Conservation. Cambridge University Press,

› water snake. *Endangered Species Update*

rvation Biology: An Evolutionary-ecological
l Mass.
, B. R. Noon, and J. Verner. 1990. A conservation
agency Scientific Committee to Address the
JSDA Forest Service, Portland, Ore.
Forsman, A. G. Gunderson, R. S. Holthausen,
l D. M. Solis. 1993. Viability assessments and
›ciated with late-successional and old-growth
:st Service National Forest System and Forest
g Office, Washington, D.C.
tal impact statement for an amendment to the
SDA Forest Service, U.S. Government Printing

population decline in birds. *Am. Birds* 38:10-13.
)2. Reintroduction as a conservation strategy
:: *Solutions from Conservation Biology*, eds.
p. 165-200. Smithsonian Institution Press,

6

AN ORGANISM-BASED PERSPECTIVE OF HABITAT FRAGMENTATION

Scott M. Pearson,[1] Monica G. Turner,[2] Robert H. Gardner,[3] and Robert V. O'Neill

Environmental Sciences Division
Oak Ridge National Laboratory
Oak Ridge, Tennessee
U.S.A.

Environmental heterogeneity in both space and time has been important in the evolution and maintenance of biodiversity. Moreover, this heterogeneity is hierarchical (O'Neill et al. 1986). Differences occur between biomes, between landscapes (within biomes), and in nested levels of organization within landscapes. For example, climatic factors, such as temperature and rainfall, determine the spatial distribution of life zones on a continent (Raunkaier 1934; Whittaker 1956). Landscapes in the southern Appalachian Mountains are dominated by deciduous forest. Although deciduous forest covers most of these landscapes, the community composition of dominant tree species varies with soil type and topography. In a given area of the same soil type and topographic exposure, the density, age structure, and seral status of trees can vary depending on the history of disturbance. These local patterns of structural variation influence levels of light levels reaching the forest floor and, therefore, the herb community. Thus, hierarchical patterns of heterogeneity are a consequence of the complexity within ecological communities (Dayton 1984). The maintenance of biodiversity depends upon the preservation of complex ecological patterns.

Natural landscapes are dynamic systems with temporal and spatial heterogeneity. However, human exploitation tends to simplify landscapes (Krummel et al. 1987). For example, agriculture and forestry tend to reduce spatial heterogeneity in biota. These land uses often change diverse communities to monocultures. Attempts to control disturbances in ecosystems, such as fire suppression and flood control, interrupt natural disturbance/recovery regimes. The challenge of preserving biodiversity in managed landscapes is to incorporate natural levels of spatial and temporal heterogeneity into management schemes.

The concept of scale has emerged as an important topic among ecologists who recognize the role of heterogeneity in natural ecosystems. Subjects related to scale, such as grain (level of detail) and extent (size of area or duration of time), are frequently used

[1] Present address: Biology Department, Mars Hill College, Mars Hill, North Carolina.
[2] Present address: Department of Zoology, University of Wisconsin, Madison, Wisconsin.
[3] Present address: Appalachian Environmental Laboratory, Frostburg, Maryland.

to determine the appropriate interpretation of ecological data (Turner et al. 1989; Wiens 1989). Likewise, considering scale is important for the application of ecological principles to the protection of biodiversity and conservation. The scale of a particular conservation effort will affect its ability to fulfill its goals. For example, the spatial extent of a reserve system must be large enough to sustain the ecological process it is intended to protect. However, the geographic boundaries are often determined by the distribution of surviving populations, political boundaries, or fiscal constraints rather than on an accurate understanding of the ecological process. Temporal scales can also be included in conservation strategies. Estimating the probability of a single population surviving for a specified period of time based on population size and environmental variability (e.g., Shaffer 1981) is an example of incorporating temporal scale. Therefore, scaling issues should be considered when designing and evaluating conservation strategies. Techniques for identifying areas deserving protection have been developed (e.g., Scott et al. 1987). However, preservation of these systems depends on protecting the broader landscapes in which they are embedded.

This chapter addresses issues related to biodiversity protection at landscape scales, areas ranging from tens to thousands of hectares. However, the working definition of landscape scale should depend on the relevant organisms and ecological processes (Wiens 1989; Wiens and Milne 1989). For example, beetles and eagles operate at different spatial scales. In this chapter, we will emphasize the importance of natural patterns of spatial and temporal heterogeneity, encourage a broader-scale perspective for conservation, and illustrate the interaction between landscape-level heterogeneity and organism-based scales of resource utilization with a simulation experiment.

RETHINKING CONCEPTS OF HETEROGENEITY

Strategies for the protection of biodiversity depend on an understanding of the ecological function of the relevant species, communities, or ecosystems. The perception of these functions might be affected by scale. For example, conclusions about a species' persistence might depend on the spatial extent over which it is studied. In source-sink populations (sensu Pulliam 1988), some populations exhibit birth rates lower than mortality rates. Although some reproduction occurs in these sink populations, they are dependent on demographic subsidies from source populations, where birth rates exceed mortality rates. A study of only one population might conclude that the population is healthy and growing, or that it is declining. Only a study of the larger metapopulation could identify the critical source populations.

The process-oriented concept of the ecological neighborhood is useful for management of biodiversity because it encourages ecologists and managers to evaluate spatial patterning of resources in the context of ecological functions. An ecological neighborhood is defined by an ecological process, the time and space scale appropriate for that process, and an organism's relationship to the process during a specific time period (Addicott et al. 1987). This concept can be applied to ecological activities as diverse as foraging by individual animals, gene flow, predator-prey interactions, or population growth and persistence. For an individual breeding bird, the ecological neighborhood might be its territory. For a flowering plant, the neighborhood would include

the activity ranges of its pollinato
Neighborhoods for community-level
the population dynamics of all the com

Addicott et al. (1987) used ecol
of heterogeneity in the environment.
only a portion of one patch, but fine-
Thus, the scale of heterogeneity d
neighborhoods of populations and
the spatial arrangement of resources
the network structure of a metapo
subpopulations exceeds the organism
and spatial arrangement of habitats
patches (Pearson 1993).

Role of Spatial Heterogene

Landscapes have natural levels of t
temporal patterns are driven by distu
Baker 1989; Turner et al. 1993) in
and climate. For example, the tree c
States change in composition wi
(Whittaker 1956). They are also af
falls affect about 1% of the landsc
mild disturbances is rapid. Thus,
dominated by mature forests with
habitat. In contrast, lodgepole pin
experience forest fires (Romme a
fires coupled with the long recover
with a mosaic of forests of differe

Changing the patterns of reso
species composition. Increasing
diversity by increasing the numb
heterogeneity provides habitat for
However, excessive levels of hete
result in the loss of species sensi
changes can have desirable or
conservation goal and the specifi
a population of black bears, he
phenology of food items, could
should have a positive effect on
items are consistently available.
unsuitable habitats, such as roa
negative effect. Therefore, hetero
the effect of changing specific
processes. All species are adapt

gical data (Turner et al. 1989; Wiens
e application of ecological principles
he scale of a particular conservation
mple, the spatial extent of a reserve
cal process it is intended to protect.
ined by the distribution of surviving
raints rather than on an accurate
al scales can also be included in
f a single population surviving for a
nd environmental variability (e.g.,
oral scale. Therefore, scaling issues
conservation strategies. Techniques
developed (e.g., Scott et al. 1987).
protecting the broader landscapes in

rsity protection at landscape scales,
However, the working definition of
sms and ecological processes (Wiens
nd eagles operate at different spatial
rtance of natural patterns of spatial
le perspective for conservation, and
rogeneity and organism-based scales
t.

GENEITY

n an understanding of the ecological
cosystems. The perception of these
nclusions about a species' persistence
studied. In source-sink populations
th rates lower than mortality rates.
populations, they are dependent on
re birth rates exceed mortality rates.
e population is healthy and growing,
population could identify the critical

gical neighborhood is useful for
ecologists and managers to evaluate
cological functions. An ecological
he time and space scale appropriate
the process during a specific time
applied to ecological activities as
low, predator-prey interactions, or
dual breeding bird, the ecological
ant, the neighborhood would include

the activity ranges of its pollinators and the distribution of the plants they visit. Neighborhoods for community-level processes are more complex because they involve the population dynamics of all the component species, which can operate at different scales.

Addicott et al. (1987) used ecological neighborhoods to describe the relative scale of heterogeneity in the environment. Heterogeneity is coarse if the neighborhood includes only a portion of one patch, but fine-scaled if the neighborhood includes several patches. Thus, the scale of heterogeneity depends on both spatial pattern and the ecological neighborhoods of populations and communities. Moreover, in fine-scaled landscapes the spatial arrangement of resources can affect persistence of a population. For example, the network structure of a metapopulation will be disrupted if the distance between subpopulations exceeds the organism's dispersal capabilities. Changes in the composition and spatial arrangement of habitats will affect the community composition of individual patches (Pearson 1993).

Role of Spatial Heterogeneity

Landscapes have natural levels of temporal and spatial heterogeneity. These spatial and temporal patterns are driven by disturbance/recovery regimes (White 1979; Romme 1982; Baker 1989; Turner et al. 1993) in addition to variation in physical forces like geology and climate. For example, the tree communities of deciduous forests of the eastern United States change in composition with elevation, topography, and soil characteristics (Whittaker 1956). They are also affected by a large number of small disturbances. Tree falls affect about 1% of the landscape annually (Runkle 1981), but recovery from these mild disturbances is rapid. Thus, natural landscapes in eastern deciduous forests are dominated by mature forests with isolated, ephemeral patches of early successional habitat. In contrast, lodgepole pine forests of the northern Rocky Mountains regularly experience forest fires (Romme and Despain 1989). Variation in the spatial extent of fires coupled with the long recovery times because of harsh climate results in a landscape with a mosaic of forests of different ages (Romme 1982).

Changing the patterns of resources and habitats at the landscape level can affect the species composition. Increasing spatial heterogeneity can increase species (gamma) diversity by increasing the number of habitat types available in the landscape. This heterogeneity provides habitat for species adapted to different habitats and seral stages. However, excessive levels of heterogeneity can, depending on the actual spatial pattern, result in the loss of species sensitive to habitat fragmentation. Thus, landscape-level changes can have desirable or undesirable effects depending upon a particular conservation goal and the specific changes that occur. For example, for the survival of a population of black bears, heterogeneity, as measured by variation in type and phenology of food items, could provide a varied, nutritious diet. Such heterogeneity should have a positive effect on population persistence by insuring that suitable food items are consistently available. Conversely, increasing spatial heterogeneity by adding unsuitable habitats, such as roads (McLellan and Shackleton 1988), would have a negative effect. Therefore, heterogeneity per se is not good or bad; its value depends on the effect of changing specific spatial and temporal patterns on specific ecological processes. All species are adapted to particular spatial and temporal patterns in the

abiotic and biotic characteristics of their environment. In general, the risk of losing biodiversity and disrupting ecological functions is greatly increased when natural patterns of heterogeneity are altered.

Characterizing Spatial Heterogeneity

The terms patch, matrix, and corridor are boldly written in the lexicon of landscape ecology (Forman and Godron 1986). The definition and use of these terms have been useful in describing the spatial structure of habitats at landscape scales. The widespread acceptance and popularity of these terms will provide a basis for the next step in understanding landscape-level processes.

These terms are especially useful in landscapes where the contrast between the patches and the matrix is sharp and has ecological meaning. The concepts of patches and corridors evolved in the context of highly manipulated landscapes as in western Europe and the northeastern United States and often reflect an anthropocentric perspective. But, in natural landscapes, patches and corridors are seldom discrete (Kotliar and Wiens 1990). If the variation between patch and matrix is greater than the variation within either patch or matrix, then patches can be easily delineated. However, discernable, nonarbitrary patches might not be apparent in landscapes showing continual gradual variation, but spatial structure might still be present (Musick and Grover 1991). Therefore, patch, matrix, and corridor can be of limited use in describing natural pattern in many landscapes.

It is difficult to define specific patches in a landscape without being arbitrary. Patches have been defined in an ecological context as a discontinuity in an ecological variable affecting an organism (Wiens 1976) or as a place where the abundance of resources or organisms is low or high relative to its surroundings (Roughgarden 1977). Both of these definitions use an organism-based perspective. Analyzing a landscape from an organism's perspective, particularly of a non-vertebrate, can reveal a very different set of environmental patterns and gradients (Wiens and Milne 1989; Buechner 1989) than the patterns apparent to humans. Even so, natural landscapes tend to have hierarchical levels of variation (O'Neill et al. 1986; Kotliar and Wiens 1990). Nested levels of heterogeneity might exist from the perspective of a single organism. If a landscape could be evaluated from the viewpoint of many species, any single map of the landscape would be arbitrary because that map would reflect the perspective of one species or a small group of similar species (Risser et al. 1984).

Community-level interactions can complicate the optimal design of patches and corridors for preserving biodiversity. For example, several pairs of antbirds existed in 1-10 ha fragments of tropical forest until corridors connecting forests were cut (Bierregaard 1990). Antbirds are obligate commensals with foraging army ants; they disappeared after army ant activity was lost in the forest fragment. The ant colonies have home ranges of several hundred hectares (Willis and Oniki 1978), and colonies did not visit the forest fragment when the corridor was cut. Bierregaard (1990) also reported that bird species dependent on foraging flocks disappeared from forest fragments when the nuclear species (bird species critical to flock organization) left the fragment.

Conservation strategies using patch networks to preserve populations rely heavily on dispersal between patches to maintain genetic variation and to avoid stochastic

extinctions (Diamond 1975). Corri
patches. However, satisfying the hab
species requires corridors of various
animals to move between patches,
distance between patch requires m
satisfy the dispersal needs of the
environmental gradients acting as
not exist. However, multiple corrid
patches. Moreover, a small archi
biodiversity can exhibit island-like
of small population sizes. In addi
concentrates on patches and corrid

The value of patches and corri
larger landscape in which they are
that landscape biodiversity can be
while ignoring the matrix. Howeve
in maintaining the biodiversity of
found that individual sites (9-50 ha
of species between years. High rate
resulting in a relative stability in
preserved by a small number of pat
depends on processes such as immi
In an Amazonian forest, a 70-m v
understory birds from the unbroke
began to fill the former clearcut,
larger forest became more common
increased as the contrast between

In a landscape dominated by
ecological processes in the matri
on the size of the patches and the
interiors (i.e. edge effects; Wilcov
it might be necessary to manage

Whereas concepts and terms
landscape-level patterns, it is ti
heterogeneity and its importance
as a whole from the perspective o
into arbitrary patch and matrix ca
preservation strategies because it
preserve patterns of heterogeneity
scale perspective has already bee
the importance of linkages betw
scale corridors (Noss 1991) that
and are wide enough to be cons
many species can complete their

The following portion of thi
level characteristics such as the a

extinctions (Diamond 1975). Corridors are intended to facilitate movement between patches. However, satisfying the habitat preferences and dispersal capabilities of different species requires corridors of various habitat types. Although satisfactory corridors permit animals to move between patches, they must be able to sustain plant populations if the distance between patch requires more than one generation to traverse. Corridors that satisfy the dispersal needs of the entire community must be short, wide, and free of environmental gradients acting as a barrier to any species. This perfect corridor might not exist. However, multiple corridors to each patch could solve this problem for some patches. Moreover, a small archipelago of patches isolated from the mainland of biodiversity can exhibit island-like dynamics like high extinction probabilities because of small population sizes. In addition to being arbitrary, a management strategy that concentrates on patches and corridors might be too narrowly focused for conservation.

The value of patches and corridors for conservation of biodiversity depends on the larger landscape in which they are embedded. The patch/matrix/corridor concepts imply that landscape biodiversity can be preserved in a selected number of refugia (patches) while ignoring the matrix. However, this implication ignores the vital role of the matrix in maintaining the biodiversity of a single site. For example, Glenn and Collins (1992) found that individual sites (9-50 ha in extent) in a Kansas prairie exhibited a high turnover of species between years. High rates of extinction were balanced by frequent immigration, resulting in a relative stability in species richness. An open system like this cannot be preserved by a small number of patches because maintenance of diversity at any one site depends on processes such as immigration which operate at the scale of the larger system. In an Amazonian forest, a 70-m wide strip of clearcut eliminated movement by forest understory birds from the unbroken forest to a forest island. However, as second growth began to fill the former clearcut, movement by these birds between the island and the larger forest became more common (Bierregaard 1990). Thus, movement between patches increased as the contrast between the patches and matrix decreased.

In a landscape dominated by a matrix of unsuitable habitats for native species, ecological processes in the matrix might overwhelm patches and corridors, depending on the size of the patches and the ability of the matrix processes to penetrate the patch interiors (i.e. edge effects; Wilcove 1985; Lovejoy et al. 1986; Janzen 1988). Therefore, it might be necessary to manage not only the patches and corridors, but also the matrix.

Whereas concepts and terms such as patches are useful for describing and discussing landscape-level patterns, it is time to take the next step in recognizing broad-scale heterogeneity and its importance to biodiversity. This step entails viewing the landscape as a whole from the perspective of different species instead of subdividing the landscape into arbitrary patch and matrix categories. This approach is more useful for formulating preservation strategies because it promotes the creation of management strategies that preserve patterns of heterogeneity critical for the persistence of biodiversity. This broad-scale perspective has already been recognized. In a recent book, Hudson (1991) noted the importance of linkages between protected regions. This book described regional-scale corridors (Noss 1991) that encompass a great deal of environmental heterogeneity and are wide enough to be considered landscapes themselves because populations of many species can complete their life cycle within the corridor itself.

The following portion of this chapter will describe an example of how landscape-level characteristics such as the abundance of suitable habitat and its spatial arrangement

affect habitat fragmentation, an important, broad-scale characteristic that can affect population persistence. Moreover, this example shows how evaluating habitat fragmentation (or connectivity) from the perspective of different organisms affects conclusions about the suitability of different landscapes. This example involves the use of a computer simulation model. Although the model simulates a simple landscape that consists of only two habitat types, it illustrates the complex interactions between habitat abundance, spatial pattern, and resource utilization of different species. The technical details of the simulations have been documented for interested readers.

LANDSCAPE CONNECTIVITY: THE INTERACTION BETWEEN LANDSCAPE PATTERN AND ORGANISMAL SCALES

Habitat fragmentation is one of the greatest threats to biodiversity (Whitcomb et al. 1981) and, therefore, conservation strategies should maintain habitat connectivity within and among landscapes. Connectivity depends on both the abundance and spatial arrangement of habitats in a landscape. In raster maps where cells of a given habitat are arranged randomly and connectivity is defined by nearest neighbor adjacencies, the habitat spans the map if it occupies about 60% or more of the landscape (Gardner et al. 1987). Below this critical percentage, connectivity is severely reduced on random maps, and the habitat occurs as numerous small isolated clusters. This trend in connectivity has also been observed in forested habitat in real landscapes (Gardner et al. 1991).

Thresholds of connectivity can exert strong influences on the dynamics of several ecological processes, such as spread of disturbance (Turner et al. 1991; O'Neill et al. 1992), utilization of resources (O'Neill et al. 1988), and the movement and dispersal of organisms (Gardner et al. 1989; Gardner et al. 1991). However, connectivity also depends on the ability of the organism or process to move across the landscape. For example, a plant with wind-dispersed seeds is more likely to colonize a small, apparently disconnected cluster of habitat than a heavy-seeded plant lacking a mechanism for long-range dispersal. Similarly, a river or a highway can be a barrier to movement for a mouse, but a bird or deer might regularly cross such obstacles. Critical thresholds in habitat abundance and connectivity can be identified for a variety of organisms, but these thresholds will depend on both landscape pattern and the scale at which the organism can use the landscape.

A series of simulation experiments was designed (1) to explore the implications of landscape pattern for organisms that perceive the landscape at different scales, and (2) to illustrate how a particular organism might respond to alternative patterns of suitable habitat across the landscape. A set of landscape maps was developed in which the abundance and spatial distribution of habitat and the degree of scale-dependent structure were varied. In addition, a set of rules was defined to describe alternative resource utilization scales (sensu O'Neill et al. 1988) for a variety of organisms. Resource utilization scale, as discussed here, represents an organism's ability to use disjunct habitat fragments. We were particularly interested in how thresholds of connectivity might differ with the scale at which an organism can utilize resources and how the scale-dependent structure of the landscape (spatial arrangement of habitat) might affect the ability of an organism to use different landscapes.

Landscape Patterns

The simulated landscape was repre
and spatial distribution of suitable h
random across the landscape with p
Turner et al. 1989) or by using a hi
1992; Gardner et al. in press). In
suitable habitat is controlled by p (
on the pattern. In hierarchical map
introduced with curdling algorithm

To create a hierarchical map, c
finer (nested) scales at which pattern
is considered a m_1 x m_1 grid in whic
within $(m_1)^2$ cells by selecting cells
contains an m_2 x m_2 grid in which p
p_2 of the cells that were selected at
time by subdividing each of these
occurs in p_3 of the cells selected at t
level are considered suitable habita
m_2 x $m_3)^2$, and the overall proportio
p_1 x p_2 x p_3.

An illustration of the curdling
$m_2 = m_3 = 3$ (i.e., a 27 x 27 grid) is
cells at each level l that were select
map at the finest level is 0.44 x 0.6

Curdled maps represent an ext
be introduced by adding "wheys" t
curdled map discussed above, wit
that were designated as unsuitable
proportion q_2 of suitable habitat. Sin
at the second level are now consid
the curdled and wheyed map (right
occupied by suitable habitat is now

$$p = [p_1 * p_2 * p_3] + [p_1 * (1-p_2) * q_3]$$

If $p_1 = p_2 = q_2 = p_3 = q_3$, the map is

Resource Utilization Scale

A set of three rules for how an org
defined to generate a range of scale
move to suitable habitat only wit
present site. Rule 2 represents an
four cardinal and four subcardinal

scale characteristic that can affect
e shows how evaluating habitat
ive of different organisms affects
pes. This example involves the use
l simulates a simple landscape that
mplex interactions between habitat
of different species. The technical
interested readers.

ERACTION ORGANISMAL SCALES

s to biodiversity (Whitcomb et al.
naintain habitat connectivity within
both the abundance and spatial
s where cells of a given habitat are
est neighbor adjacencies, the habitat
he landscape (Gardner et al. 1987).
rely reduced on random maps, and
ers. This trend in connectivity has
apes (Gardner et al. 1991).
luences on the dynamics of several
(Turner et al. 1991; O'Neill et al.
and the movement and dispersal of
However, connectivity also depends
ross the landscape. For example, a
ize a small, apparently disconnected
mechanism for long-range dispersal.
ovement for a mouse, but a bird or
hresholds in habitat abundance and
ms, but these thresholds will depend
organism can use the landscape.
d (1) to explore the implications of
dscape at different scales, and (2) to
to alternative patterns of suitable
naps was developed in which the
degree of scale-dependent structure
d to describe alternative resource
a variety of organisms. Resource
nism's ability to use disjunct habitat
esholds of connectivity might differ
urces and how the scale-dependent
abitat) might affect the ability of an

Landscape Patterns

The simulated landscape was represented as a 512 by 512 grid in which the abundance and spatial distribution of suitable habitat was varied. Suitable habitat was distributed at random across the landscape with probability p (Gardner et al. 1987; O'Neill et al. 1988; Turner et al. 1989) or by using a hierarchical map-generating algorithm (O'Neill et al. 1992; Gardner et al. in press). In random maps, the size, shape, and arrangement of suitable habitat is controlled by p (Gardner et al. 1987) and no spatial scale is imposed on the pattern. In hierarchical maps (O'Neill et al. 1992), scale-dependent structure is introduced with curdling algorithms from fractal geometry (Mandelbrot 1983).

To create a hierarchical map, consider that a landscape contains three successively finer (nested) scales at which pattern will be generated. At the broadest scale, the landscape is considered a $m_1 \times m_1$ grid in which potentially suitable habitat is distributed randomly within $(m_1)^2$ cells by selecting cells with probability p_1. Each of these selected cells then contains an $m_2 \times m_2$ grid in which potentially suitable habitat is distributed randomly in p_2 of the cells that were selected at the first level. This process is then repeated a third time by subdividing each of these sites into a $m_3 \times m_3$ grid in which suitable habitat occurs in p_3 of the cells selected at the previous level. Cells that are selected at this third level are considered suitable habitat. The total number of cells in the landscape is $(m_1 \times m_2 \times m_3)^2$, and the overall proportion, p, of the landscape occupied by suitable habitat is $p_1 \times p_2 \times p_3$.

An illustration of the curdling algorithm for a map with three scales in which $m_1 = m_2 = m_3 = 3$ (i.e., a 27 x 27 grid) is shown to the left in Figure 6.1. Black cells represent cells at each level l that were selected at a probability of p_l. The overall p of the curdled map at the finest level is 0.44 x 0.66 x 0.55 = 0.16.

Curdled maps represent an extreme case of scaled pattern. More subtle patterns can be introduced by adding "wheys" to the "curds." A wheyed map can be described by the curdled map discussed above, with the following additions. At the second level, cells that were designated as unsuitable at the first level are now considered to contain a proportion q_2 of suitable habitat. Similarly, at the third level, cells designated as unsuitable at the second level are now considered to contain a proportion q_3 of suitable habitat. In the curdled and wheyed map (right side, Fig. 1), the overall proportion p of the landscape occupied by suitable habitat is now:

$$p = [p_1 * p_2 * p_3] + [p_1 * (1-p_2) * q_3] + [(1-p_1) * q_2 * p_3] + [(1-p_1) * (1-q_2) * q_3].$$

If $p_1 = p_2 = q_2 = p_3 = q_3$, the map is quite similar to a random map.

Resource Utilization Scales

A set of three rules for how an organism might perceive and move in a landscape was defined to generate a range of scales (Figure 6.2). Rule 1 represents an organism that can move to suitable habitat only within the four cardinal directions from the organism's present site. Rule 2 represents an organism that can move to suitable habitat within the four cardinal and four subcardinal directions. Under Rule 2, an organism can move to a

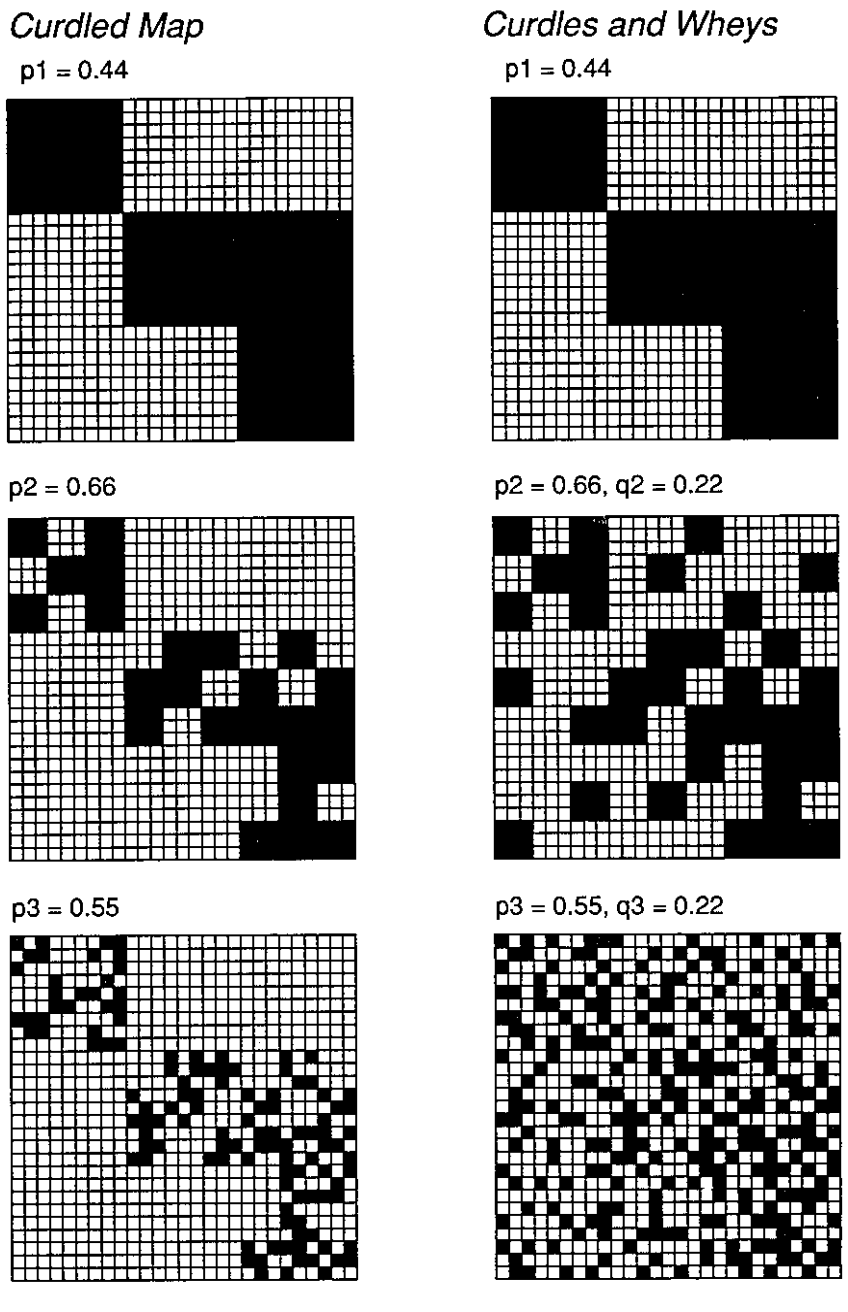


Figure 6.1. Hierarchically structured maps created by using curdling and wheying algorithms. The three maps in the left column were created by curdling at three nested levels (p_1, p_2, and p_3). The maps on the right were created using both curdling and wheying. Wheys are introduced at the second level by turning on some cells (at q_2=0.22) which were turned off at the coarser first level. See text for a further explanation of these techniques.

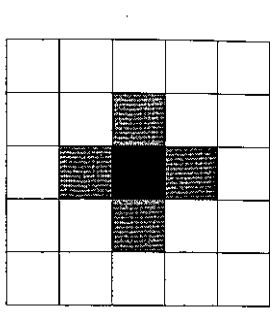


Figure 6.2. Three resource utilizati
The solid square indicates the cell cc
covered by the shaded cells are co
three successively broader scales of

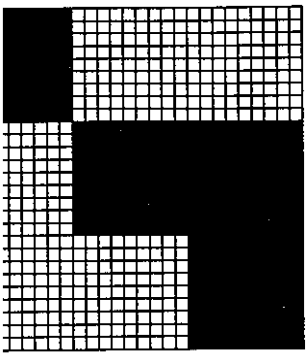
suitable habitat on adjacent or diag
Rule 1. Rule 3 expands the scale of
adjacent and diagonal neighbors, bu
current position. Thus, Rule 3 allo
or to jump over a pixel of unsuital
rules in two sets of simulations to
organisms perceive the landscape

Experiment I: Organisms C Random Landscapes.

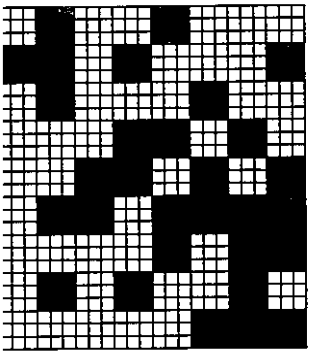
First, we address the question of hc
scales respond to the abundance c
random maps was generated with th
habitats ranging from 0.1 to 0.9. Tl
compare how organisms operating a
of suitable habitat on each map w
above. Resource clusters were ident
as a set of resource cells are accessib
cells not accessible to an organism w
clusters were identified using each
of resource clusters (S_{avg}) was dete
area that an organism can use is oft
largest resource cluster on the map
determined by dividing its size (LC
maximum cluster size is given by p_1
Thus, suitable habitat across the la
LC_{rel} is inversely related to the deg

dles and Wheys

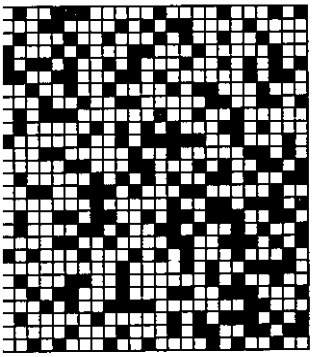
= 0.44



= 0.66, q2 = 0.22



= 0.55, q3 = 0.22



ıg curdling and wheying algorithms.
lling at three nested levels (p_1, p_2,
curdling and wheying. Wheys are
at q_2=0.22) which were turned off
ın of these techniques.

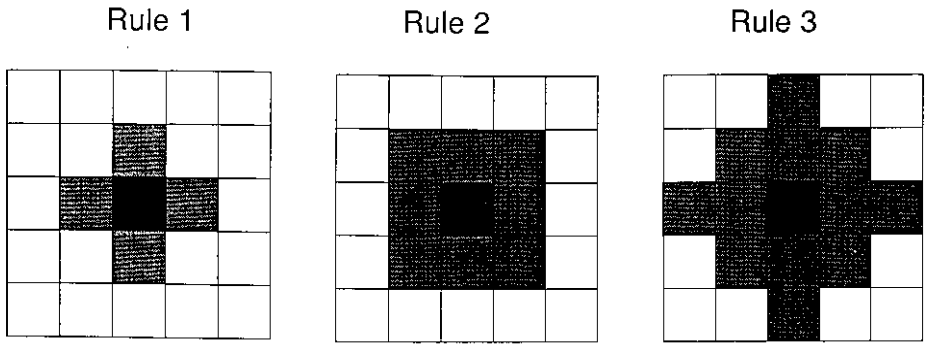


Figure 6.2. Three resource utilization rules used to identify clusters of connected habitat. The solid square indicates the cell containing suitable habitat. Other cells of suitable habitat covered by the shaded cells are considered connected to solid cell. The rules represent three successively broader scales of resource use.

suitable habitat on adjacent or diagonal cells and exploit more suitable habitat than under Rule 1. Rule 3 expands the scale of movement from Rule 2 to include not only the eight adjacent and diagonal neighbors, but also cells that are two cells away from the organism's current position. Thus, Rule 3 allows an organism to move to adjacent or diagonal sites or to jump over a pixel of unsuitable habitat in the cardinal directions. We used these rules in two sets of simulations to explore the interaction between the scale at which organisms perceive the landscape the scale of pattern on the landscape.

Experiment I: Organisms Operating at Different Scales in Random Landscapes.

First, we address the question of how organisms that perceive the landscape at different scales respond to the abundance of suitable randomly distributed habitat. A series of random maps was generated with the proportion, p, of the landscape occupied by suitable habitats ranging from 0.1 to 0.9. Three replicate maps were created for each p level. To compare how organisms operating at different scales can use these landscapes, the pattern of suitable habitat on each map was quantified with each of the three rules described above. Resource clusters were identified by the movement rule. A single cluster is defined as a set of resource cells are accessible by an organism moving within the cluster. Resource cells not accessible to an organism within one cluster belong to separate clusters. Resource clusters were identified using each resource utilization rule, and the weighted mean size of resource clusters (S_{avg}) was determined. Because the size of the largest contiguous area that an organism can use is often important for conservation, we then identified the largest resource cluster on the map. The relative size of the largest cluster (LC_{rel}) was determined by dividing its size (LC) by the maximum cluster size possible (LC_{max}). The maximum cluster size is given by pm^2, when all suitable habitat occurs in a single cluster. Thus, suitable habitat across the landscape becomes contiguous as LC_{rel} approaches 1. LC_{rel} is inversely related to the degree of fragmentation of suitable habitat.

The weighted mean size of resource clusters (S_{avg}) varied with both the rule and the proportion, p, of the landscape occupied by suitable resources (Figure 6.3) on the random maps in which p was varied. Values of S_{avg} increased rapidly as p increased, but the value of p at which this increase occurred varied among the rules. For Rule 1, which represents the most restricted movement, mean cluster size increased rapidly near $p = 0.6$, the critical threshold for connectivity reported from percolation theory (Stauffer 1985). Rapid increases in S_{avg} occurred near $p = 0.4$ for Rule 2 and near $p = 0.3$ for Rule 3. As p increased to approximately 0.7, there was little or no difference in the change in S_{avg} among the different rules. Similarly, when p was very low on these random maps, e.g., < 0.25, S_{avg} was very low, and no differences among the rules were found.

The relative size of the largest resource cluster, LC_{rel}, also varied with p and among the rules (Figure 6.4). The value of LC_{rel} approached zero for all four rules at low p and reached a value of 1 at some higher value of p. The transition between 0 and 1 was abrupt, but the value of p at which this abrupt transition occurred varied among the rules. For Rule 1, the rapid increase again occurred near $p = 0.6$. As with the rapid increases in S_{avg}, the value of LC_{rel} increased rapidly near $p = 0.4$ for Rule 2 and near $p = 0.3$ for Rule 3. The p values at which these rapid changes occur represent the critical threshold, p_{crit}, at which randomly distributed sites of suitable habitat become connected across the landscape for organisms that operate at the scales defined by each rule.

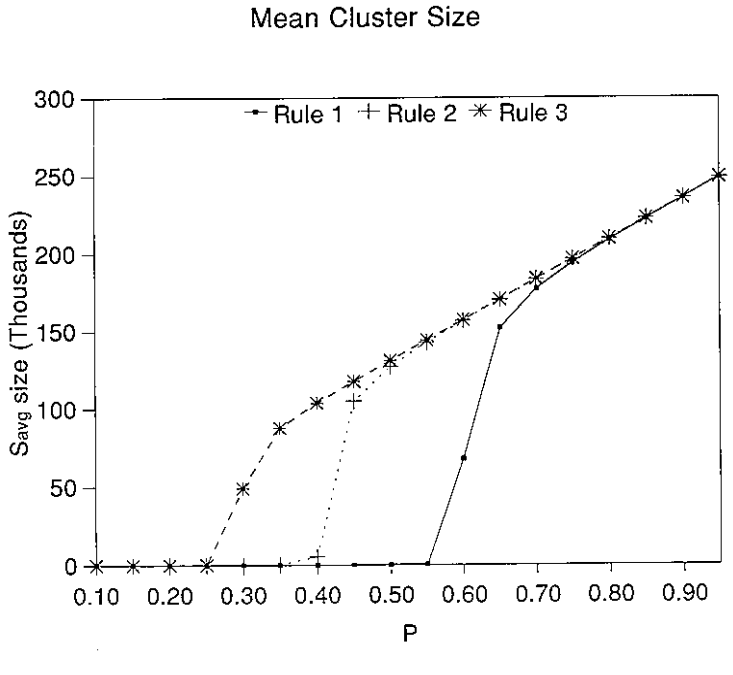


Figure 6.3. Relationship between average cluster size and frequency of suitable habitat. The average number of cells in habitat clusters (S_{avg}) increases as the proportion of the landscape covered by suitable habitat, p, increases. Habitat clusters were measured by three resource utilization rules (see Figure 6.2).

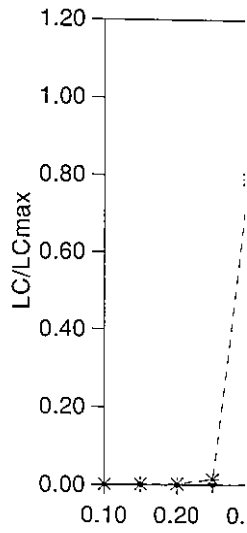


Figure 6.4. Relationship betwee
The relative size of the largest clus
the suitable habitat on the landsc
1 and highly fragmented when *LC*
shown here for clusters measured
increases as the proportion of the

Experiment II: Scaled La

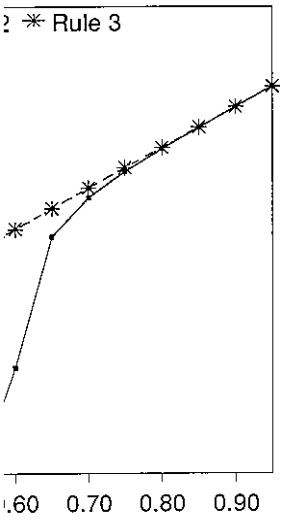
Next, we address how organism
landscapes which have the same
habitat is different. We held p c
varied the pattern in the landsc
maps, and random maps. Suitabl
= $m3 = 8$ (i.e., a 512 x 512 grid). F
two alternative patterns to repre
higher value of p at the finest sc
curdled-bottom or wheyed-botto
coarsest level, and we refer to th
of a set of these maps with the sa
used to generate the maps are sh
was again quantified with each
described above.

Consider first a landscape i
0.328. If an organism uses reso

$_{avg}$) varied with both the rule and the
esources (Figure 6.3) on the random
rapidly as p increased, but the value
rules. For Rule 1, which represents
ncreased rapidly near p = 0.6, the
lation theory (Stauffer 1985). Rapid
and near p = 0.3 for Rule 3. As p
no difference in the change in S_{avg}
y low on these random maps, e.g., <
he rules were found.

LC_{rel}, also varied with p and among
l zero for all four rules at low p and
he transition between 0 and 1 was
nsition occurred varied among the
ed near p = 0.6. As with the rapid
near p = 0.4 for Rule 2 and near p =
changes occur represent the critical
f suitable habitat become connected
he scales defined by each rule.

ze



ze and frequency of suitable habitat.
g) increases as the proportion of the
. Habitat clusters were measured by

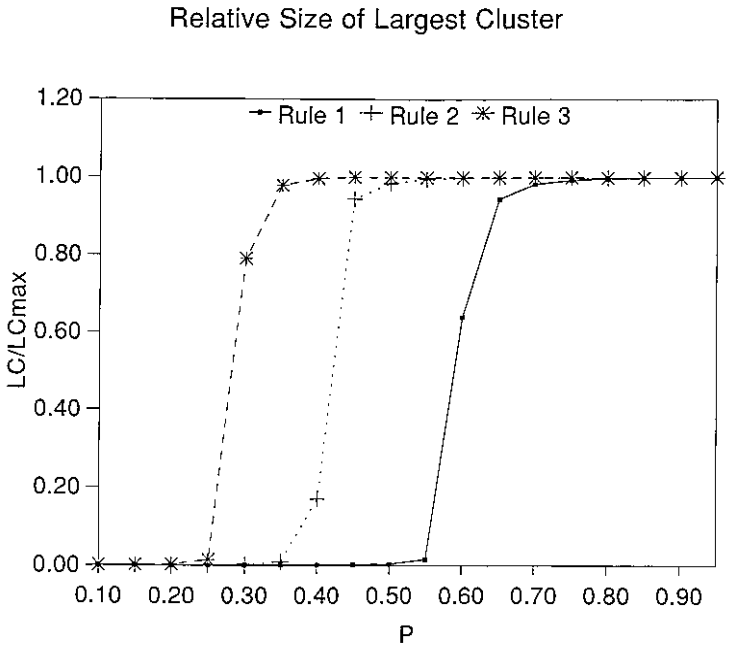


Figure 6.4. Relationship between habitat connectivity and frequency of suitable habitat. The relative size of the largest cluster (LC/LC_{max}) indicates the level of connectivity among the suitable habitat on the landscape. Habitat is highly connected when LC/LC_{max} is near 1 and highly fragmented when LC/LC_{max} is near 0. LC/LC_{max} for a random landscape is shown here for clusters measured by three resource utilization rules (See Fig. 2). LC/LC_{max} increases as the proportion of the landscape covered by suitable habitat, p, increases.

Experiment II: Scaled Landscape Patterns

Next, we address how organisms with the same resource utilization rule respond to landscapes which have the same abundance of suitable sites, but the spatial patterns of habitat is different. We held p constant at three levels (p = 0.328, 0.422, 0.656) and varied the pattern in the landscape by generating curdled maps, curdled and wheyed maps, and random maps. Suitable habitat was generated at three levels in which $m_1 = m_2 = m3 = 8$ (i.e., a 512 x 512 grid). For both curdled and curd-and-whey maps, we generated two alternative patterns to represent a range of potential patterns. One pattern had the higher value of p at the finest scale, i.e., the third level, and we refer to these maps as curdled-bottom or wheyed-bottom. The other pattern had the higher value of p at the coarsest level, and we refer to these maps as curdled-top or wheyed-top. An illustration of a set of these maps with the same p is shown in Figure 6.5, and the values of p_1 and q_1 used to generate the maps are shown in Table 6.1. The landscape pattern on each map was again quantified with each of the three rules and determining S_{avg} and LC_{rel} as described above.

Consider first a landscape in which suitable habitat is not very abundant, e.g., p = 0.328. If an organism uses resources as defined by Rule 1 (the most restrictive rule

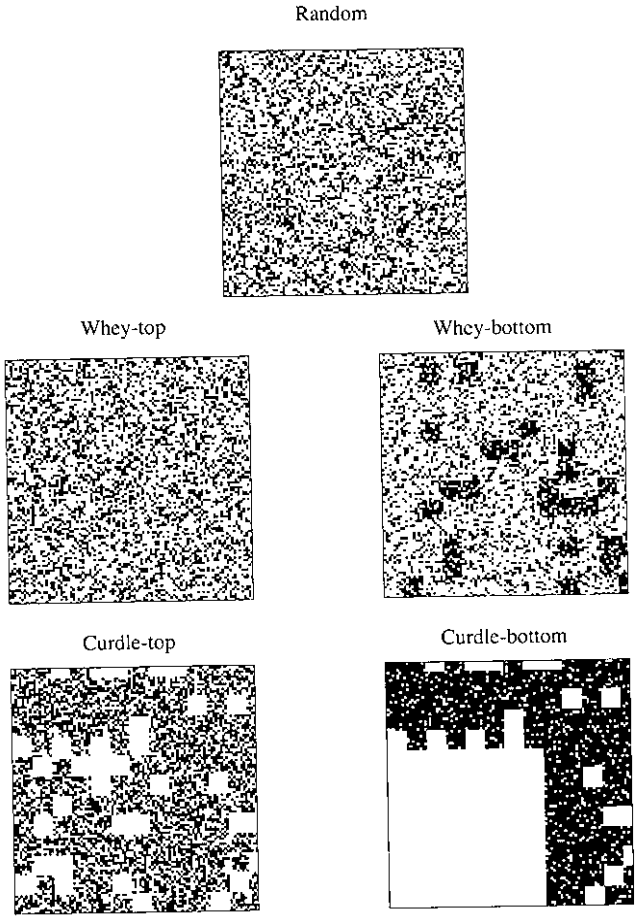


Figure 6.5. Hierarchical landscape patterns. Landscape-level pattern is strongly affected by hierarchical structure. These 100 x 100 cell maps are covered by the same amount of suitable habitat (32.8%) but were produced by random, curdling, and curdling-and-wheying algorithms. Shaded cells represent suitable habitat, and open cells represent unsuitable habitat.

allowing movement only to the adjacent neighbors), the weighted mean cluster size (S_{avg}), as perceived by this organism, is very low on the random and wheyed-top maps, slightly higher on curdled-top and wheyed-bottom, but dramatically larger on the curdled-bottom map (Table 6.2). Similarly, the relative size of the largest cluster (LC_{rel}) is approximately 0.5 on the curdled-bottom map but is near zero for the other patterns. Thus, the suitable habitat of this organism is more connected on the curdled-bottom map than on the other maps.

An organism using resources as defined by Rule 2 perceives small clusters on the random, wheyed-bottom, and wheyed-top maps, but perceives large, more connected

Table 6.1. Values of the proportion were used at each of three nested description of the methods for gene

Map pattern[1]	p_1	
Curdled-bottom	0.500	
Wheyed-bottom	0.125	
Curdled-top	0.875	
Wheyed-top	0.875	
Curdled[2]	0.75	
Wheyed-bottom	0.250	
Wheyed-top	0.875	
Curdled-bottom	0.750	
Wheyed-bottom	0.125	
Curdled-top	1.000	
Wheyed-top	1.000	

[1] The terms 'bottom' and 'top' refer to wh level ($l = 1$) or at the finest level ($l = 3$).

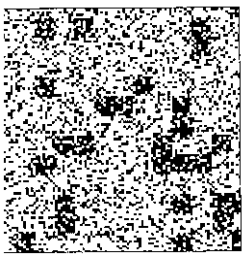
[2] There is a finite set of values that can be 0.422 it was impossible to generate a curd

clusters on both the curdled-botto (Table 6.2). Thus, increasing the r permits an organism under Rule 2 scale-dependent patterns. Further i results in an increase in S_{avg} and L LC_{rel} remain relatively low on the

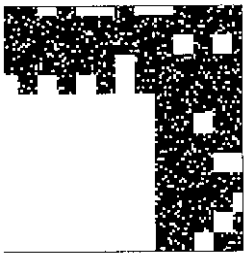
When the abundance of suit Rule 1 organism is similar to that perceives relatively small disconn when the largest cluster comprises (Table 6.2). The Rule 2 organism clusters are still relatively small Rule 3 organism, in contrast, perc The values of S_{avg} are all high a indicating that almost all suitable

When the abundance of suit effect of scale-dependent landscap That is, suitable habitat is sufficie the organisms. Even for the Rule

Whey-bottom



Curdle-bottom



:ape-level pattern is strongly affected by
s are covered by the same amount of
)m, curdling, and curdling-and-wheying
t, and open cells represent unsuitable

)ors), the weighted mean cluster size
on the random and wheyed-top maps,
but dramatically larger on the curdled-
size of the largest cluster (LC_{rel}) is
ut is near zero for the other patterns.
connected on the curdled-bottom map

Rule 2 perceives small clusters on the
but perceives large, more connected

Table 6.1. Values of the proportion (p_l) of the landscape occupied by suitable habitat that were used at each of three nested levels (l) to generate hierarchical maps. See text for description of the methods for generating hierarchical landscape maps.

Map pattern[1]	p_1			q_1		
	p_1	p_2	p_3	q_1	q_2	q_3
	$p = 0.328$					
Curdled-bottom	0.500	0.750	0.875	0	0	0
Wheyed-bottom	0.125	0.375	0.750	0	0.125	0.250
Curdled-top	0.875	0.750	0.500	0	0	0
Wheyed-top	0.875	0.625	0.375	0	0.625	0.250
	$p = 0.422$					
Curdled[2]	0.75	0.75	0.75	0	0	0
Wheyed-bottom	0.250	0.375	0.625	0	0.125	0.375
Wheyed-top	0.875	0.625	0.375	0	0.625	0.500
	$p = 0.656$					
Curdled-bottom	0.750	0.875	1.000	0	0	0
Wheyed-bottom	0.125	0.250	0.750	0	0.250	0.625
Curdled-top	1.000	0.875	0.750	0	0	0
Wheyed-top	1.000	0.750	0.625	0	0.875	0.750

[1] The terms 'bottom' and 'top' refer to whether the highest values of p and q were used at the most coarse level ($l = 1$) or at the finest level ($l = 3$).

[2] There is a finite set of values that can be used to generate a hierarchical map with a given p, and for $p = 0.422$ it was impossible to generate a curdled-top and curdled-bottom.

clusters on both the curdled-bottom and curdled-top maps, as indicated by S_{avg} and LC_{rel} (Table 6.2). Thus, increasing the resource utilization scale to include diagonal neighbors permits an organism under Rule 2 to perceive a relatively connected landscape with two scale-dependent patterns. Further increasing the resource utilization scale to Rule 3 again results in an increase in S_{avg} and LC_{rel} on most of the maps (Table 6.2). However, S_{avg} and LC_{rel} remain relatively low on the wheyed-bottom map, even with Rule 3.

When the abundance of suitable habitat is increased to $p = 0.422$, the trend for a Rule 1 organism is similar to that observed when $p = 0.328$. The Rule 1 organism still perceives relatively small disconnected resource clusters except on the curdled landscape, when the largest cluster comprises more than 90% of the suitable habitat in the landscape (Table 6.2). The Rule 2 organism perceives a more connected landscape, but resource clusters are still relatively small and discontinuous on the wheyed-bottom map. The Rule 3 organism, in contrast, perceives connected suitable habitat in all the landscapes. The values of S_{avg} are all high and consistent, and LC_{rel} approaches 1.0 (Table 6.2), indicating that almost all suitable habitat occurs in a single resource cluster.

When the abundance of suitable habitat increases again to $p = 0.656$, there is little effect of scale-dependent landscape pattern among the different resource utilization rules. That is, suitable habitat is sufficiently abundant for habitat connectivity to be high for all the organisms. Even for the Rule 1 organism, more than 95% of the suitable habitat is

Table 6.2. Values of the weighted mean cluster size (S_{avg}) and the relative size of the largest cluster (LC_{rel}) as determined using three rules that represent different resource utilization scales. Within each value of p, the proportion of the landscape occupied by suitable habitat, five different spatial arrangements of habitat were simulated by generating scale-dependent landscape pattern. See text for definition of the rules and the scale-dependent pattern.

	Weighted mean cluster size (S_{avg})			Relative size of largest cluster (LC_{rel})		
Map pattern	Rule 1	Rule 2	Rule 3	Rule 1	Rule 2	Rule 3
			$p = 0.328$			
Random	6	55	77,671	0.001	0.004	0.951
Curdled-bottom	31,581	54,398	54,399	0.529	0.742	0.742
Wheyed-bottom	68	176	3,550	0.009	0.020	0.141
Curdled-top	26	62,448	84,695	0.002	0.844	0.993
Wheyed-top	6	57	77,469	0.000	0.005	0.949
			$p = 0.422$			
Random	16	69,174	110,819	0.001	0.790	0.999
Curdled	95,622	106,776	106,824	0.926	0.982	0.982
Wheyed-bottom	37	12,800	109,705	0.004	0.304	0.996
Wheyed-top	15	71,341	109,949	0.001	0.802	0.997
			$p = 0.656$			
Random	156,085	171,914	172,064	0.953	1.000	1.000
Curdled-bottom	166,510	166,685	166,685	0.983	0.983	0.983
Wheyed-bottom	156,888	171,913	172,030	0.955	1.000	1.000
Curdled-top	169,519	172,002	172,032	0.993	1.000	1.000
Wheyed-top	156,830	171,921	172,031	0.955	1.000	1.000

located in a single resource cluster (Table 6.2), and Rule 2 and Rule 3 organisms essentially perceive one resource cluster.

Discussion of Simulation Results

Connectivity in the landscape is a direct consequence of the abundance of suitable habitat, spatial patterning of the habitat in the landscape, and the organism's scale of resource utilization. Results of the simulations illustrate that when suitable habitat is abundant, landscape-level patterning (i.e., random or hierarchical patterns) and resource utilization scale are not important because the landscape is sufficiently connected when suitable habitat occupies more than 60% of the landscape.

When suitable habitat is less abundant, patterning and resource utilization scales became increasingly important. Whereas the patterning in the random and wheyed-top landscapes appears fine, the curdled-bottom landscape appears more coarse. That is, large contiguous blocks of habitat occur more frequently in the curdled-bottom maps than in random and wheyed-top maps (Figure 6.5).

Landscape-level patterning interac
connectivity at intermediate levels of re
broad scales of resource utilization (
connected. However, organisms with r
perceive only the coarser curdled-botto

At intermediate levels of habitat
abundance of habitat can have profour
The abundance level at which these c
spatial patterning in the landscape and t
example, p_{crit} is around 0.60 for Rule
6.2). P_{crit} on random maps decreases t
However, landscape-level spatial patte
some hierarchical maps, like wheyed-b
(Figure 6.5), disconnect the habitat eve
the random map (see p=0.422, Table
abundances less than p_{crit} for random n
For example, Rule 2 organisms find t
perceive the other landscapes as disco

These results suggest that fine-sca
connectivity than the same percentage
Moreover, fine-scale fragmentation i
Therefore, edge-avoiding species find
fragmentation. This result agrees with
recommendations for forest manageme
clearcuts and preserving large patches

The benefits of coarse-scale struc
et al. (1991) compared landscapes fr
Georgia. Forest species could easily t
forest. In this region, forest dominated
to the valleys, imposing structure on
region were relatively disconnected v
areas of non-forest land use, not res
scaled manner throughout the landsc

The results also suggest that
conservation is at low and intermed
predict the consequences of habitat
abundance because of complex inte
scale. Biodiversity, by definition, re
mobility and dispersal capabilities.
amount and spatial pattern of habitat
landscape, like protecting large bloc
can preserve connectivity in the face
The same amount of habitat loss in
landscape further.

) and the relative size of the largest
esent different resource utilization
scape occupied by suitable habitat,
ıted by generating scale-dependent
ıd the scale-dependent pattern.

	Relative size of largest cluster (LC_{rel})		
	Rule 1	Rule 2	Rule 3
28			
	0.001	0.004	0.951
	0.529	0.742	0.742
	0.009	0.020	0.141
	0.002	0.844	0.993
	0.000	0.005	0.949
22			
	0.001	0.790	0.999
	0.926	0.982	0.982
	0.004	0.304	0.996
	0.001	0.802	0.997
556			
	0.953	1.000	1.000
	0.983	0.983	0.983
	0.955	1.000	1.000
	0.993	1.000	1.000
	0.955	1.000	1.000

le 2 and Rule 3 organisms essentially

of the abundance of suitable habitat,
ıd the organism's scale of resource
: when suitable habitat is abundant,
:al patterns) and resource utilization
ıfficiently connected when suitable

ıing and resource utilization scales
ning in the random and wheyed-top
cape appears more coarse. That is,
quently in the curdled-bottom maps

Landscape-level patterning interacts with the resource utilization scales to affect connectivity at intermediate levels of resource abundance. At p=0.422, organisms with broad scales of resource utilization (Rule 3, Table 6.2) perceive all landscapes as connected. However, organisms with more restrictive scales of resource use (Rule 1) perceive only the coarser curdled-bottom map (Figure 6.3) as connected.

At intermediate levels of habitat abundance, small amounts of change in the abundance of habitat can have profound effects on the connectivity of the landscape. The abundance level at which these changes in connectivity occur (p_{crit}) depends on spatial patterning in the landscape and the resource utilization scale of the organism. For example, p_{crit} is around 0.60 for Rule 1 organisms operating on random maps (Figure 6.2). P_{crit} on random maps decreases to around 0.35 for Rule 2 and 0.25 for Rule 3. However, landscape-level spatial patterning can change this relationship. For Rule 2, some hierarchical maps, like wheyed-bottom maps with the finest scale of heterogeneity (Figure 6.5), disconnect the habitat even when the abundance of habitat is above p_{crit} for the random map (see p=0.422, Table 6.2). Similarly, connectivity can occur at habitat abundances less than p_{crit} for random maps, if heterogeneity in the landscape is coarser. For example, Rule 2 organisms find the curdled landscapes connected at p=0.328 but perceive the other landscapes as disconnected.

These results suggest that fine-scale fragmentation poses a greater risk to landscape connectivity than the same percentage reduction of habitat arranged in a coarser pattern. Moreover, fine-scale fragmentation increases the amount of edge in the landscape. Therefore, edge-avoiding species find less suitable habitat in a landscape with fine-scale fragmentation. This result agrees with the findings of Franklin and Forman (1987) whose recommendations for forest management include reducing the number of small, dispersed clearcuts and preserving large patches of primeval forest.

The benefits of coarse-scale structure can be observed in real landscapes. Gardner et al. (1991) compared landscapes from the ridge-and-valley and piedmont regions of Georgia. Forest species could easily traverse the ridge-and-valley landscapes with 43% forest. In this region, forest dominated the ridges whereas non-forest lands were confined to the valleys, imposing structure on the landscape. Some landscapes in the piedmont region were relatively disconnected when forest covered 68% of the landscape because areas of non-forest land use, not restricted by topography, were dispersed in a fine-scaled manner throughout the landscape.

The results also suggest that the greatest opportunity for intervention with conservation is at low and intermediate levels of habitat abundance. It is difficult to predict the consequences of habitat fragmentation at intermediate values of habitat abundance because of complex interactions between pattern and resource utilization scale. Biodiversity, by definition, refers to a variety of organisms which differ in their mobility and dispersal capabilities. Such organisms are differentially affected by the amount and spatial pattern of habitat reduction. Imposing coarse scale structure on the landscape, like protecting large blocks of habitat or creating regional-scale corridors, can preserve connectivity in the face of some acceptable amount of habitat destruction. The same amount of habitat loss in a fine-scale pattern is more likely to fragment the landscape further.

INCORPORATING SCALING ISSUES INTO CONSERVATION

The following suggestions should be useful for protecting biodiversity in managed landscapes. The suggestions are phrased negatively to emphasize management choices which might endanger biodiversity.

(1) *Do not focus on single, simple concepts like patches and corridors* (regional scale corridor excepted). Expand the management perspective to include viewing the landscape as a whole. Use landscape-level indices to measure pattern at multiple scales. The spatial extent of protection must be equal to or broader than the spatial extent of the ecological system needing protection.

(2) *Do not destroy the natural levels of heterogeneity* (spatial and temporal). Instead, match exploitative/disruptive activities to natural patterns of heterogeneity. Natural processes (such as fire and flooding) create and maintain heterogeneity and should not be disrupted. Consider the question, "Under the proposed management scheme, will the appearance of (levels of heterogeneity in) future landscape be similar to those of a natural landscape?"

(3) *Do not fragment the landscape.* Maintain connectivity by keeping the amount of native habitats above potential thresholds for connectivity and/or imposing coarse-scale structure on the landscape. Limiting the amount and spatial extent of exploitative activities that result in habitats which starkly contrast with native habitats (e.g., agriculture versus forest) promotes connectivity.

(4) *Do not ignore the effects of critical thresholds.* The methods and results presented here show that small changes in habitat abundance and pattern can suddenly fragment an otherwise well-connected landscape at some (but not all) resource utilization scales.

CONCLUSIONS

Natural patterns of heterogeneity are related to biodiversity and affect ecological processes. However, the role of heterogeneity differs between species and between ecological processes. Therefore, protection strategies using a single species perspective can result in an array of complex management strategies likely to contain contradictory prescriptions. Taking a broader scale perspective and implementing protection at the landscape level is a more robust protection strategy. An intact landscape will preserve the natural processes and patterns of heterogeneity that its ecosystems and species require. A landscape-level characteristic such as habitat connectivity can be preserved by controlling the spatial extent and pattern of habitat loss. The challenge to conservation is to recognize critical landscape-level patterns and to minimize human effects on natural patterns and processes.

ACKNOWLEDGMENTS

V. H. Dale, D. DeAngelis, G. Orians, R. C. Szaro, D. W. Johnston, and an anonymous reviewer contributed useful suggestions on earlier drafts of this chapter. Funding for this research was provided by the Office of Health and Environmental Research, Department

of Energy under contract No. DE
Systems, Inc. S. M. Pearson receive
Fellowship from Oak Ridge Assoc
of the Environmental Sciences Div

LITERATURE CITED

Addicott, J. F., J. M. Aho, M. R. Antol
Ecological neighborhoods: scal
Baker, W. L. 1989. Landscape ecology
Area, Minnesota. *Ecology* 70:2
Buechner, M. 1989. Are small-scale la
mammal dispersal sinks? *Land*
Bierregaard, R. O., Jr. 1990. Avian con
In *Biogeography and Ecology o*
Academic Publishing, The Hag
Dayton, P. 1984. Processes structuring
Communities: Conceptual Issu
G. Abele, and A. B. Thistle, pp
Diamond, J. M. 1975. The island dilem
of natural reserves. *Biol. Conse*
Franklin, J. R., and R. T. T. Forman. 19
consequences and principles. *L*
Forman, R. T. T., and M. Godron. 198
Gardner, R. H., B. T. Milne, M. G. Tur
of broad-scale landscape patte
Gardner, R. H., R. V. O'Neill, M. G.
effects of animal movement w
Gardner, R. H., M. G. Turner, R. V. O'N
effects of landscape boundari
Role of Landscape Bounda
Environments, eds. M. M. Ho
and Hall, New York.
Glenn, S. M., and S. L. Collins. 1992.
extinction of species in prairie
Hudson, W. 1991. *Landscape Linkag*
Janzen, D. H. 1988. Tropical dry fores
ed. E. O. Wilson, pp. 130-137
Kotliar, N. B., and J. A. Wiens. 1990. M
framework for the study of he
Krummel, J. R., R. H. Gardner, G. Su
patterns in a disturbed enviror
Lovejoy, T. E., R. O. Bierregaard, A.
Brown, Jr., A. H. Powell, G. V.
other effects of isolation on
Soulé, pp. 257-285. Sinauer A
McLellan, B. N., and D. M. Shackle
effects of roads on behavior, I

CONSERVATION

ting biodiversity in managed
ıphasize management choices

tches and corridors (regional
ective to include viewing the
sure pattern at multiple scales.
er than the spatial extent of the

spatial and temporal). Instead,
rns of heterogeneity. Natural
heterogeneity and should not
management scheme, will the
be similar to those of a natural

ivity by keeping the amount of
and/or imposing coarse-scale
extent of exploitative activities
ıbitats (e.g., agriculture versus

methods and results presented
ıttern can suddenly fragment
ıll) resource utilization scales.

/ersity and affect ecological
etween species and between
ıg a single species perspective
ikely to contain contradictory
ıplementing protection at the
ntact landscape will preserve
cosystems and species require.
ctivity can be preserved by
ıe challenge to conservation is
nize human effects on natural

Johnston, and an anonymous
f this chapter. Funding for this
mental Research, Department

of Energy under contract No. DE-AC05-84OR21400 with Martin Marietta Energy Systems, Inc. S. M. Pearson received support from an Alexander Hollaender Postdoctoral Fellowship from Oak Ridge Associated Universities. This is publication number 4060 of the Environmental Sciences Division of Oak Ridge National Laboratory.

LITERATURE CITED

Addicott, J. F., J. M. Aho, M. R. Antolin, D. K. Padilla, J. S Richardson, and D. A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. *Oikos* 49:340-346.

Baker, W. L. 1989. Landscape ecology and nature reserve design in the Boundary Waters Canoe Area, Minnesota. *Ecology* 70:23-35.

Buechner, M. 1989. Are small-scale landscape features important factors for field studies of small mammal dispersal sinks? *Landscape Ecol.* 2:191-199.

Bierregaard, R. O., Jr. 1990. Avian communities in the understory of Amazonian forest fragments. In *Biogeography and Ecology of Forest Bird Communities*, ed. A. Keast, pp. 333-343. SPB Academic Publishing, The Hague.

Dayton, P. 1984. Processes structuring some marine communities: are they general? In *Ecological Communities: Conceptual Issues and the Evidence*, eds. D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, pp. 181-195. Princeton University Press, Princeton, N. J.

Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biol. Conserv.* 7:129-146.

Franklin, J. R., and R. T. T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecol.* 1:5-18.

Forman, R. T. T., and M. Godron. 1986. *Landscape Ecology*. John Wiley and Sons, New York.

Gardner, R. H., B. T. Milne, M. G. Turner, and R. V. O'Neill. 1987. Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecol.* 1:19-28.

Gardner, R. H., R. V. O'Neill, M. G. Turner, and V. H. Dale. 1989. Quantifying scale-dependent effects of animal movement with simple percolation models. *Landscape Ecol.* 3:217-227.

Gardner, R. H., M. G. Turner, R. V. O'Neill, and S. Lavorel. 1991. Simulation of the scale-dependent effects of landscape boundaries on species persistence and dispersal. In *Ecotones: The Role of Landscape Boundaries in the Management and Restoration of Changing Environments*, eds. M. M. Holland, P. G. Risser, and R. J. Naiman, pp. 76-89. Chapman and Hall, New York.

Glenn, S. M., and S. L. Collins. 1992. Effects of scale and disturbance on rates of immigration and extinction of species in prairies. *Oikos* 63:273-280.

Hudson, W. 1991. *Landscape Linkages and Biodiversity*. Island Press, Washington, D.C.

Janzen, D. H. 1988. Tropical dry forests: the most endangered tropical ecosystem. In *Biodiversity*, ed. E. O. Wilson, pp. 130-137. National Academy Press, Washington, D.C.

Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253-260.

Krummel, J. R., R. H. Gardner, G. Sugihara, R. V. O'Neill, and P. R. Coleman. 1987. Landscape patterns in a disturbed environment. *Oikos* 48:321-324.

Lovejoy, T. E., R. O. Bierregaard, A. B. Rylands, J. R. Malcom, C. E. Quintela, L. H. Harper, S. Brown, Jr., A. H. Powell, G. V. N. Powell, H. O. R. Schubart, and M. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. In *Conservation Biology*, ed. M. Soulé, pp. 257-285. Sinauer Associates, Inc. Sunderland, Mass.

McLellan, B. N., and D. M. Shackleton. 1988. Grizzly bears and resource-extraction industries: effects of roads on behavior, habitat use and demography. *J. Appl. Ecol.* 25:451-460.

Mandelbrot, B. B. 1983. *The Fractal Geometry of Nature*. W. H. Freeman and Co., San Francisco, Calif.

Musick, H. B., and H. D. Grover. 1991. Image textural measures as indices of landscape pattern. In *Quantitative Methods in Landscape Ecology: the Analysis and Interpretation of Landscape Heterogeneity*, eds. M. G. Turner and R. H. Gardner, pp. 77-103. Ecological Studies, vol. 82. Springer-Verlag Inc., New York.

Noss, R. F. 1991. Landscape connectivity: different functions at different scales. In *Landscape Linkages and Biodiversity*, ed. W. Hudson, pp. 27-39. Island Press, Washington, D.C.

O'Neill,, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. *A Hierarchical Concept of Ecosystems*. Princeton University Press, Princeton, N.J.

O'Neill, R. V., B. T. Milne, M. G. Turner, and R. H. Gardner. 1988. Resource utilization scales and landscape pattern. *Landscape Ecol.* 2:63-69.

O'Neill, R. V., R. H. Gardner, M. G. Turner, and W. H. Romme. 1992. Epidemiology theory and disturbance spread on landscapes. *Landscape Ecol.* 7:19-26.

Pearson, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. *Landscape Ecol.* 8:3-18.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. *Am. Nat.* 132:652-661.

Raunkaier, C. 1934. *The Life Form of Plants and Statistical Plant Geography*. Clarendon, Oxford.

Risser, P. G., J. R. Karr, and R. T. T. Forman. 1984. *Landscape Ecology, Directions and Approaches*. Special Publication No. 2, Illinois Natural History Survey, Champaign, Ill.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecol. Monogr.* 52:199-221.

Romme, W. H., and D. G. Despain. 1989. Historical perspective on the Yellowstone fires of 1988. *BioScience* 39:695-699.

Roughgarden, J. D. 1977. Patchiness in the spatial distribution of a population caused by stochastic fluctuations in resources. *Oikos* 29:52-59.

Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62:1041-1051.

Scott, J. M., B. Csuti, J. D. Jacobi, and J. E. Estes. 1987. Species richness: a geographic approach to protecting future biological diversity. *BioScience* 37:782-788.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31:131-134.

Shaffer, M. 1987. Minimum viable populations: coping with uncertainty. In *Viable Populations for Conservation*, ed. M. E. Soulé, pp. 69-86. Cambridge University Press, Cambridge.

Stauffer, D. 1985. *Introduction to Percolation Theory*. Taylor and Francis, London.

Turner, M. G., V. H. Dale, and R. H. Gardner. 1989. Predicting across scales: theory development and testing. *Landscape Ecol.* 3:245-252.

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 1991. Potential responses of landscape boundaries to global climate change. In *Ecotones: The Role of Landscape Boundaries in the Management and Restoration of Changing Environments*, eds. M. M. Holland, P. G. Risser and R. J. Naiman, pp. 52-75. Chapman and Hall, New York.

Turner, M. G., W. H. Romme, R. H. Gardner, R. V. O'Neill, and T. K. Kratz. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. *Landscape Ecol.* 8:213-227.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of eastern deciduous forest. In *Forest Island Dynamics in Man-dominated Landscapes*, eds. R. L. Burgess and D. M. Sharpe. Springer-Verlag, New York.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Bot. Rev.* 45:229-299.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* 26:1-80.

Wiens, J. A. 1976. Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* 7:81-120.

Wiens, J. A. 1989. Spatial scaling in ec

Wiens, J. A., and B. T. Milne. 1989. Sc
ecology from a beetle's perspecti

Wilcove, D. S. 1985. Nest predation in fo
66:1211-1214.

Willis, E. O., and Y. Oniki. 1978. Birds

N. H. Freeman and Co., San Francisco,

asures as indices of landscape pattern.
nalysis and Interpretation of Landscape
r, pp. 77-103. Ecological Studies, vol.

ions at different scales. In *Landscape*
9. Island Press, Washington, D.C.
llen. 1986. *A Hierarchical Concept of*
N.J.
. 1988. Resource utilization scales and

mme. 1992. Epidemiology theory and
7:19-26.
of landscape-level factors on wintering

tion. *Am. Nat.* 132:652-661.
Plant Geography. Clarendon, Oxford.
e Ecology, Directions and Approaches.
Survey, Champaign, Ill.
lpine forests of Yellowstone National

ctive on the Yellowstone fires of 1988.

on of a population caused by stochastic

forests of the eastern United States.

ecies richness: a geographic approach
37:782-788.
conservation. *BioScience* 31:131-134.
ith uncertainty. In *Viable Populations*
ridge University Press, Cambridge.
lor and Francis, London.
ing across scales: theory development

tial responses of landscape boundaries
dscape Boundaries in the Management
f. M. Holland, P. G. Risser and R. J.

ill, and T. K. Kratz. 1993. A revised
bility on scaled landscapes. *Landscape*

, M. K. Klimkiewicz, and D. Bystrak.
f eastern deciduous forest. In *Forest*
ds. R. L. Burgess and D. M. Sharpe.

in vegetation. *Bot. Rev.* 45:229-299.
ntains. *Ecol. Monogr.* 26:1-80.
nents. *Ann. Rev. Ecol. Syst.* 7:81-120.

Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecol.* 3:385-397.
Wiens, J. A., and B. T. Milne. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecol.* 3:87-96.
Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211-1214.
Willis, E. O., and Y. Oniki. 1978. Birds and army ants. *Ann. Rev. Ecol. Syst.* 9:243-263.