number of individuals of each age/stage class. PATCH also tracks the effective aggregate survival rates and fecundities, on an age/stage class basis, as mean values taken over all of the replicate runs. This output data can be thought of as consisting of a unique population projection matrix for each year of a model simulation. The mean population size on an age/stage class basis, taken over the all of the replicate runs, can be reproduced exactly from this time series of projection matrices using matrix multiplication. This output data lets the user track the changes in the survival rates and fecundities, for each age/stage class, taking place through time.

Lastly, the PATCH model has features that both estimate, and then actually track, whether portions of the landscape function as demographic sources or sinks. This analysis is performed on a hexagon by hexagon basis, but it is only done for suitable breeding sites. The potential of a hexagon to function as a source or sink is evaluated by computing the value of the dominant eigenvalue (λ) of the projection matrix associated with the site. The computation of λ incorporates information about the site quality, the survival and fecundity information supplied to the model, and the interpolation functions that are being used to assess survival and fecundity in hexagons of arbitrary quality. This information then provides the user with an initial estimate of the importance of portions of the landscape for the model species.

The PATCH model also tracks the immigration into, and emigration from, each breeding site, and uses this information to identify effective demographic sources and sinks throughout the landscape. Specifically, what PATCH does is to increment a counter each time an individual leaves a breeding site, and decrement the same counter each time an individual enters the site.

These counters are referred to as "utility values", and a separate utility value is compiled for each breeding site. The user specifies at what time the utility data should start being collected, and then the immigration and emigration data is gathered for every subsequent year. Individuals in motion that simply pass through a site produce no net change in its utility value. On the other hand, when individuals are born in, and subsequently disperse from a breeding site, this produces an incremental gain in utility. When individuals move into a breeding site, and then die, this produces an incremental loss in utility.

PATCH's source-sink analysis is then presented to the user in three files. The first is a table that displays the score, lambda-value, and utility value for each breeding site. The second and third files are raster images of the lambda-values and utility scores, respectively, which can be directly compared to the territory map.

A Case Study

Methods

I developed a case study that exhibits some of the features of the PATCH model described in the preceding text, but that also addresses the theme of the 1996 AMIGO workshops. The focus of these workshops was cross-biome comparisons of the consequences of habitat fragmentation. This case study examined the response of two wildlife species to two types of habitat fragmentation in two contrasting landscapes. The model species included a "large" organism characterized by low reproductive output, high survival, and a large territory size. Also modeled was a "small" organism characterized by high reproductive output, low survival, and a small territory size. Both of these species exhibited identical habitat affinities. The two types of habitat

fragmentation mimicked "aggregated" vs. "dispersed" clear-cutting. Aggregated clear-cutting was approximated by removing large (100 x 100 pixel) squares of habitat. Dispersed clear-cutting was approximated by removing small (10 x 10 pixel) squares of habitat. Landscapes were either subjected to the aggregated or dispersed cutting, not both, and the frequency of dispersed cuts was always 100 times that of the aggregated cuts. A sequence of landscapes exhibiting increasing degrees of habitat removal was generated by imposing a specific number of cuts, saving the resultant image, and then proceeding on with additional cuts. The cuts were placed randomly across the landscapes, and no attempt was made to prevent their overlapping one-another. Areas that were clear-cut remained in this state for the duration of a model run.

The landscapes used in this study (figure 2) were simply fabrications intended to illustrate very different types of underlying habitat pattern. Landscape 1 (figure 2) might typify habitats distributed along an topographic gradient, whereas landscape 2 could characterize a patchy array of vegetative communities or habitat patterns resulting from intensive management. Habitat utility indices (HUI), which are relative measures that designate each habitat's suitability for the model species, were specified for the different categories present in the two landscapes. The category depicted in black in figure 2 was assigned a HUI of six, the darkest gray color was given a HUI value of five, and so on down to the habitat colored white, which was assigned an HUI of one. Clear-cuts were assigned an HUI of zero. Prior to fragmentation, landscape 1 held identical numbers of pixels of each habitat type. Landscape 2 held similar, but not quite identical, areas of each of the habitat types.

The larger model species had a territory size that was ten times that of the smaller species, and each landscape could hold 6960 of the large territories and 68,854 of the smaller territories. The

minimum and maximum territory sizes were set to 1/2 and 3/2 the hexagon size, respectively. The population projection matrices, and associated lambda values (Caswell 1989), used for the two species were

$$\text{small organism} \rightarrow \begin{bmatrix} 0.74 & 1.20 \\ 0.20 & 0.50 \end{bmatrix} \quad ; \quad \text{lambda} = 1.124$$

$$\text{large organism} \rightarrow \begin{bmatrix} 0.00 & 0.50 \\ 0.50 & 0.90 \end{bmatrix} \quad ; \quad \text{lambda} = 1.123$$

For both organisms, the interpolation functions for survival and fecundity were set to linear, and the movement routine used was a random walk. Individuals searching for available breeding sites were allowed to take a maximum of 25 steps from hexagon to hexagon. Dispersing juveniles were obligated to move at least 5 steps before settling. The range of burning rates was set at the maximum possible (0 - 100%) and the landscape was initialized with every breeding site filled with an adult. Simulations were conducted for each combination of landscape, organism, and cutting regime (aggregated vs. dispersed) at each of 26 different levels of habitat fragmentation. In every case, five replicate simulations were performed, and the results were averaged across replicates. Utility data, used to identify demographic sources and sinks, were collected only after the first 100 years so that transient effects of the model parameterization could die down.

Because the two model species had identical habitat preferences, and nearly identical values for lambda, they could be expected to perform equally well in the absence of complications arising from spatial pattern. Observed differences in the performance of the two species should be tied to interactions between the landscape patterns, life history attributes, and the cutting regimes.

The goal of this analysis was a qualitative examination of the relative importance of each of these contributions to the overall success of the model species.

Results

Habitat loss was tracked as the percent degradation of a landscape's quality. The equation used to obtain percent degradation was

$$100 \times \frac{\sum \text{pre-fragmentation pixel weights} - \sum \text{post-fragmentation pixel weights}}{\sum \text{pre-fragmentation pixel weights}},$$

and thus degradation measured the loss of habitat, weighted by the quality of that habitat. Defined this way, percent degradation served as a unitless metric for making comparisons between landscapes and disturbance regimes. The two study landscapes were subjected to 25 different levels of habitat fragmentation, for each cutting regime, plus the original pre-fragmentation images. Habitat degradation resulting from this fragmentation spanned a range from zero to 64 percent.

Because the sample landscapes could support larger numbers of the smaller organisms than the larger ones, comparisons of the model results between species were conducted using a relative measure of population size. The measure that was used for the relative population size was

$$\frac{\text{mean population size in the pre-fragmentation landscape}}{\text{mean population size in the post-fragmentation landscape}},$$

where the mean values were computed from the last 50 model years of five replicate simulations. (five replicate simulations were performed for each combination of model parameters reported

here). The standard deviations derived from the five replicate model simulations were small compared to the population size. This measure of relative population size provided a unitless estimate of the amount by which the populations declined under the fragmentation pressure. The relative population size parameter took on values between zero and one.

The principal results of the case study are displayed in figure 3. Relative population size was tracked as a function of percent degradation for both landscapes, disturbance regimes, and species. Underlying landscape pattern appeared less important than disturbance regime or life history strategy in determining the population response to habitat loss. Not surprisingly, interactions between body size and disturbance regime played a large role in species persistence, as evidenced by the differential responses of the two species under the dispersed cutting regime. These results are encouraging because they suggest that cross-biome comparisons of wildlife responses to habitat fragmentation may be useful in spite of inherent differences in landscape pattern.

Estimates of population size, while critical to viability analyses, provide little or no insight into the spatial patterns of habitat use by model organisms. Summary data exhibiting patterns of habitat use, if collected at all, are typically presented as rates of habitat occupancy. PATCH is designed instead to track immigration and emigration rates into breeding habitat, and from this information it compiles data on demographic sources and sinks (see Model Description, above). Source/sink data are arguably superior to occupancy rate information because they better indicate the importance of different localities for the population under study. Source/sink data were compiled for each of the model simulations conducted in this study, and these data provide a visual analogue to the results displayed in figure 3. For the sake of brevity, I examine here only the

source/sink data acquired from the pre-fragmentation landscapes, and from landscapes that were degraded by approximately 42%.

The top panels of each of set of three images in figure 4 display the pre-fragmentation source/sink data associated with the different landscapes and species. The best sources are colored dark black, while poorer sources and then sinks are displayed in increasingly lighter shades of gray. Habitats that were not suitable for breeding, or for which immigration and emigration were exactly balanced (including those that were never occupied) are displayed in the lightest shade of gray. Immigration and emigration were compiled on a hexagon by hexagon basis, but for the purposes of constructing figure 4, these hexagons have been collapsed into small squares (this is done to minimize the disk space necessary to store the images). Hexagons (shown as the little squares) that, as a result of fragmentation, contained no habitat whatsoever are colored white in figure 4. Hexagons that experienced some fragmentation, but that still contained some habitat, are shown in one of the shades of gray (note in particular that the source/sink maps with the large species and small clear-cuts contain no white areas).

The source/sink images corresponding to the pre-fragmentation landscapes provide baselines for the evaluation of the source/sink data in the post-fragmentation landscapes. The center panels in figure 4 display the source/sink data resulting from simulations conducted with aggregated clear-cutting. Remnants of the pre-fragmentation source/sink patterns can be clearly observed in the post-fragmentation images exhibiting these large disturbances. This is less true of the source/sink data resulting from the dispersed clear-cutting (bottom panels in figure 4). There, the patterns become blurred, and in the case of the large species plus the dispersed cutting, evidence of the underlying landscape patterns is lost altogether.

Figure 4 reinforces the notion, derived from the data of figure 3, that underlying landscape pattern is a less critical determinant of the response to fragmentation than are relationships between the spatial scales associated with the model species and the disturbance. figure 4 shows that the effect of the large disturbances is to dramatically lower the quality of some large pieces of the landscape, while leaving other areas intact. Both the large and small organisms were still able to construct many high quality territories in these landscapes, and these areas buoyed up the simulated populations even at high levels of habitat degradation. The effect of the small disturbances, however, was to dramatically reduce the likelihood that a territory of high quality could be constructed anywhere in the landscape. And this effect became more pronounced as the territory size increased. Consequently, the small model species fared more poorly in the midst of the dispersed clear-cutting, and the large organisms did the worst overall. These results suggest that, all other things being equal, the consequences of habitat loss that is aggregated across a landscape may be less severe than losses that are more uniformly distributed in space. However, no attempt was made here to realistically mimic any type of anthropogenic disturbance, Moreover, in nature, all other things are never equal and compensations associated with large-scale disturbances might negate any advantages suggested by this analysis.

CONCLUSIONS

The PATCH model was designed to help investigators examine the importance of landscape pattern for an array of terrestrial vertebrate species. The model is based on a population projection matrix, and it requires the user to specify a minimum of parameters. While PATCH's life history module is simple, its coupling to spatial pattern through GIS imagery adds a great deal of complexity to the overall model behavior. Landscape categories can be assigned different habitat

utility indices, and these in turn affect the survival, reproduction, and movements of the model organisms. Individuals compete for high quality breeding sites, and this introduces density dependence and, at times, metapopulation-like dynamics. PATCH's many outputs allow an investigator to conduct viability analyses, to examine the differential effects of habitat pattern (or loss) on individual age or stage classes, and to both predict and track the importance to the population of specific habitat units through an analysis of demographic sources and sinks.

A case study was conducted that illustrated some of the workings of the PATCH model, and that examined an issue central to the 1996 AMIGO workshops. The importance of underlying landscape pattern, types of anthropogenic disturbance, and species life history characteristics, were examined in the context of a population viability analysis. The results of the case study suggest that inherent differences in landscape pattern will not preclude cross-biome comparisons of the effects of habitat fragmentation on certain wildlife species. The results suggest that the severity of the impacts to wildlife will instead be determined largely by interactions between the spatial scales of disturbance and the spatial scales important to the organisms responding to the disturbance. While this analysis is simple and esoteric, it may be useful to investigators designing better theoretical and empirical studies of biotic responses to landscape change.

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FIGURE CAPTIONS

Figure 1. The PATCH model's control windows. The windows used for displaying imagery are not shown. The separate panel at the bottom is a second view of the panel directly above it, as indicated by the arrow. Population projection matrices are entered into the array of numeric fields immediately above the arrow.

Figure 2. The two sample landscapes used in the study. Each image was 2384 pixels wide and 1031 pixels tall. The proportions of landscape 1 in each of the six habitat types were identical, while they were only roughly equal in landscape 2.

Figure 3. Results from the model simulations showing the population response to habitat loss. See the text for the definitions of habitat degradation and relative population size. The upper figure displays the responses of the small model species to habitat loss in the two landscapes, while the lower figure is for the large model species. The types of anthropogenic disturbance that were used in the simulations are indicated next to the curves for which they apply.

Figure 4. The source/sink maps derived from the PATCH model. The best sources are colored dark black, while poorer sources and then sinks are displayed in increasingly lighter shades of gray. Habitats not suitable for breeding, or for which immigration and emigration were balanced, are displayed in the lightest shade of gray. Squares containing no habitat are colored white. In each case, the upper panel is the pre-fragmentation source/sink map, and the bottom two panels show the results obtained from approximately 42% habitat degradation. The small model species appear in images A and C, and the large model species are in images B and D. Landscape 1 is shown in images A and B, while landscape 2 is displayed in images C and D.

Figure 1
DRAFT

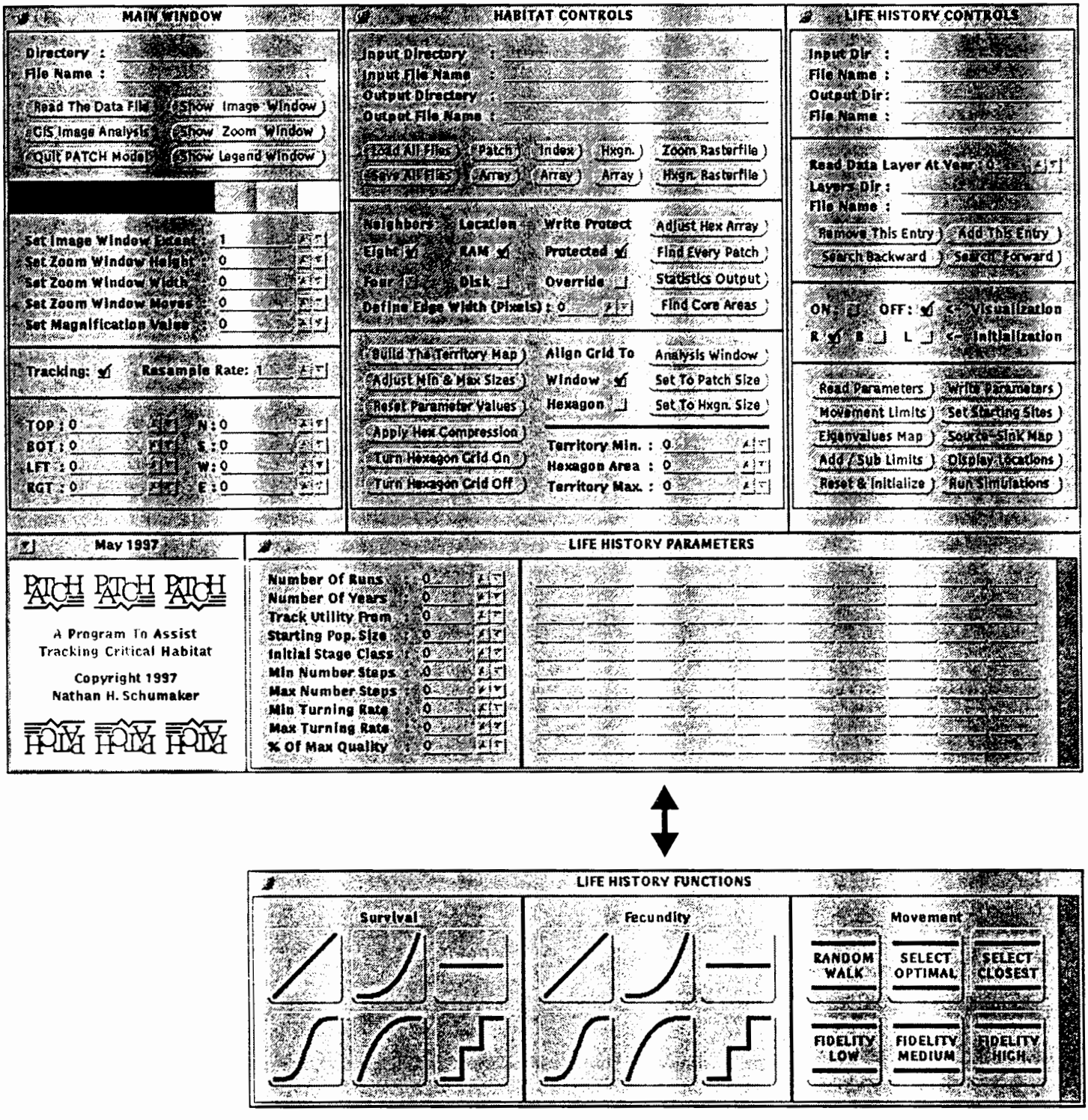
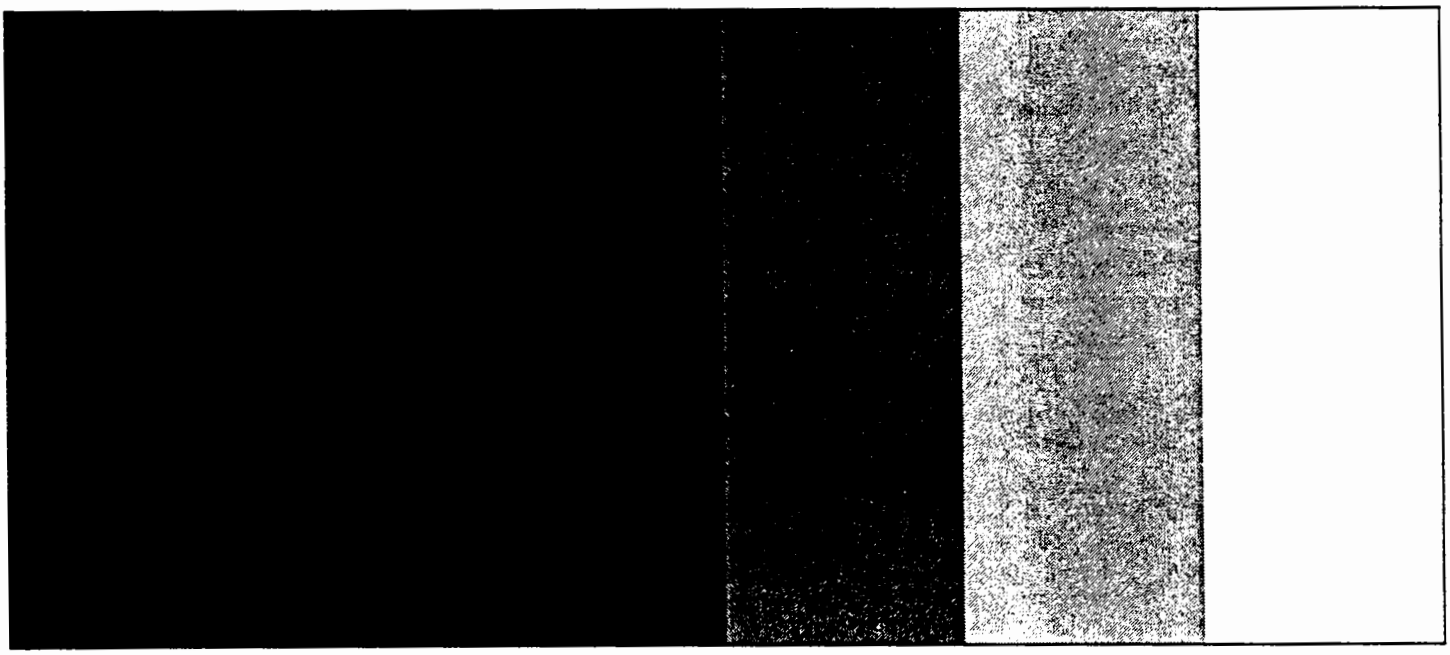


Figure 2
DRAFT

Landscape 1



Landscape 2

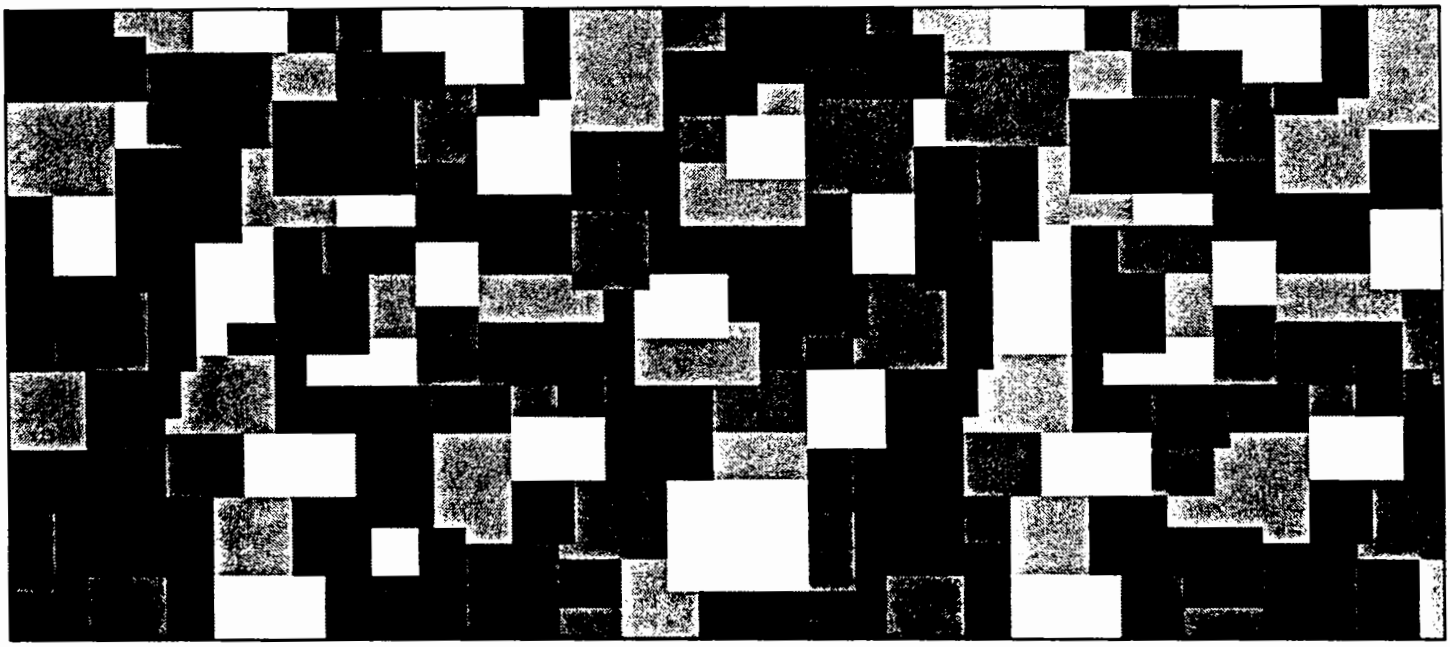
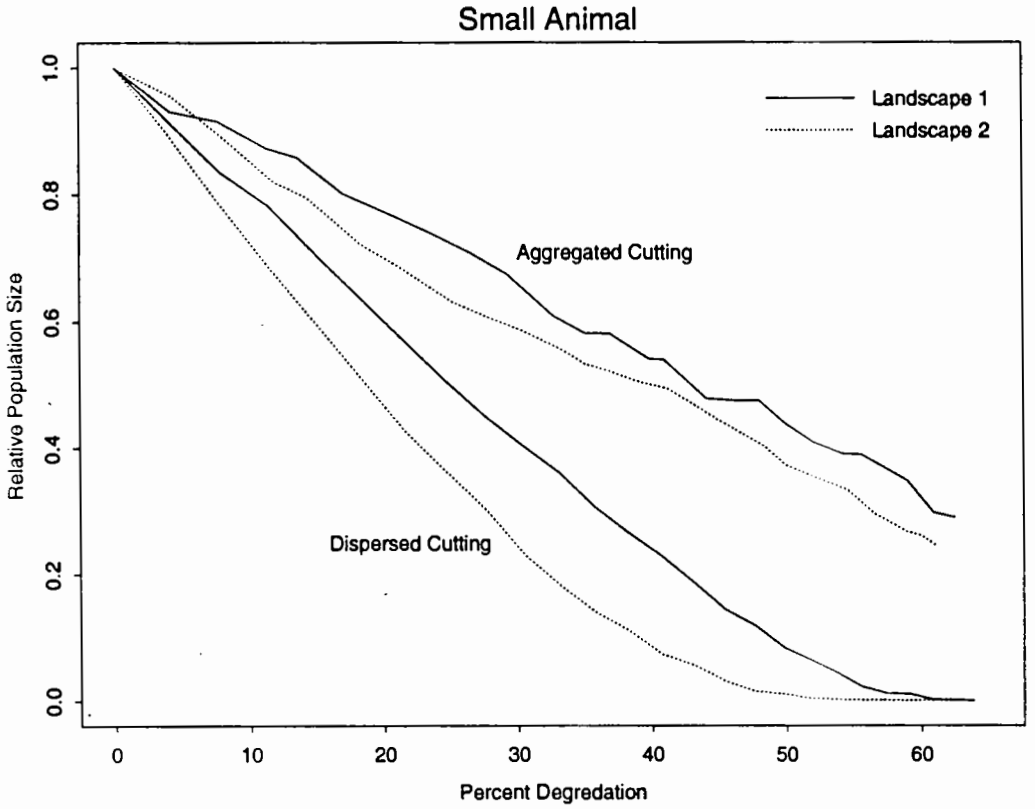


Figure 3
DRAFT



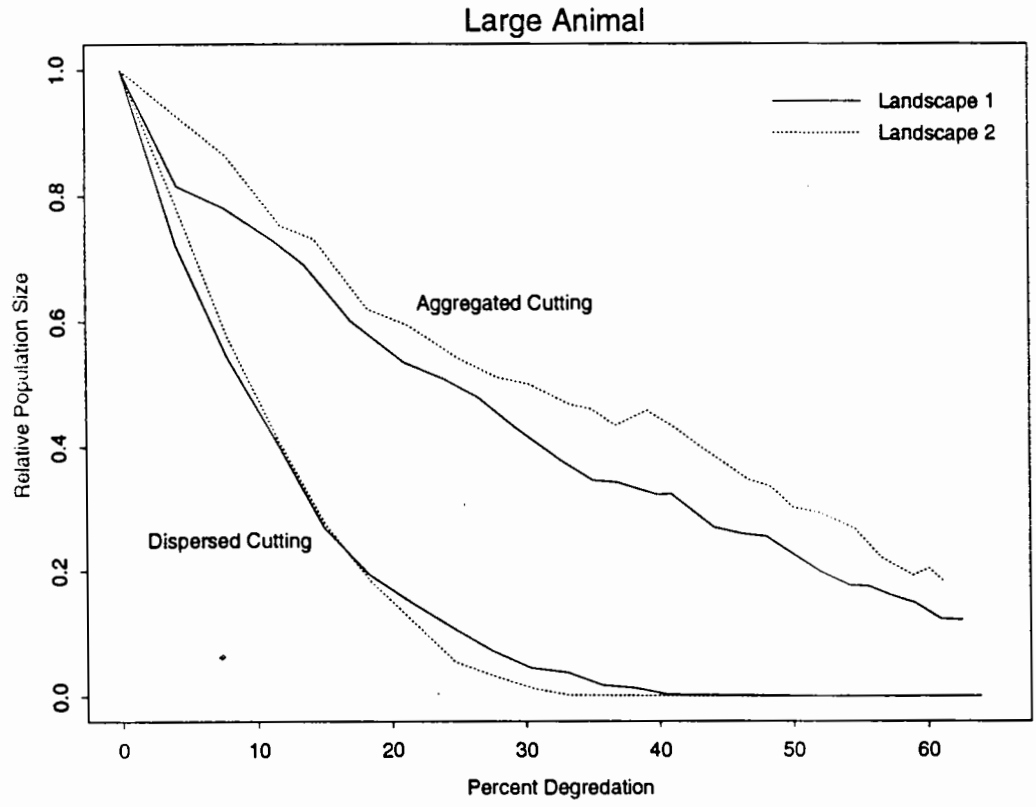


Figure 4
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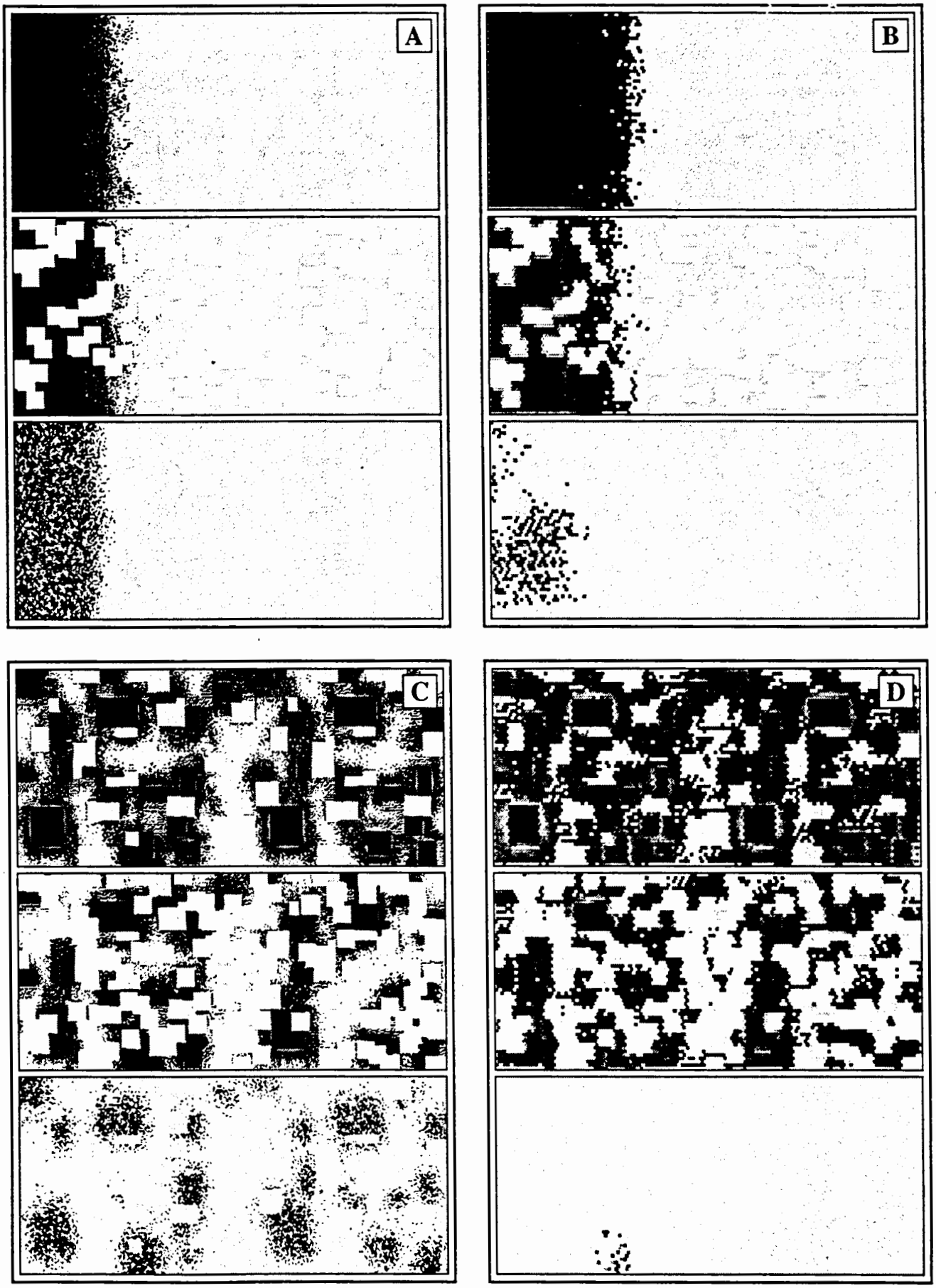

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16. Abstract:

A significant need exists for tools that can help resource managers project the consequences of land management for biodiversity. In an attempt to provide one such tool, a new spatially explicit life history simulator has been developed to aid researchers exploring the possible influences of habitat pattern on the viability of populations of terrestrial vertebrates. The model is especially useful for evaluating the consequences for wildlife species of habitat change through time. The model is discussed in the manuscript, and a case study is presented that illustrates its use. Results from the case study suggest that relationships between population viability and anthropogenic stressors developed for one region may, in certain cases, be extrapolated to other very different regions. This research will be useful for investigators involved in the development of theory linking population viability analysis to landscape structure and anthropogenic disturbance.

17. KEY WORDS AND DOCUMENT ANALYSIS

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Landscape ecology, conservation biology, viability analysis, simulation model, projection matrix, anthropogenic disturbance.		
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