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Human-induced fragmentation of forests is increasing, yet the consequences of these landscape changes to vertebrate communities are poorly understood. Despite progress in our understanding of how bird communities respond to forest fragmentation caused by agricultural or urban development, we have little understanding of these dynamics in landscapes undergoing intensive forest management, where mature forest islands are separated by younger forest stands of varying ages. I developed a conceptual framework on vertebrate-habitat relationships in spatially complex landscapes and applied this landscape ecological perspective in the design and implementation of a field study on the relationship between landscape structure and breeding bird abundance patterns in the central Oregon Coast Range. I sampled 10 subbasins (250-300 ha) in each of 3 basins based on the proportion of subbasin in a large sawtimber condition and the spatial distribution pattern of that sawtimber within the subbasin. I systematically sampled each subbasin for birds during the breeding season and developed digital vegetation cover maps for each subbasin. I developed a spatial analysis program for quantifying landscape structure using the Arc/Info Geographic Information System. Using analysis of variance and regression procedures, I quantified the independent effects of habitat area and habitat pattern on several bird species, focussing on species associated with large sawtimber. Species varied dramatically in the strength and nature of the relationship between abundance and several gradients in habitat area and pattern at the subbasin scale. Relationships between bird abundance and landscape structure were generally weak; landscape structure typically explained less than one-third to one-half of the variation in each species' abundance among the 30 subbasins. Most species were positively associated with gradients in increasing landscape heterogeneity or fragmentation of their habitats; that is, they were associated with the more fragmented habitats. Only winter wrens showed consistent evidence of association with the least fragmented landscapes. The results are interpreted within the context of the conceptual framework outlined in the second chapter and within the scope and limitations of the study.

RELATIONSHIP BETWEEN LANDSCAPE STRUCTURE AND AVIAN ABUNDANCE PATTERNS IN THE OREGON COAST RANGE

by

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CHAPTER 1

INTRODUCTION

Ecologists increasingly are recognizing the importance of heterogeneity and scale in the structure and function of natural ecosystems. This recognition has led to a greatly expanded understanding of ecosystem structure and dynamics and has opened new pathways for understanding vertebrate population distribution and dynamics. In particular, this appreciation has spurred interest in expanding the range of spatio-temporal scales investigated by ecologists and has led to the emergence of landscape ecology as a separate discipline (Forman and Godron 1986). Moreover, this recognition has enhanced our understanding of vertebrate-habitat relationships and challenged us to recognize the complex manner in which land management activities affect vertebrate communities.

The 3 chapters that follow represent 3 stages in the development and completion of my dissertation research: (1) formulation of a conceptual framework to guide the development, implementation, and interpretation of the research, (2) development of the methodology and tools with which to conduct the research, and (3) the implementation and interpretation of the field study.

Landscape processes (e.g., forest fragmentation), in particular, can only be understood within the context of a broad conceptual framework built upon the concepts of heterogeneity and scaling. Consequently, in the second chapter, I develop a conceptual framework on vertebrate-habitat relationships from a landscape ecological perspective. This model consists of several premises that together provide a strong framework for understanding vertebrate populations in spatially complex environments. Perhaps most importantly, this framework helps to identify many of the limitations that constrain studies on wildlife-habitat relationships, and, in this respect, provides the context within which the results of the field study (presented in Chapter 4) can be interpreted.

In the third chapter, I present a detailed discussion on the measurement of landscape structure using a program that Barbara Marks (OSU, Forest Science Department) and I developed called FRAGSTATS. FRAGSTATS is a spatial analysis program for quantifying landscape structure. This program was developed specifically to assist in the analysis of 30 landscapes in the central Oregon Coast Range as part of the field study. However, interest in the program was so great that we expanded the program into a versatile software package that has broad applicability.

Finally, in the fourth chapter, I present the results of a field study on the relationship between landscape structure and breeding bird abundance patterns in the central Oregon Coast Range. Specifically, I evaluated the relationship between both habitat area and habitat pattern and the abundance of species associated with large sawtimber habitats. The conceptual framework presented in chapter 2 provides the intellectual framework within which I designed and conducted the study and interpreted the results. Program FRAGSTATS, presented in chapter 3, provided the analytical capability to conduct the necessary landscape analysis.

There has been much discussion and disagreement regarding the appropriate conduct of wildlife research to gain reliable knowledge (e.g. Sinclair 1991, Murphy and Noon 1991, Nudds and Morrison 1991, Romesburg 1981). My field study was designed as an initial exploratory investigation on the relationship between landscape structure and breeding birds in the central Oregon Coast Range. Exploratory, pattern-oriented studies such as mine have been heavily criticized because they do not address process hypotheses derived in a hypothetico-deductive manner using experimental designs and confirmatory procedures in the traditional reductionist manner. Part of this criticism stems from the belief that research of the latter type qualifies as "good" science, whereas all other approaches represent inferior science. Part of the criticism also stems from a lack of appreciation of how a particular study fits into an overall research program. Therefore, in order to evaluate my study properly, it is important to understand how it was designed in the context of my overall research program.

The overall goal of my research program is to understand how landscape structure affects vertebrate populations and communities, with the aim of providing land managers the information necessary to evaluate the potential impacts of landscape management strategies on vertebrate populations. To accomplish this goal, ultimately we must understand how changes in landscape structure, including changes in habitat area, edge-to-interior ratio, insularity, and other aspects of landscape structure, affect processes (e.g., competition, predation, dispersal, etc.) that affect population abundance, distribution, and dynamics. Ultimately, we must understand the myriad of process pathways by which landscape structure affects population viability. Unfortunately, while there has been a great deal of theoretical and conceptual work on populations in spatially complex environments, there have been few empirical studies to confirm or refute these ideas, and none at an appropriate scale for bird species or in a regional landscape context similar to western Oregon and Washington. Consequently, there is not a strong empirical basis for assuming that 1 process pathway is more important than another; it would therefore be premature to focus the initial research on 1 process pathway. My study was designed as phase 1 in this research program. Specifically, my study was designed to determine whether or not I could demonstrate that landscape structure was related to bird abundance patterns and to what extent, and if so, to explore patterns in the relationship between landscape structure and bird abundance. If relationships could be demonstrated, phase 2 studies would be designed to explore possible mechanisms for the observed patterns. Hopefully, the results from phase 1 will help determine which of the many process pathways may be most important, so that intensive process-oriented research employing costly manipulative experiments can be conducted with a greater likelihood of success.

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CHAPTER 2

A LANDSCAPE ECOLOGICAL PERSPECTIVE ON WILDLIFE-HABITAT RELATIONSHIPS

INTRODUCTION

Wildlife ecologists often have assumed that the most important ecological processes effecting wildlife populations and communities operate at local spatial scales. Vertebrate species richness and abundance, for example, are often considered to be functions of variation in local resource availability, vegetation structure, and the size of the habitat patch (MacArthur and MacArthur 1961, Willson 1974, Cody 1985). Correspondingly, most wildlife research and management activities have focussed on the within-patch scale, typically small plots or forest stands (e.g., Rosenberg and Raphael 1986, Lehmkuhl et al. 1991, McGarigal and McComb 1992).

Ecologists increasingly are recognizing the importance of heterogeneity and scale in the structure and function of natural ecosystems ((Allen and Star 1982, Forman and Godron 1986, Wiens 1989a, Kolasa and Pickett 1991). This recognition has greatly expanded our perspective on ecosystem structure and dynamics and has opened new pathways for understanding vertebrate population distribution and dynamics. In particular, this appreciation has spurred interest in expanding the range of spatial and temporal scales investigated by ecologists and has led to the emergence of landscape ecology as a discipline (Forman and Godron 1986, Urban et al. 1987, Turner 1989). Correspondingly, wildlife ecologists have become increasingly aware that habitat variation and its effects on ecological processes and vertebrate populations occurs at a wide range of spatial scales (Wiens 1989a,b). In particular, there has been increasing awareness of the potential importance of coarse-scale habitat patterns to wildlife populations, and there has been a corresponding surge in landscape ecological investigations that examine vertebrate distributions and population dynamics over broader spatial scales (e.g., this study). The recent attention on metapopulation theory (Gilpin and Hanski 1991) and the proliferation of mathematical models on dispersal and spatially distributed populations (Kareiva 1990) are testimony to these changes. Moreover, recent conservation efforts for the Northern Spotted Owl demonstrate the willingness and ability of public land management agencies to analyze and manage wildlife populations at the landscape scale (Lamberson et al. 1992, Murphy and Noon 1992, Thomas et al. 1990).

From these developments there has emerged a landscape ecological perspective on wildlife-habitat relationships that provides a strong conceptual framework for considering how vertebrate populations function in spatially complex environments. This perspective has enhanced our understanding of vertebrate-habitat relationships and challenged us to recognize the complex manner in which land management activities affect vertebrate communities. Effects of landscape processes such as forest fragmentation on vertebrate communities, for example, can only be fully understood within the context of a broad conceptual framework built upon the concepts of heterogeneity and scaling. Through this conceptual framework not only can we better appreciate the potential importance of landscape and patch dynamics to vertebrate populations, but we also can identify many of the limitations and constraints on wildlife studies (Wiens 1989a,b). In this chapter, I briefly describe my understanding of this conceptual framework and outline some of the key underlying premises. Further, I discuss some of the research and management implications derived from this perspective.

CONCEPTUAL FRAMEWORK

> "In the real world, environments are patchy. Factors influencing the proximate physiological or behavioral state or the ultimate fitness of individuals (and the dynamics of populations) exhibit discontinuities on many scales in time and space. The patterns of these discontinuities produce an environmental

> patchwork which exerts powerful influences on the distributions of organisms, their interactions, and their adaptations" (Wiens 1976).

This idea that environments are patchy or heterogeneous at many scales and that these patterns can exert a strong influence on the distribution and dynamics of vertebrate populations is the foundation of a landscape ecological perspective on vertebrate-habitat relationships. Judging from the date of this quote, obviously this landscape ecological perspective is not new to ecologists; yet, only recently has it become popular among ecologists. As a result of its growing popularity, this conceptual framework increasingly is guiding land management practices even though the underlying premises are not recognized or fully understood. Unfortunately, a misunderstanding of this conceptual framework can lead to erroneous management decisions. Therefore, it is imperative that this conceptual framework be clearly understood and rigorously challenged. The following premises contribute toward the development of this conceptual framework. Separately, these premises are simple, straightforward and intuitive concepts that are widely understood. However, these concepts have not been synthesized into a single coherent conceptual model that wildlife ecologists and managers can benefit from.

(1) <u>Multidimensional Environment</u>.--The environment in which each animal lives is multidimensional; that is, there are a multitude of characteristics representing different physical or biological parameters (e.g., elevation, moisture, canopy height, herbaceous cover, etc.) of the environment that characterize each animal's environment over space and time (Fig. 2.1).

From a landscape ecological perspective, there are at least 3 important points derived from this premise. First, although the environment can be characterized by a multitude of physical and biological parameters, each species' environment can be characterized effectively by a space with many fewer dimensions, corresponding to those parameters that assume a disproportionate

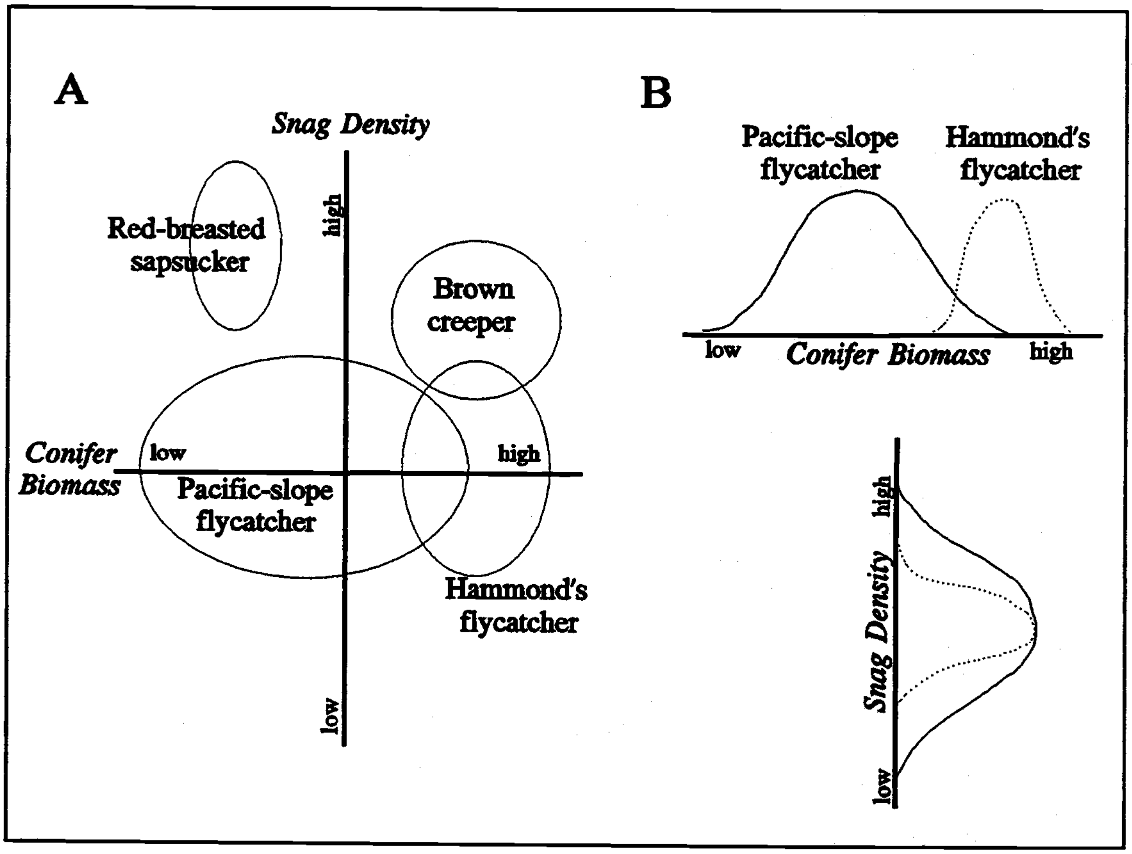

Figure 2.1. Hypothetical distribution of bird species in 2-dimensional space, where each dimension represents an important environmental gradient for ≥ 1 species represented (A), and the corresponding Gaussian response curves along those dimensions for 2 species (B). The width of an ellipse represents the species' niche breadth along the corresponding dimension. If the ellipse crosses the origin along a dimension, then the species' use of environments along that dimension does not differ significantly from the average condition.

role in limiting or regulating the population(s), as in the concept of the species' 'niche'. The distinction here between the autecological or individualistic focus of the Grinnellian niche concept (Grinnell 1917, 1924, 1928) and the synecological or community focus of the Hutchinsonian niche concept (Elton 1927, Hutchinson 1957) is trivial. In either view, important environmental parameters (dimensions) may correspond to different life history requirements of the species (e.g., nest sites, roost sites, food resources, etc.). The range along each of these dimensions or the multidimensional space occupied by a species is its niche breadth and this may vary over space and time in response to changes in resource availability, intra- and interspecific interactions (e.g., competition, predation), habitat patterns, and other factors (Wiens 1989b). Niche breadth is often portrayed graphically as Guassian, or bell-shaped, frequency distributions along environmental resource gradients or as frequency ellipses or spheres in 2- or 3-dimensional space, respectively (Fig. 2.1). Niche breadth may be viewed as an index to habitat specificity along each dimension from an organism-centered perspective. For example, Hammond's flycatchers (Empidonax hammondii) occupy relatively pure conifer stands during the breeding season in the Oregon Coast Range (i.e., narrow niche breadth) and thus exhibit a high degree of specificity along the hardwood-conifer gradient; whereas, Pacific slope flycatchers (Empidonax difficilis) select a wider range of conditions along this gradient (i.e., broader niche breadth) and thus exhibit less specificity (McGarigal and McComb, unpubl. data). From a landscape ecological perspective, the important point is that niche breadth varies among species along each environmental dimension.

Second, according to niche theory, ecologically similar species coexist by virtue of niche differences; that is, each species has a unique niche (Wiens 1989b). Because resource use by species may be scaled on a variety of dimensions, species that exhibit high overlap on ≥ 1 dimension should differ on at least 1 other dimension (MacArthur 1972, Schoener 1974). Indeed, the notion of resource partitioning as a consequence of natural selection to allow coexistence of species is nothing more than the shifting and/or narrowing of a species' niche position and/or breadth along 1 or more environmental dimensions. Thus, each species has at least 1 unique resource utilization function and therefore occupies a slightly different portion of the total environmental space. In the previous example, Hammond's flycatchers occupy the conifer end of the gradient, whereas Pacific slope flycatchers occupy the hardwood and mixed portions of the gradient (Fig. 2.1).

Third, and most importantly, environmental dimensions important to 1 species may or may not be functionally important to another species. In other words, each species' niche may be characterized by different dimensions, either those that limit or regulate the distribution or abundance of the species (as in the Grinnellian niche concept) or those along which potentially competing species partition resources (as in the Hutchinsonian niche concept). For example, the proportional abundance of hardwoods in a mixed hardwood-conifer forest stand may be important to Hammond's and Pacific slope flycatchers and may be a gradient along which these species partition resources, but it may be meaningless to winter wrens (Troglodytes) because of differences in life history requirements (Fig. 2.1).

Based on this premise of a multidimensional environment, each species uses only a portion of the total environmental space available (i.e., habitat partitioning), presumably because evolutionary forces have resulted in differential habitat selection among species to allow for coexistence. On any particular environmental gradient, some species are habitat specialists and occupy a relatively narrow range of environmental conditions (i.e., narrow niche breadth), whereas other species are habitat generalists and occupy a relatively broad range of environmental conditions (i.e., broad niche breadth). Moreover, each species uses a different portion of the total environmental space; that is, each species occupies a slightly different niche, distinguished on the basis of 1 or more environmental dimensions. Species may overlap or coincide with other species on many or nearly all environmental dimensions, but exclusively occupy a portion of at least 1 dimension (i.e., unique niches).

By appreciating the multidimensional character of each species' niche and recognizing that environmental parameters affect species differently, we can better appreciate why manipulations of landscape patterns through timber management practices, for example, may affect some species and not others. More generally, our limited ability to perceive of and measure the functionally important dimensions for each species limits our ability to characterize a species' niche accurately and predict responses to management activities.

(2) Heterogeneity Domains.--The environment in which each animal lives is heterogeneous in both the spatial and temporal domains, and there may be multiple dimensions to heterogeneity within each of these domains (Fig. 2.2).

Within the spatial domain, heterogeneity is typically expressed in the horizontal dimension because this corresponds to our (human) own perception of the environment and it is relatively simple to measure. However, the vertical dimension (or perhaps the 3-dimensional perspective) may be equally or more important for certain environmental attributes. In other words, some environmental parameters may exhibit greater heterogeneity or patterning in the vertical dimension than the horizontal dimension (Fig. 2.2). Moreover, species may be differentially responsive to heterogeneity in different dimensions. For example, some bird species may select vegetation patches on the same scale in the horizontal dimension, yet discriminate between patches on the basis of vertical heterogeneity (e.g., foliage height diversity). In addition, temporal heterogeneity often constitutes a major source of spatial patchiness. For example, localized stochastic disturbances such as fire or windthrow over time may be responsible for creating the spatial patchiness.

The important point is that heterogeneity is not unidimensional. By recognizing that species may be differentially responsive to environmental heterogeneity in the different domains (spatial and temporal) and along different dimensions (e.g., horizontal and vertical), we can better understand why manipulations of landscape patterns in the horizontal dimension of the spatial domain may affect some species and not others. For example, as a habitat becomes progressively fragmented in the horizontal plane, species sensitive to heterogeneity in the vertical dimension may be affected only to the degree that horizontal fragmentation affects vertical structure. Studies on forest fragmentation have traditionally only measured heterogeneity in the horizontal plane. Stronger relationships might be found for some species if vertical heterogeneity was measured as well.

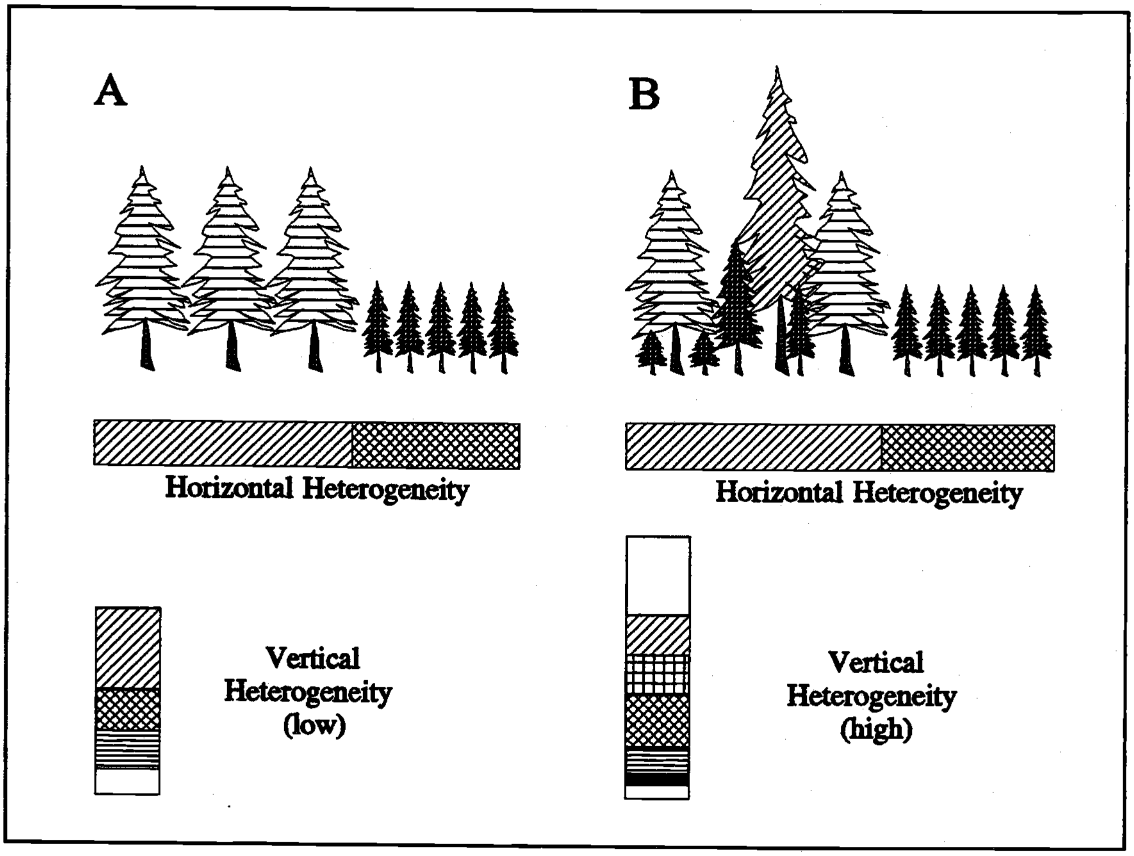

Figure 2.2. Hypothetical representation of 2 landscapes with identical horizontal heterogeneity but different vertical heterogeneity. On the horizontal axis, both landscapes contain 2 patches (e.g., conifer sawtimber and conifer pole patches in landscape A, and conifer old-growth and conifer pole patches in landscape B) represented by hatched bars as they might be mapped in a typical landscape mosaic. Thus, although the composition of these landscapes differs, horizontal patchiness is the same. On the vertical axis, landscape A contains fewer vertical strata (represented by hatched bars), based on vertical changes in the composition and density of foliage, than landscape B. Thus, although landscape A and B have equal horizontal patchiness, they differ in vertical patchiness because the patches in landscape B are structurally and/or compositionally more diverse than the patches in landscape A.

(3) Patchy Environment.--The environment in which each animal lives is comprised of a heterogeneous mosaic of patches at many spatial and temporal scales (Fig. 2.3). That is, the dimensions of each animal's environment often contain sharp discontinuities and are thus distributed heterogeneously as a patchwork mosaic on many scales in time and space.

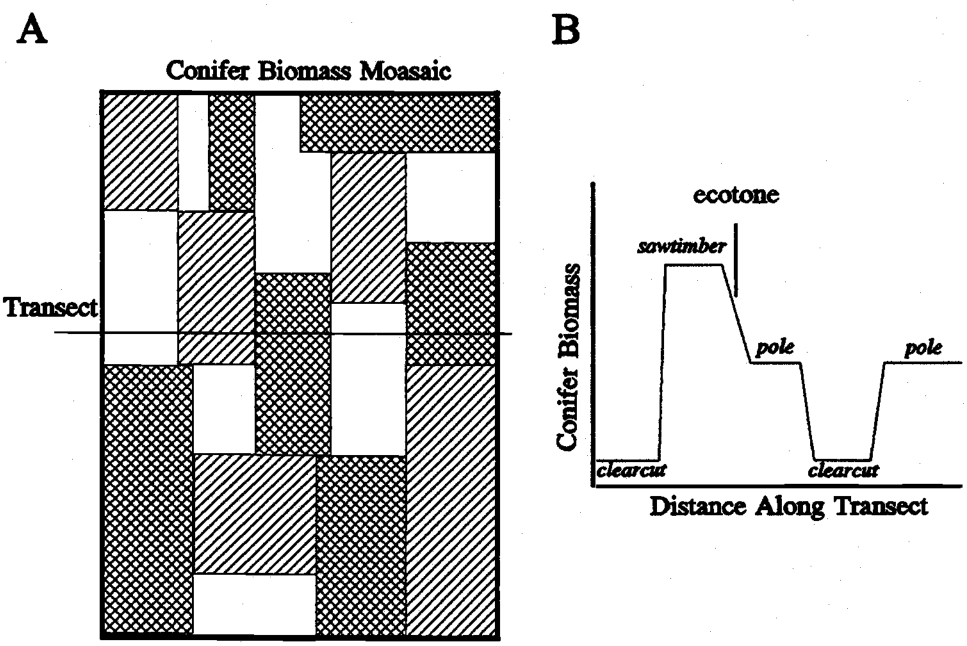

Figure 2.3. Hypothetical representation of conifer biomass distribution as a 2-dimensional mosaic of relatively discrete patches (rectangular areas with a common fill pattern)[A], and the variation in conifer biomass along a transect across that landscape mosaic (B). Within patches, conifer biomass is relatively similar throughout. Among patches, however, conifer biomass varies significantly relative to the level of homogeneity within patches.

Patches represent relatively discrete areas (spatial domain) or periods (temporal domain) of relatively homogeneous environmental conditions where the patch boundaries are distinguished by discontinuities in environmental character states from their surroundings of magnitudes that are perceived by or relevant to the animal under consideration (Wiens 1976). From a strictly organism-centered view, patches may be defined as environmental units between which fitness prospects, or "quality", differ. In practice, however, patches may be more appropriately defined by nonrandom distribution of activity or resource utilization among environmental units, as recognized in the concept of "Grain Response" (see below).

Patches are dynamic (Pickett and White 1985) and occur on a variety of spatial and temporal scales that vary as a function of each animal's perceptions (Wiens 1976). In other words, a patch at any given scale has an internal structure that is a reflection of patchiness at finer scales, and the mosaic containing that patch has a structure that is determined by patchiness at broader scales (Kotliar and Wiens 1990). Thus, a landscape does not contain a single patch mosaic, but contains a hierarchy of patch mosaics across a range of scales. From an organism-centered perspective, the smallest scale at which an organism perceives and responds to patch structure is its "grain" (Kotliar and Wiens 1990). This lower threshold of heterogeneity is the level of resolution at which the patch size becomes so fine that the individual or species stops responding to it, even though patch structure may actually exist at a finer resolution (Kolasa and Rollo 1991). The lower limit to grain is set by the physiological and perceptual abilities of the organism and therefore varies among species. Similarly, "extent" is the coarsest scale of heterogeneity, or upper threshold of heterogeneity, to which an organism responds (Kotliar and Wiens 1990, Kolasa and Rollo 1991). At the level of the individual, extent is determined by the lifetime home range of the individual (Kotliar and Wiens 1990) and varies among individuals and species. More generally, however, extent varies with the organizational level (e.g., individual, population, metapopulation) under consideration; for example the upper threshold of patchiness for the population would probably greatly exceed that of the individual.

Patch boundaries are artificially imposed and are meaningful only when referenced to a particular scale (i.e., grain size and extent). For example, a relatively discrete patch boundary between an aquatic surface (e.g., lake) and terrestrial surface (e.g., adjacent forest) becomes a continuous gradient as one moves to a finer and finer resolution. Most environmental attributes possess 1 or more "domains of scale" at which the individual spatial or temporal units can be treated as functionally homogeneous and the variation among units is most pronounced (i.e., strong patterning); at intermediate scales the environmental dimensions appear more as gradients of continuous variation in character states (Wiens 1989a). These scale domains may be arranged hierarchically in a simple or nested hierarchy (Fig. 2.4). For example, conifer biomass (attribute) may exhibit a strong pattern at the scale of thousands of square kilometers (e.g., physiographic provinces). Within each landscape unit at this coarse scale, conifer biomass may exhibit a secondary pattern at the scale of several hectares (e.g., forest stands). This secondary pattern may be scaled similarly among landscape units (i.e., simple hierarchy) or differently among landscape units (i.e., nested hierarchy), and there may be multiple levels in the hierarchy representing multiple domains of scale.

In addition, the domains of scale for different environmental attributes may be coincident, nested, or completely independent because of similarities or differences in the underlying processes (e.g., disturbance regime) that produced the environmental patterns (Fig. 2.5). For example, at any particular scale, some attributes may be jointly heterogeneously distributed (i.e., coincident domains of scale), whereas others may be functionally homogeneous (i.e., no scale domain). For example, at the scale of canopy gaps, tree foliage biomass, shrub cover, and soil temperature (attributes) might exhibit joint heterogeneity (i.e., they all exhibit a great degree of variation from 1 gap-sized area to the next), whereas coarse woody debris biomass might exhibit little variation at that scale, but itself might be strongly patterned at slightly finer (e.g., presence or absence of individual wood pieces) and slightly coarser (e.g., woody debris clumps) scales. Other attributes may have largely independent domains of scale. For example, snag biomass (attribute) might be patterned at 3 dominant scales (e.g., clumps of a few to several snags; stands of trees; regions within a mountain range) reflecting the disturbance regime; whereas, slope/aspect (attribute) might be heterogeneously distributed at several different scales (e.g., first-order drainages, second-order drainages, and so on) reflecting geomorphological patterns. Relative to the landscape ecological conceptual

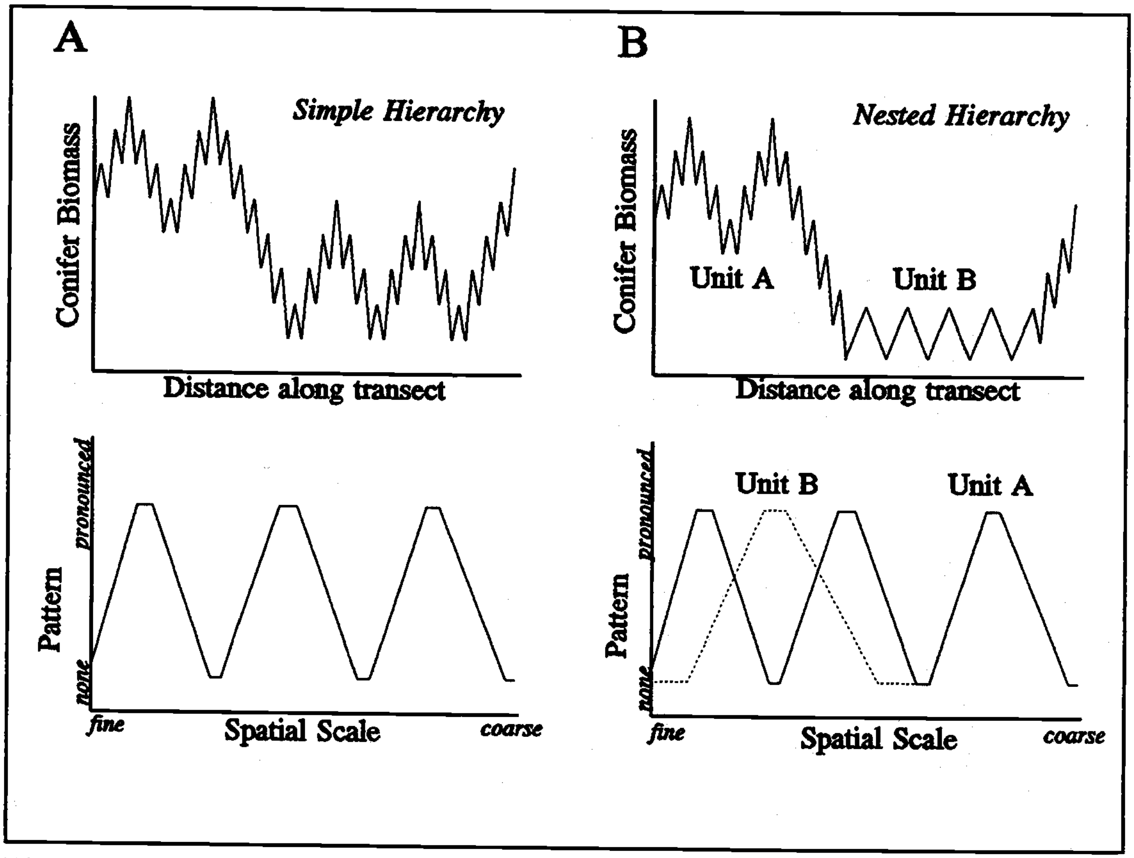

Figure 2.4. Hypothetical patterns of spatial variation in conifer biomass, including a simple hierarchy of patterns (landscape A) and a nested hierarchy of patterns (landscape B). Top figures represent the variation in conifer biomass along a transect in each landscape. Bottom figures represent the corresponding scales at which spatial pattern is revealed. In landscape A, conifer biomass varies periodically along a transect at 3 different spatial scales. The finest scale at which pattern is pronounced is represented by the smallest periodic change in conifer biomass and may correspond to the scale of individual trees. The second scale at which pattern is revealed is represented by the intermediate periodic change in conifer biomass and may correspond to the scale of several trees (e.g., influenced by topo-edaphic variation). The coarsest scale at which pattern is again prevalent is represented by the largest periodic change in conifer biomass and may correspond to the scale of stands of trees (e.g., influenced by fire disturbance). Landscape B has similar patterns, except that the finest and intermediate scales in unit B (e.g., a stand in the landscape mosaic) have dissolved into a single intermediate scale, perhaps reflecting the uniform spacing of trees in a managed planation. The spatial patterns represented are purely hypothetical but illustrate the concept that environmental parameters may be patterned at multiple scales.

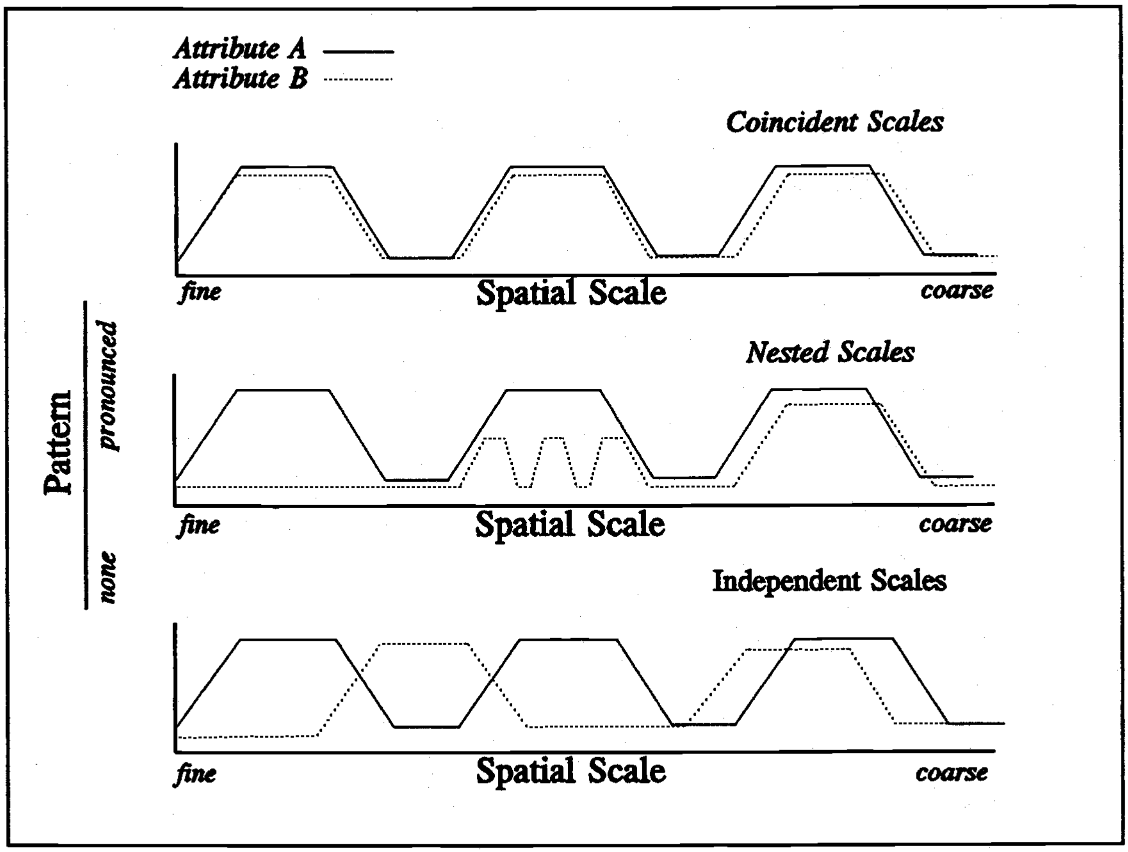

Figure 2.5. Hypothetical patterns of spatial variation in 2 environmental parameters, including coincident, nested, and independent domains of scale. The solid and dotted lines represent the spatial scale at which patterns in the spatial variation in these 2 environmental parameters are most pronounced, similar to the bottom graphs in figure 2.4. Peaks or high plateaus along these lines represent spatial scales at which the corresponding environmental parameter exhibits strong patterning (i.e., high spatial variation). At intermediate scales along these lines, the environmental parameters do not exhibit any discernable spatial patterning. The 3 figures represent hypothetically different ways in which environmental parameters may be scaled relative to each other.

framework, it is not important whether the scale domains of different environmental parameters are coincident, nested, independent, or related in some other way. The important point is that each environmental attribute has its own domains of scale; these may or may not be related to each other, depending on the underlying causal mechanisms that produced the environmental patterns.

Fortunately, many environmental attributes can be patterned similarly because of common causal mechanisms and thus exhibit similar domains of scale. For example, disturbances such as fire affect many environmental attributes similarly. This provides an opportunity to characterize much of the (multidimensional) environmental heterogeneity in fewer domains of scale. Furthermore, this facilitates the use of composite measures of environmental attributes (e.g., stand condition) that actually summarize a number of environmental parameters that have coincident domains of scale.

While much scientific attention has been given to the question of whether environmental variation is continuous or discrete, it is clear that this is merely a function of scale. Even continuous environmental gradients can be discretized by changes in scale, and vice versa. My point is not to argue whether environments are really continuous or discrete; at some scale(s) all environmental dimensions can be treated as a heterogeneous mixture of relatively discrete and homogeneous patches. Considering the environment as a patch mosaic at 1 or more scales is fundamental to landscape ecological investigations and management of wildlife populations. By recognizing that this patchiness occurs at multiple domains of scale, even for a single species, we can appreciate why attempts to map and quantify landscape patterns at a single, usually anthropocentrically-defined, scale may not effectively characterize the full range of habitat heterogeneity important to the species under consideration.

(4) Animal Scaling.--The scales at which animals sense (or perceive) and respond to their environment varies among species; that is, each animal scales their environment differently. For example, the scales at which salamanders and owls perceive their environments probably differ dramatically. Consequently, species likely vary in their responsiveness to habitat changes at different scales. In addition, the scales at which "individuals" sense and respond to the environment (corresponding to grain and extent) are generally much finer than the scales at which the respective "population" dynamics are

influenced. The consequences of environmental heterogeneity may be very different at the "individual" scale where it may affect foraging patterns, than at the "population" scale where it may affect the spatial structure of the population.

Although it is convenient to distinguish between the "individual" and "population" scale, for most species inhabiting heterogeneous environments, it may be more meaningful to consider a hierarchy of more subtle relative scale domains (Fig. 2.6). A species geographic range often constitutes the coarsest scale of interest (i.e., the extent or upper threshold of heterogeneity for the species). Within the range of the species, typically individuals are aggregated into populations that function demographically as somewhat independent units. Populations may be further segregated into spatially disjunct subpopulations that each experience somewhat independent demographic changes but remain "connected" to other subpopulations (i.e., flow of genetic information) through periodic dispersal of individuals (e.g., as in a metapopulation structure; Gilpin and Hanski 1991). Subpopulations represent the smallest demographic unit and are comprised of individuals or pairs, often arranged into breeding territories. Subpopulations may be subdivided into smaller aggregations that do not form functionally semi-independent demographic units. Within each territory or home range, individuals may use only selected resource patches that fulfill life history requirements (e.g., as often portrayed by optimal foraging theory models); that is, they may utilize resources, including space, in a nonrandom or "coarse-grained" manner (see below). Finally, within a selected resource patch, individuals may use only selected microsites (e.g., individual trees or logs, or locations in the canopy, etc.). Of course, there may be finer or other intermediate scales at which resource selection occurs for many species, but the previous hierarchy probably captures the most important scale domains from the perspective of the animal.

The prominence of these scale domains for each species depends on the degree to which the species specializes on certain habitat conditions and the

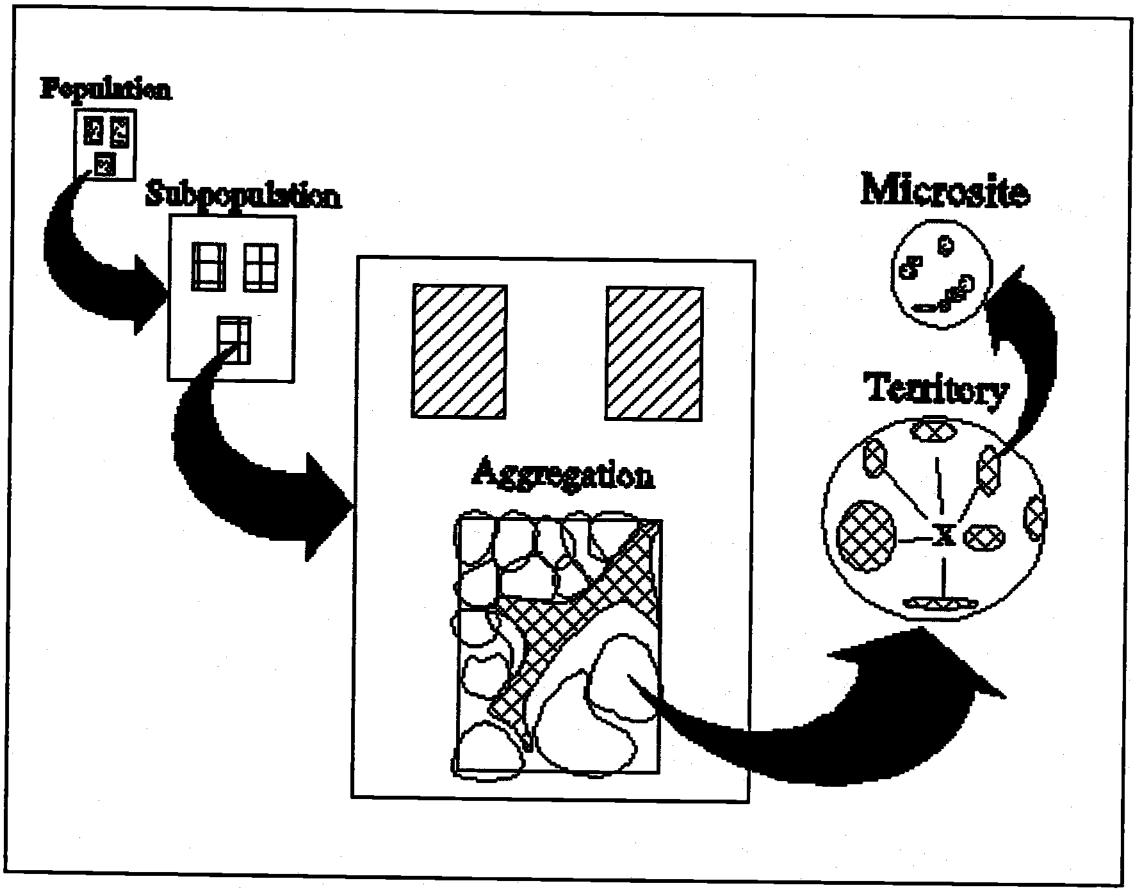

Figure 2.6. Hypothetical example of a hierarchy of spatial scales potentially important to a species, ranging from the species' distributional range to individual microsite resources used by a species.

degree to which the required habitat conditions are heterogeneously distributed at the appropriate scales. In other words, a population will be subdivided into distinct subpopulations (as in a metapopulation) only if the appropriate habitat is distributed accordingly. In addition, these scale domains are relative in the sense that what constitutes the population or individual scale in absolute terms for 1 organism will not be the same for another. For example, a typical forest stand may correspond to the subpopulation scale for a small rodent, the home range scale for a passerine, and the foraging patch scale for an owl. In this case, the stand scale represents a prominent scale domain for all 3 species because they are all affected by the heterogeneous distribution of habitat at that scale, albeit in different ways.

By recognizing that each species scales the environment differently in both relative and absolute terms, we can appreciate why habitat modifications (e.g., as caused by forest management activities) may affect some species and not others and may affect within-territory use patterns for some species yet affect the structure and demographics of populations for other species.

(5) Grain Response.--Grain Response is a concept used to describe ways organisms (at either the individual- or population-level) respond to or perceive heterogeneous resource mixtures (King 1971, MacArthur and Levins 1964, MacArthur and Wilson 1967). Grain Response also is used to describe the relations between the sizes of environmental patches and individual mobility (Hutchinson and MacArthur 1959, Levins 1968). In both cases, Grain Response is an attempt to combine the previous concepts of patchy environments and animal scaling into 1 concept that has a useful functional interpretation. Much of the following discussion was extracted from Wiens (1976).

A *fine-grained response* is one in which the units of the mosaic (i.e., 'grains') are used in direct proportion to their frequency of occurrence (i.e., in a random fashion); no habitat selection occurs at that scale for that environmental mosaic, either because the animal does not perceptually discriminate among mosaic units that we recognize as discrete or it discerns a difference but does not act upon that information. Hence, while the environment at that scale is measurably heterogeneous, it is functionally homogeneous. The organism is said to be "patch-indifferent" to that particular patch mosaic at that scale (Kotliar and Wiens 1990).

A *coarse-grained response* is one in which the units of the mosaic are used nonrandomly or disproportionate to availability; animals exhibit patch selection or preference either through active choice among recognized alternatives or passively, as a result of the actions of some external agent (e.g., predation pressure on prey populations). Hence, the environment is both measurably and functionally heterogeneous. The organism is said to be "patch-sensitive" to that particular patch mosaic at that scale (Kotliar and Wiens 1990).

The Grain Response concept may apply to individuals or populations, but the response patterns of the 2 do not necessarily coincide in a given situation. For example, the population may be clumped into well-separated aggregations of individuals reflecting coarse-scale patchiness (i.e., coarse-grained response), yet these same individuals may distribute their use randomly throughout their individual home ranges (i.e., fine-grained response). Conversely, individuals may be more or less uniformly (or perhaps randomly) distributed throughout their range (i.e., fine-grained response, at least at some scale) perhaps because of strong territorial behavior, yet forage among fine-scale, within-territory patches in a decidedly nonrandom manner (i.e., coarse-grained response), as is often portrayed in optimal foraging models. In addition, the environmental mosaic may be used in a fine-grained fashion for some functions (e.g., feeding) and a coarse-grained manner for other functions (e.g., nesting).

Grain Response is often interpreted as a "behavioral" response to an environmental mosaic (Wiens 1976). Animals may be classified as fine-grained or coarse-grained only in reference to use of the resources associated with a particular life-history function, and categorization of species as fine- or coarse-grained without specifying the context is inappropriate. In this sense, "patch" applies to the physical environmental or resource units upon which the Grain Response is expressed.

If patches differ in "quality" (relative to the fitness conferred to the individual) then individuals should exhibit patch selection. The magnitude of this selection is related to the Grain Response. Thus, Grain Response is a function of the degree of habitat selectivity. At a functionally important scale, a coarse-grained strategy should be optimal if environmental patches differ in "quality" and are relatively stable or predictable over time. As environmental variation increases, habitat selection tends increasingly toward a fine-graininess and this is intensified if the patch variations are relatively predictable. In general, the tendency toward fine-grained response might be expected to increase as the difference between patches (in environmental state), patch size, and/or interpatch distance decreases, or as the temporal instability of the patch structure increases (Wiens 1976, Fig. 2.7).

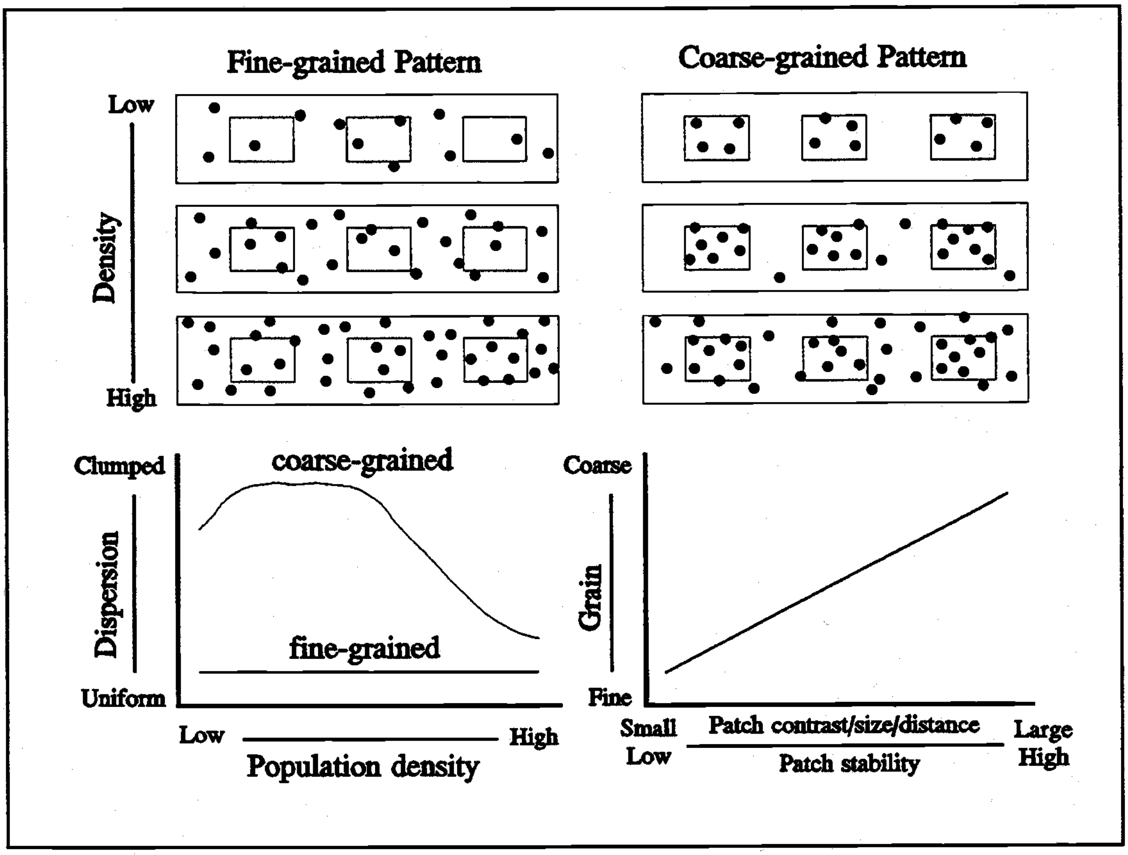

Figure 2.7. Habitat occupancy patterns for a fine-grained (top left) and coarse-grained (top right) population as density increases; changes in dispersion as population density increases (bottom left); and changes in grain response in relation to several patch characteristics (bottom right). Modified from Wiens (1976).

In addition, Grain Response is a density-dependent behavior (Wiens 1976). Under field conditions, the expression of individual habitat selection is strongly influenced by population densities in the various patch types. In an "ideal" (i.e., other things being equal) situation, individuals should select habitat patches on the basis of fitness prospects, which may be a function of the intrinsic "quality" of the habitat type and the population density (intensity of competition) in the habitat patch. According to the Fretwell-Lucas model of habitat selection and distribution (Fretwell and Lucas 1969), at low total population sizes, only the optimal or highest quality patch types should be occupied, but as density increases (and the costs of maintaining a territory increase because of increasing competition), the quality of that habitat decreases, so that a point is reached at which some other habitat type has equal potential quality. At this point, patch occupancy should expand to include the additional habitat of now equal quality, given the assumption of perfect choice capabilities of the organisms. With further increases in population density, the range of habitat types which are of equal quality continues to increase. Thus, habitat quality and habitat selection are a function of population density; marginal or low quality habitat at low densities may have a 'marginal' value equal to the optimal habitat at higher densities. A major consequence of this ideal distribution is relative equality of individual success in the various habitats. Departures from this expectation may reflect the influences of other factors, such as territorial behavior, upon population densities. Although the "ideal" assumptions are probably never met exactly in natural populations, it is nonetheless apparent from field studies that density does influence patterns of habitat occupancy (Wiens 1976, 1989b).

The manner in which changes in population density effect the distribution of individuals among habitats is influenced by the grain-response pattern (Wiens 1976, Fig. 2.7). Individuals exhibiting a fine-grained response may spread randomly over patch types as density increases. Thus, the population maintains a fine-grained spatial pattern at any density (i.e., uniform or random distribution of individuals among patches); tendencies toward aggregation may appear only if social effects intervene. On the other hand, the dispersion of individuals in a coarse-grained population, may initially be highly aggregated ("ideal-free distribution"), and become less so at higher densities as a broader range of habitat types becomes equally suitable (as predicted by the Fretwell-Lucas model). At very high densities, a coarse-grained population may converge toward a fine-grained population in dispersion pattern. In addition, it also has been suggested that poor habitat patches (i.e., low fitness quality) can, under extreme conditions, contain greater densities than optimal habitat patches ("ideal-despotic distribution"). This may result because intraspecific competition results in the dominant individuals establishing themselves in and protecting their grip on a disproportionately high share of the best places to the exclusion of subordinate individuals. The result is that marginal patches may actually contain higher densities of individuals; although each individual has a lower fitness than individuals occupying the preferred habitat. The practical implication of this is that marginal or poor quality patches can, under the right conditions and based on density estimates alone, seem to be the preferred and optimal habitat, when actually the opposite is true.

Summary.--Based on these premises, the environment can be conceptualized as a multidimensional, heterogeneous mosaic of patches where each dimension is patterned at different scale(s), from which may emerge several domains of scale that capture the dominant overall heterogeneity in the environment. Each species occupies a slightly different portion of this multidimensional environmental space and is subject to environmental influence at different scales. Environmental heterogeneity, therefore, must be viewed on scales that reflect different environmental parameters for different organisms. Moreover, the Grain Response of individuals and populations to environmental heterogeneity at any scale may vary in relation to population density.

RESEARCH AND MANAGEMENT IMPLICATIONS

This conceptual framework forms the basis of a landscape ecological perspective on wildlife-habitat relationships. This framework essentially applies the concepts of ecological heterogeneity and scaling to the study of wildlife populations. Despite the utility of this landscape ecological perspective, there is not much evidence of its application in the study and management of wildlife populations, although this is changing rapidly. Based on this conceptual framework, it is apparent that changes in environmental parameters (e.g., through forest management activities) occurring at 1 or more scales will affect species differently. Each species may have a unique response to environmental changes occurring at a particular scale or set of scales and these responses may change in relation to population density. Thus, there are many conditions under which, and reasons why, we may not detect animal responses to measured environmental heterogeneity (i.e., the patterns that we perceive and measure). This recognition has considerable implications for our understanding of how and why land management activities affect species differently. Perhaps most importantly, this framework provides a powerful means of identifying limitations and constraints on wildlife investigations and management efforts, and in this respect, has great potential to improve future wildlife research and management.

What humans perceive to be important heterogeneous patterns in the landscape (i.e., measured heterogeneity) may not be features of the environment important to a particular species or at scales appropriate to that species (i.e., functional heterogeneity). Environmental heterogeneity will influence a species' distribution or population dynamics only if it occurs at a functionally relevant scale from the organism's perspective. That is, measured heterogeneity has utility only if it corresponds to the individual's perceived environment at an appropriate scale (e.g., effects foraging patterns) or it influences the population dynamics of the species (e.g., creates a metapopulation structure). For example, if forest fragmentation creates a heterogeneous landscape at a scale larger than (e.g., salamander) or smaller than (e.g., large mammal) the scale(s) functionally important to a species, then it may not impact the species. This may well explain why studies on forest fragmentation often fail to demonstrate impacts on a large number of species; the scale at which fragmentation is quantified does not match the scale(s) relevant to the species.

Given the wide range of spatial and temporal scales likely to be functional to the vast array of vertebrate species occupying any landscape, it behooves us to design studies from a multi-scale perspective. That is, in designing studies, we should give greater consideration to the wide range of potentially important ecological scales, and when possible, investigate a range of scales rather than a single scale, as traditionally done in the past (Allen and Star 1982, Wiens 1989a). For example, instead of centering on the plot or forest stand as the sampling unit, we could establish a hierarchy of sampling units ranging in scale from the plot-level to the landscape level. This would increase the likelihood of detecting significant vertebrate-habitat relationships for a wider range of species. Ideally, we should make greater attempts to shed our own conceptions of environmental scale and instead concentrate on the perceptions of the animals, and attempt to view environmental structure through their senses (Wiens 1976, 1989a). Specifically, we should design experiments and measure environments at scales relevant to the species under consideration and not at scales convenient for work. Only in this way can we hope to measure heterogeneity at functionally important scales. What constitutes a "landscape" for a salamander is probably not the same as for an owl. The pattern or fragmentation of each organism's landscape has the same biological implications even though the spatial scales may be different by several orders of magnitude.

Given the wide range of environmental parameters likely affecting vertebrate distribution and population dynamics, we should recognize the likelihood that our choice of environmental parameters to measure (and our ability to measure them) may not include the parameters of primary importance to some or even most species. For example, in quantifying landscape patterns, we usually measure only gross vegetation patterns (e.g., stand condition); the multidimensional environment is collapsed into a single measurable parameter that generally is quantified in the spatial domain and horizontal dimension (i.e., we portray the landscape as a mosaic of two-dimensional, planar units). This simplification may be inappropriate for species that are regulated by the distribution of other environmental attributes that are not adequately represented by the chosen landscape mosaic, or species responsive to environmental heterogeneity in the vertical dimension. For example, species affected more by the distribution of coarse woody debris or shrub cover than the distribution of general vegetation classes (e.g., stand condition) may not show any measurable response to forest fragmentation. Alternatively, these species may show only minor (i.e., statistically insignificant) responses because the "measured" forest fragmentation is only partially correlated with the environmental attributes (and/or at scales) important to those species.

Given the possible effect of population density on Grain Response, we must give more emphasis to fitness responses than responses in relative abundance when investigating vertebrate-habitat relationships. Otherwise, we stand the chance of reaching erroneous conclusions for species with an ideal-despotic distribution.

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CHAPTER 3

FRAGSTATS: A SPATIAL PATTERN ANALYSIS PROGRAM FOR QUANTIFYING LANDSCAPE STRUCTURE

INTRODUCTION

Growing concerns over the loss of biodiversity has spurred land managers to seek better ways of managing landscapes at a variety of spatial and temporal scales. A number of developments have made possible the ability to analyze and manage entire landscapes to meet multi-resource objectives. The developing field of landscape ecology has provided a strong conceptual and theoretical basis for understanding landscape structure, function and change (Forman and Godron 1986, Urban et al. 1987, Turner 1989). Growing evidence that habitat fragmentation is detrimental to many species and may contribute substantially to the loss of regional and global biodiversity (Saunders et al. 1991) has provided empirical justification for the need to manage entire landscapes, not just the component parts. The development of GIS technology, in particular, has made a variety of analytical tools available for analyzing and managing landscapes. In response to the growing theoretical and empirical support and technical capabilities, public land management agencies have begun to recognize the need to manage natural resources at the landscape scale.

A good example of these changes is in the field of wildlife science. Wildlife ecologists often have assumed that the most important ecological processes affecting wildlife populations and communities operate at local spatial scales (Dunning et al. 1992). Vertebrate species richness and abundance, for example, often are considered to be functions of variation in local resource availability, vegetation composition and structure, and the size of the habitat patch (MacArthur and MacArthur 1961, Willson 1974, Cody 1985). Correspondingly, most wildlife research and management activities have focussed on the within-patch scale, typically small plots or forest stands. Wildlife ecologists have become increasingly aware, however, that habitat variation and its affects on ecological processes and vertebrate populations occurs at a wide range of spatial scales (Wiens 1989a,b). In particular, there has been increasing awareness of the potential importance of coarse-scale habitat patterns to wildlife populations, and there has been a corresponding surge in landscape ecological investigations that examine vertebrate distributions and population dynamics over broader spatial scales (e.g., this study). The recent attention on metapopulation theory (Gilpin and Hanski 1991) and the proliferation of mathematical models on dispersal and spatially distributed populations (Kareiva 1990) are testimony to these changes. Moreover, recent conservation efforts for the northern spotted owl (Strix occidentalis caurina) demonstrate the willingness and ability of public land management agencies to analyze and manage wildlife populations at the landscape scale (Lamberson et al. 1992, Murphy and Noon 1992, Thomas et al. 1990).

The emergence of landscape ecology to the forefront of ecology is testimony to the growing recognition that ecological processes affect and are affected by the dynamic interaction among ecosystems. This surge in interest in landscape ecology also has become manifest in a wave of recent efforts to incorporate a landscape perspective into policies and guidelines for managing public lands. Landscape ecology embodies a way of thinking that many see as very useful for organizing land management approaches. Specifically, landscape ecology focusses on 3 characteristics of the landscape (Forman and Godron, 1986):

> "(1) **Structure**, the spatial relationships among the distinctive ecosystems or "elements" present--more specifically, the distribution of energy, materials, and species in relation to the sizes, shapes, numbers, kinds, and configurations of the ecosystems.

> (2) **Function**, the interactions among the spatial elements, that is, the flows of energy, materials, and species among the component ecosystems.
>
> (3) **Change**, the alteration in the structure and function of the ecological mosaic over time."

Thus, landscape ecology involves the study of landscape patterns, the interactions among patches within a landscape mosaic, and how these patterns and interactions change over time. In addition, landscape ecology involves the application of these principles in the formulation and solving of real-world problems. Landscape ecology considers the development and dynamics of spatial heterogeneity and its affects on ecological processes, and the management of spatial heterogeneity (Risser et al. 1984).

Landscape ecology is largely founded on the notion that the patterning of landscape elements (patches) strongly influences ecological characteristics, including vertebrate populations. The ability to quantify landscape structure is prerequisite to the study of landscape function and change. For this reason, much emphasis has been placed on developing methods to quantify landscape structure (e.g., O'Neill et al. 1988, Li 1990, Turner 1990a, Turner and Gardner 1991). Most of the efforts to date have been tailored to meet the needs of specific research objectives and have employed user-generated computer programs to perform the analyses. Such user-generated programs allow for the inclusion of customized analytical methods and easy linkages to other programs such as spatial simulation models, yet generally lack the advanced graphics capabilities of commercially available GIS (Turner 1990a). Most of these user-generated programs are limited to a particular hardware environment or are embedded within a larger software package designed to accomplish a specific research objective (e.g., to model fire disturbance regimes). Of the available software programs that I am aware of, none offer a broad array of landscape metrics and all are designed to analyze raster images only.

Barbara Marks (OSU, Forest Science Dept.) and I developed a versatile software package called FRAGSTATS for analyzing landscape structure that includes a comprehensive selection of landscape metrics. Moreover, the program is almost completely automated and thus requires little technical training. In this chapter, I describe program FRAGSTATS in detail, including both the technical aspects of the program as well as its ecological applicability. Specifically, I discuss a number of important concepts and definitions critical to the assessment of landscape structure; describe the overall structure, organization, and limitations of FRAGSTATS; describe each metric computed by FRAGSTATS, including technical aspects of the algorithms and their ecological applicability; and, describe how to run FRAGSTATS.

CONCEPTS AND DEFINITIONS

It is beyond the scope and purpose of this document to provide a glossary of terms and a comprehensive discussion of the many concepts embodied in landscape ecology. Instead, I define and discuss a few key terms and concepts essential to the use of FRAGSTATS and the measurement of spatial heterogeneity; a thorough understanding of these concepts is prerequisite to the effective use of FRAGSTATS.

Landscape.--What is a "landscape"? Surprisingly, there are many different interpretations of this well-used term. The disparity in definitions makes it difficult to communicate clearly, and even more difficult to establish consistent management policies. Definitions of landscape invariably include an area of land containing a mosaic of patches or landscape elements. Forman and Godron (1986) defined landscape as a heterogeneous land area composed of a cluster of interacting ecosystems that is repeated in similar form throughout. The concept differs from the traditional ecosystem concept in focusing on groups of ecosystems and the interactions among them. There are many variants of the definition depending on the research or management context. For example, from a wildlife perspective, we might define landscape as an area of land containing a mosaic of *habitat* patches, often within which a particular "focal" or "target" habitat patch is embedded (Dunning et al. 1992). Because habitat patches can only be defined relative to a particular organism's perception of the environment (Wiens 1976)(i.e., each organism defines habitat patches differently and at different scales), landscape size would differ among organisms. However, landscapes generally occupy some spatial scale intermediate between an organism's normal home range and its regional distribution. In-other-words, because each organism scales the environment differently (i.e., a salamander and a hawk view their environment on different scales), there is no absolute size for a landscape; from an organism-centered perspective, the size of a landscape varies depending on what constitutes a mosaic of habitat or resource patches meaningful to that particular organism (Fig. 3.1).

This definition most likely contrasts with the more anthropocentric definition that a landscape corresponds to an area of land equal to or larger than, say, a large basin (e.g., several thousand hectares). Indeed, Forman and Godron (1986) suggested a lower limit for landscapes at a "few kilometers in diameter", although they recognized that most of the principles of landscape ecology apply to ecological mosaics at any level of scale. While this may be a more pragmatic definition than the organism-centered definition and perhaps corresponds to our human perception of the environment, it has limited utility in managing wildlife populations if you accept the fact that each organism scales the environment differently. From an organism-centered perspective, a landscape could range in absolute scale from an area smaller than a single forest stand (e.g., a individual log) to an entire ecoregion. If you accept this organism-centered definition of a landscape, 1 logical consequence of this is a mandate to manage wildlife habitats across the full range of spatial scales; each scale, whether it be the stand or watershed, or some other scale, will likely be important for a subset of species.

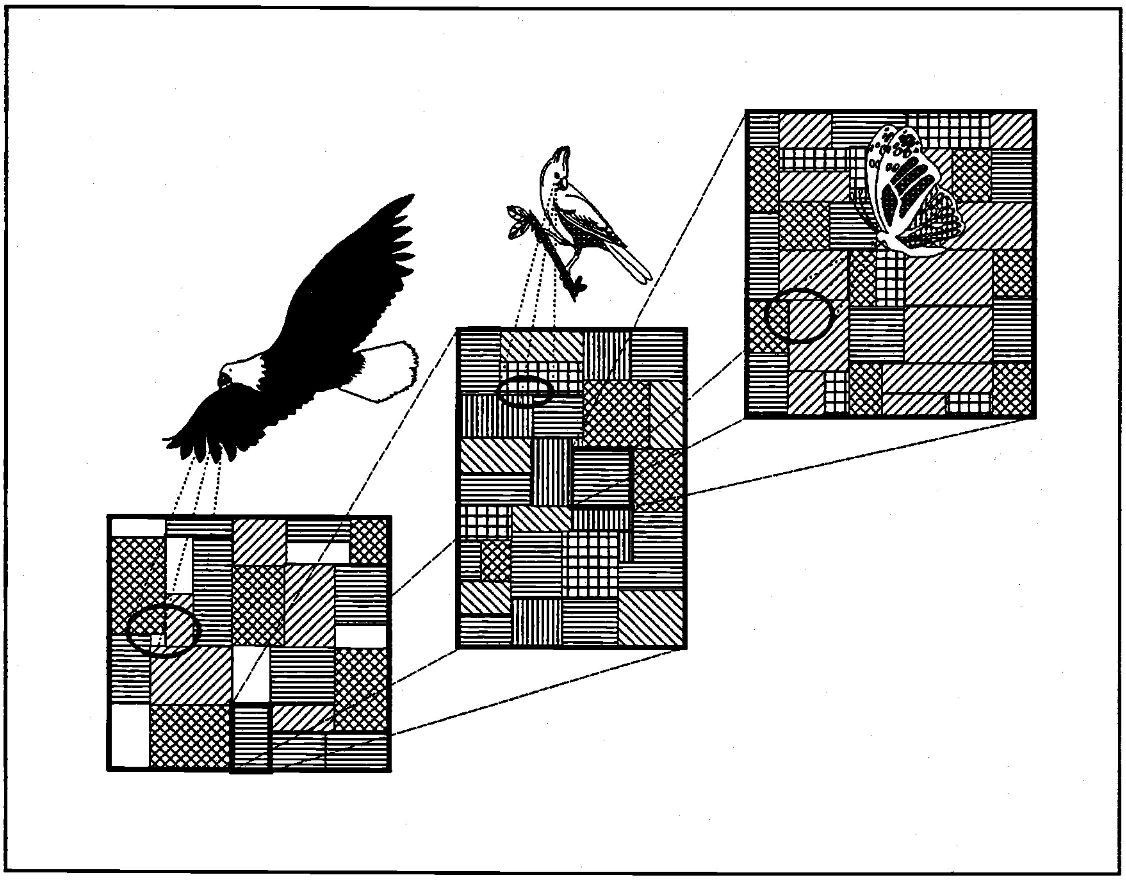


Figure 3.1. Multi-scale view of "landscape" from an organism-centered perspective. Because the eagle, cardinal, and butterfly perceive their environments differently and at different scales, what constitutes a single habitat patch for the eagle may constitute an entire landscape or patch-mosaic for the cardinal, and a single habitat patch for the cardinal may comprise an entire landscape for the butterfly that perceives patches on an even finer scale.

It is not my intent to argue for a single definition of landscape. Rather, I wish to point out that there are many appropriate ways to define landscape depending on the phenomenon under consideration. It is incumbent upon the investigator or manager to define landscape in an appropriate manner. I believe that the first step in any landscape-level research or management endeavor should be to define landscape.

Patch.--What makes up a landscape? Landscapes are composed of a mosaic of patches (Urban et al. 1987). Landscape ecologists have used a variety of terms to refer to the basic elements or units that make up a landscape, including ecotope, biotope, landscape component, landscape element, landscape unit, landscape cell, geotope, facies, habitat, and site (Forman and Godron 1986). I prefer the term patch, but any of these terms, when defined, are satisfactory according to the preference of the investigator. Like the landscape, patches comprising the landscape are not self-evident; patches must be defined relative to the phenomenon under consideration. For example, from a timber management perspective a patch may correspond to the forest stand. However, the stand may not function as a patch from an organism's perspective. From an ecological perspective, patches represent relatively discrete areas (spatial domain) or periods (temporal domain) of relatively homogeneous environmental conditions where the patch boundaries are distinguished by discontinuities in environmental character states from their surroundings of magnitudes that are perceived by or relevant to the organism or ecological phenomenon under consideration (Wiens 1976). From a strictly organism-centered view, patches may be defined as environmental units between which fitness prospects, or "quality", differ; although, in practice, patches may be more appropriately defined by nonrandom distribution of activity or resource utilization among environmental units, as recognized in the concept of "Grain Response" (Wiens 1976).

Patches are dynamic and occur on a variety of spatial and temporal scales that, from an organism-centered perspective, vary as a function of each animal's perceptions (Wiens 1976 and 1989a, Wiens and Milne 1989). A patch at any given scale has an internal structure that is a reflection of patchiness at finer scales, and the mosaic containing that patch has a structure that is determined by patchiness at broader scales (Kotliar and Wiens 1990). Thus, regardless of the basis for defining patches, a landscape does not contain a single patch mosaic, but contains a hierarchy of patch mosaics across a range of scales. For example, from an organism-centered perspective, the smallest scale at which an organism perceives and responds to patch structure is its "grain" (Kotliar and Wiens 1990). This lower threshold of heterogeneity is the level of resolution at which the patch size becomes so fine that the individual or species stops responding to it, even though patch structure may actually exist at a finer resolution (Kolasa and Rollo 1991). The lower limit to grain is set by the physiological and perceptual abilities of the organism and therefore varies among species. Similarly, "extent" is the coarsest scale of heterogeneity, or upper threshold of heterogeneity, to which an organism responds (Kotliar and Wiens 1990, Kolasa and Rollo 1991). At the level of the individual, extent is determined by the lifetime home range of the individual (Kotliar and Wiens 1990) and varies among individuals and species. More generally, however, extent varies with the organizational level (e.g., individual, population, metapopulation) under consideration; for example the upper threshold of patchiness for the population would probably greatly exceed that of the individual. Therefore, from an organism-centered perspective, patches can be defined hierarchically in scales ranging between the grain and extent for the individual or population of each species.

Patch boundaries are artificially imposed and are in fact meaningful only when referenced to a particular scale (i.e., grain size and extent). For example, even a relatively discrete patch boundary between an aquatic surface (e.g., lake) and terrestrial surface becomes more and more like a continuous gradient as one moves to a finer and finer resolution. However, most environmental dimensions possess 1 or more "domains of scale" (Wiens 1989a) at which the individual spatial or temporal patches can be treated as functionally homogeneous; at intermediate scales the environmental dimensions appear more as gradients of continuous variation in character states. Thus, as one moves from a finer resolution to coarser resolution, patches may be distinct at some scales (i.e., domains of scale) but not at others.

Again, it is not my intent to argue for a particular definition of patch. Rather, I wish to point out the following: (1) that patch must be defined relative to the phenomenon under investigation or management; (2) that, regardless of the phenomenon under consideration (e.g., timber management, single species, geomorphological disturbances, etc), patches are dynamic and occur at multiple scales; and (3) that patch boundaries are only meaningful when referenced to a particular scale. It is incumbent upon the investigator or manager to establish the basis for delineating among patches (i.e., patch type classification system) and at a scale appropriate to the phenomenon under consideration.

Matrix.--A landscape is composed typically of several types of landscape elements (patches). Of these, the matrix is the most extensive and most connected landscape element type, and therefore plays the dominant role in the functioning of the landscape (Forman and Godron 1986). For example, in a large contiguous area of mature forest embedded with numerous small disturbance patches (e.g., timber harvest patches), the mature forest constitutes the matrix element type because it is greatest in areal extent, is mostly connected, and exerts a dominant influence on the area flora and fauna. In most landscapes, the matrix type is obvious to the investigator or manager. However, in some landscapes or at a certain point in time during the trajectory of a landscape, the matrix element will not be obvious. Indeed, it may not be appropriate to consider any element as the matrix. Moreover, the designation of a matrix element is largely dependent upon the phenomenon under consideration. For example, in the study of geomorphological processes, the geological substrate may serve to define the matrix and patches; whereas in the study of vertebrate populations, vegetation structure may serve to define the matrix and patches. In addition, what constitutes the matrix is dependent on the scale of investigation or management. For example, at a particular scale, mature forest may be the matrix with disturbance patches embedded within; whereas, at a coarser scale, agricultural land may be seen as the matrix with mature forest patches embedded within.

It is incumbent upon the investigator or manager to determine whether a matrix element exists and should be designated given the scale and phenomenon under consideration. This should be done prior to the analysis of landscape structure since this decision will influence the choice and interpretation of landscape metrics.

Scale.--The ability to detect pattern is a function of scale, and the spatial scale of ecological data encompasses both extent and grain (Forman and Godron 1986, Turner et al. 1989, Wiens 1989). Extent is the overall area encompassed by an investigation or the area included within the landscape boundary. From a statistical perspective, the spatial extent of an investigation is the area defining the population we wish to sample. Grain is the size of the individual units of observation. For example, a fine-grained map might structure information into 1-ha units, whereas a map with an order of magnitude coarser resolution would have information structured into 10-ha units (Turner et al. 1989). Extent and grain define the upper and lower limits of resolution of a study and any inferences about scale-dependency in a system are constrained by the extent and grain of investigation (Wiens 1989). From a statistical perspective, we cannot extrapolate beyond the population sampled, nor can we infer differences among objects smaller than the experimental units. Likewise, in the assessment of landscape structure, we cannot generalize beyond the extent of the investigation or landscape and we cannot detect pattern below the resolution of the grain (Wiens 1989).

As with the concept of landscape and patch, it may be more ecologically meaningful to define scale from the perspective of the organism or ecological phenomenon under consideration. For example, from an organism-centered perspective, grain and extent may be defined as the degree of acuity of a stationary organism with respect to short- and long-range perceptual ability (Kolasa and Rollo 1991). Thus grain is the finest component of the environment that can be differentiated up close by the organism, and extent is the range at which a relevant object can be distinguished from a fixed vantage point by the organism (Kolasa and Rollo 1991). Unfortunately, while this is ecologically an ideal way to define scale, it is not very pragmatic. Indeed, in practice, extent and grain are often dictated by the scale of the imagery (e.g., aerial photo scale) being used or the technical capabilities of the computing environment.

It is critical that extent and grain be defined for a particular study and represent, to the greatest possible degree, the ecological phenomenon or organism under study, otherwise the landscape patterns detected will have little meaning and there is a good chance of reaching erroneous conclusions. For example, it would be meaningless to define grain as 1-ha units when the organism under consideration perceives and responds to habitat patches at a resolution of 1-m^2. A strong landscape pattern at the 1-ha resolution may have no significance to the organism under study. Likewise, it would be unnecessary to define grain as 1-m^2 units when the organism under consideration perceives habitat patches at a resolution of 1-ha. Typically, however, we do not know what the appropriate resolution should be. In this case, it is much safer to choose a finer grain than is believed to be important. Remember, the grain sets the minimum resolution of investigation. Once set, we can always dissolve to a coarser grain. In addition, we can always specify a minimum mapping unit that is coarser than the grain. That is, we can specify the minimum patch size to be represented in a landscape, and this can easily be manipulated above the grain size.

Information may be available at a variety of scales and it may be necessary to extrapolate information from 1 scale to another. In addition, it may be necessary to integrate data represented at different spatial scales. It has been suggested that information can be transferred across scales if both grain and extent are specified (Allen et al. 1987), yet it is unclear how observed landscape patterns vary in response to changes in grain and extent and whether landscape metrics obtained at different scales can be compared. The limited work on this topic suggests that landscape metrics vary in their sensitivity to changes in scale and that qualitative and quantitative changes in measurements across spatial scales will differ depending on how scale is defined (Turner et al. 1989). In investigations of landscape structure, until more is learned it is critical that (1) scale be clearly specified, (2) any observed patterns or relationships are described relative to the scale of the investigation, and (3) any attempts to compare landscapes measured at different scales be done cautiously.

Landscape Structure.--Landscapes are distinguished by particular spatial relationships among component parts and consist of 2 key aspects: landscape composition and landscape pattern (sometimes referred to as landscape physiognomy or landscape configuration)(Dunning et al. 1992, Turner 1989). A landscape can be characterized by both its composition and pattern, and these 2 aspects of a landscape can independently or in combination effect ecological processes and organisms. The difference between landscape composition and pattern is analogous to the difference between floristics (e.g., the types of plant species present) and vegetation structure (e.g., foliage height diversity) so commonly considered in wildlife-habitat studies at the within-patch scale.

Landscape composition refers to features associated with the presence and amount of each patch type within the landscape, but without being spatially explicit. In other words, landscape composition represents the types and amounts of patch types within a landscape, but not the placement or location of patches within the mosaic. Landscape composition is important to many ecological processes and organisms. For example, many vertebrate species require specific habitat types, and these habitats must be present in sufficient areal extent for them to occupy and persist in a landscape. Therefore, the total amount of suitable habitat (a function of landscape composition) likely influences the occurrence and abundance of these vertebrate species. There have been many attempts to model animal populations within landscapes based on landscape composition alone; such models have been referred to as "island models" by Kareiva (1990). Island models do represent the discrete patchwork mosaic of the landscape; the key feature of these models is population subdivision. Yet they do not specify the relative distances between patches or their positions relative to each other. Thus, although they provide strong analytical solutions, they may be overly simplified for most natural populations. It is important to note, however, that we have learned much about population dynamics in spatially complex environments based on models of landscape composition alone (Kareiva 1990).

There are many quantitative measures of landscape composition, including the proportion of the landscape in each patch type, patch richness, patch evenness, and patch diversity. Indeed, because of the many ways in which diversity can be measured, there are literally hundreds of possible ways to quantify landscape composition. It is incumbent upon the investigator or manager to choose the formulation that best represents their concerns.

Landscape pattern refers to features associated with the physical distribution or configuration of patches within the landscape. Some of these features, such as patch isolation or patch contagion, are measures of the placement of patch types relative to other patch types, the landscape boundary, or other features of interest. Other features, such as patch size and shape, are measures of the spatial character of the patches. There have been many attempts to explicitly incorporate landscape pattern into models of ecological processes and population dynamics within heterogeneous landscapes; such models have been referred to as "stepping-stone models" by Kareiva (1990). In contrast to island models, stepping-stone models have an explicit spatial dimension and can account for dispersal distances and environmental variability with a spatial structure. Recently, there have been dramatic increases in the level of sophistication in stepping-stone models and the results of some efforts have had profound effects on the design of managed landscapes (e.g., Lamberson et al. 1992, McKelvey et al. 1992).

There are many aspects of landscape pattern and the literature is replete with methods and indices developed for representing them. Landscape pattern can be quantified using statistics in terms of the landscape unit itself (i.e., the patch) as well as the spatial relationship of the patches and matrix comprising the landscape. Landscape metrics quantified in terms of the individual patches (e.g., mean patch size, mean patch shape, patch density, etc.) are spatially explicit at the level of the individual patch. The spatial pattern being represented is that of the spatial character of the individual patches. The location of patches relative to each other in the landscape (i.e., the configuration of patches within the landscape, is not explicitly represented. Such metrics represent a recognition that the ecological properties of a patch are influenced by the surrounding neighborhood (i.e., edge effects) and that the magnitude of these influences are affected by patch size and shape. These metrics simply quantify, for the landscape as a whole, the average patch characteristics or some measure of variability in patch characteristics. Although these metrics are not spatially explicit at the landscape level, they have clear ecological relevance when considered from a patch dynamics standpoint (Pickett and White 1985). For example, a number of bird species have been shown to be sensitive to patch core area (a function of patch size and shape) because of negative intrusions from the surrounding landscape (e.g., Temple 1986, Robbins et al. 1989). Quantifying mean patch core area across the landscape could provide a good index to landscape suitability for such species.

Landscape metrics quantified in terms of the spatial relationship of patches and matrix comprising the landscape (e.g., nearest neighbor, contagion) incorporate spatial explicitness at the landscape level. The relative location of individual patches within the landscape is represented in some way. Such metrics represent a recognition that ecological processes and organisms are affected by the interspersion and juxtaposition of patch types within the landscape. For example, the population dynamics of species with limited dispersal ability are likely affected by the distribution of suitable habitat patches. Both the distance between suitable patches and the spatial arrangement of suitable patches can influence population dynamics (e.g., sensu Kareiva 1990, Lamberson et al. 1992, McKelvey et al. 1992). Likewise, patch juxtaposition is especially important to organisms that require ≥ 2 habitat types because the close proximity of resources provided by different patch types is critical for their survival and reproduction.

A number of landscape pattern metrics can be formulated either in terms of the individual patches or in terms of the whole landscape, depending on the emphasis sought. For example, fractal dimension is a measure of shape complexity (Mandelbrot 1982, Burrough 1986, Milne 1988) that can be computed for each patch and then averaged for the landscape, or it can be computed from the landscape as a whole (e.g., using the box-count method, Morse et al. 1985). Similarly, core area can be computed for each patch and then represented as mean patch core area for the landscape, or it can be computed simply as total core area in the landscape. Obviously, 1 form can be derived from the other if the number of patches is known and are largely redundant; the choice of formulations is dependent upon user preference or the emphasis (patch or landscape) sought. The same is true for a number of other common landscape metrics. Typically, these metrics are spatially explicit at the patch level but not at the landscape level.

There are some landscape metrics that represent pattern complexity but are not spatially explicit at all. These metrics vary as a function of the heterogeneity of the landscape, but do not depend explicitly on the relative location of patches within the landscape or their individual spatial character. For example, total edge or edge density is a function of the amount of border between patches. For a given edge density there could be 2 patches or 10 patches, they could be clustered together or maximally dispersed, or they could be on 1 side of the landscape or in the middle.

Finally, it is important to understand how measures of landscape structure are influenced by the designation of a matrix element. If a matrix element is designated and therefore presumed to function as such (i.e., has a dominant influence on landscape dynamics), then it should not be included as another "patch" type in any metric that simply averages some characteristic across all patches (e.g., mean patch size, mean patch shape). Otherwise the matrix will dominate the metric and serve more to characterize the matrix than the patches within the landscape; although for some uses this may be meaningful. From a practical standpoint, it is important to recognize this because in program FRAGSTATS there is no automatic way to exclude a patch type (designated matrix) from the landscape-level statistics. In this case, it would be more meaningful to use the class-level statistics for each patch type and simply ignore the patch type (designated matrix). From a conceptual standpoint, it is important to recognize that the choice and interpretation of landscape metrics must ultimately be evaluated in terms of their ecological meaningfulness, which is dependent upon how the landscape is defined, including the choice of patch types and matrix.

Hopefully I have stressed the importance of fully understanding each landscape metric before it is used. Specifically, these questions should be asked of each metric before it is used: does it represent landscape composition or pattern; what aspect of pattern does it represent; what scale, if any, is spatially explicit; how is it effected by the designation of a matrix element? Based on answers to these questions, does the metric represent landscape structure in a manner ecologically meaningful to the phenomenon under consideration? Only after answering these questions should one attempt to draw conclusions about the structure of the landscape analyzed.

FRAGSTATS OVERVIEW

FRAGSTATS is a spatial pattern analysis program for quantifying landscape structure. The landscape subject to analysis is user-defined and can represent any spatial phenomenon. FRAGSTATS quantifies the areal extent and spatial distribution of polygons on a map coverage; it is incumbent upon the user to establish a sound basis for defining and scaling the landscape (including the extent and grain of the landscape) and the scheme upon which patches within the landscape are classified and delineated. Most importantly, the output from FRAGSTATS is meaningful only if the landscape mosaic is meaningful relative to the phenomenon under consideration.

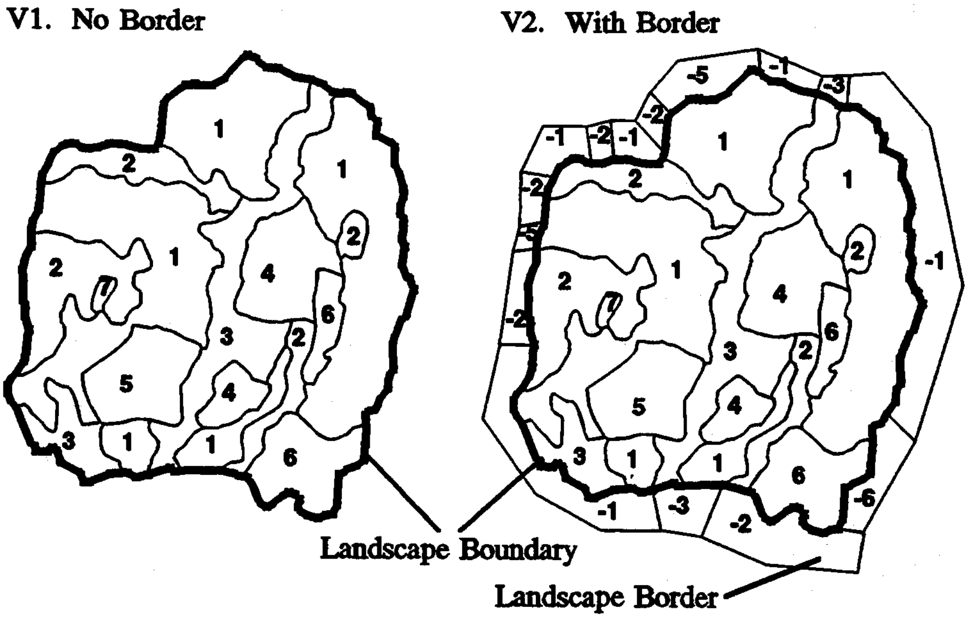
FRAGSTATS does not limit the scale (extent or grain) of the landscape subject to analysis. However, the distance- and area-based metrics computed in FRAGSTATS are reported in meters and hectares, respectively. Thus, landscapes of extreme extent and/or resolution may result in rather cumbersome numbers and/or be subject to rounding errors. However, FRAGSTATS outputs data files in ASCII format that can be manipulated using any data base management program to rescale metrics or to convert them to other units (e.g., converting hectares to acres).

FRAGSTATS is not a Geographic Information System. FRAGSTATS quantifies the landscape structure of a single image (i.e., landscape mosaic). It is incumbent upon the user to create, using GIS or some other means, an appropriate landscape image to analyze. However, FRAGSTATS can be used interactively with GIS. For example, in the process of building and modifying coverages within a GIS environment to satisfy some research and/or management objective (e.g., to evaluate alternative landscape management scenarios), FRAGSTATS can be run as a routine (e.g., within a Macro) to produce statistics for each coverage.

FRAGSTATS accepts either vector or raster images. The vector version of the program is an Arc/Info AML. It was developed on a SUN workstation in a UNIX operating environment using Arc/Info version 6.1; it will not run with earlier versions of Arc/Info. The AML calls up several C programs that were compiled with the SUNOS cc compiler and may not compile with other compilers. The raster version of the program also was developed on a SUN workstation in a UNIX operating environment. It is written in C and compiled with the SUNOS cc compiler. It may not compile with other C compilers. In both vector and raster versions of the program, a single command line comprised of several arguments is all that is required to run the program (see Appendix B for FRAGSTATS user guidelines). It is important to realize that vector and raster images depict edges differently. Vector images portray a line in its true form as it is digitized. Raster images, however, portray lines in stair-step fashion. Consequently, the measurement of edge length is biased upward in raster images; that is, measured edge length is always more than the true edge length. The magnitude of this bias varies in relation to the grain or resolution of the image, and the consequences of this bias with regards to the use and interpretation of edge-based metrics must be weighed relative to the phenomenon under investigation. As a result of this bias, the vector and raster versions of FRAGSTATS will not produce identical results for a landscape.

FRAGSTATS accepts images in several formats (described in detail below), depending on whether the image contains a *background* and whether the landscape contains a *border* (Figs. 3.2 and 3.3). A *landscape boundary* defines the perimeter of the landscape and surrounds the patch mosaic of interest. A *background* is an undefined area within which the landscape of interest is situated and is an explicit consideration only for raster images; for vector images, Arc/Info handles the background internally. The background value can be any non-patch code, although it typically is set to a negative integer. The background does not effect any of the metrics, it serves only to tell FRAGSTATS to ignore that area of the image. A *landscape border* is a strip of land surrounding the landscape of interest (i.e., outside the landscape boundary) within which patches have been delineated and classified. An image containing a landscape border consists of a landscape mosaic containing defined patches (i.e., coded polygons or pixels) surrounded by patches that are explicitly defined as belonging to the landscape border. The landscape border provides information on patch type adjacency for patches on the edge of the landscape.

Under most circumstances, it is probably not valid to assume that all edges function the same. Indeed, there is good evidence that edges vary in their affects on ecological processes and organisms depending on the nature of the edge (e.g., type of adjacent patches, degree of structural contrast, orientation, etc.)[Hansen and Castri 1992]. Accordingly, the user can specify a file containing weights for each combination of patch types (classes). These weights represent the magnitude of edge contrast between adjacent patch types


V1. No Border

V2. With Border

Figure 3.2. Alternative image formats accepted in the vector version of FRAGSTATS. Landscape boundary and border are defined in the text.

and must range between 0 (no contrast) and 1 (maximum contrast). Edge contrast weights are used to compute several edge-based metrics (see Edge Metrics below). The weight file is optional if the image does not contain a landscape border; it must be present, however, if a border is present because the only reason for specifying a border is when information on edge contrast is deemed important. Any scheme can be used to establish weights as long as it is meaningful given the phenomenon under investigation. A true edge is defined as an edge with a contrast weight > 0. Regardless of which image format is used (Figs. 3.2 and 3.3), I strongly recommend the use of an edge contrast weight file.

FRAGSTATS uses the patch type information from patches in the landscape border to determine edge contrasts. Thus, most metrics (i.e., those unaffected by edge contrast) are unaffected by the presence of a border. Border patches must be set to the negative of the appropriate patch type code.

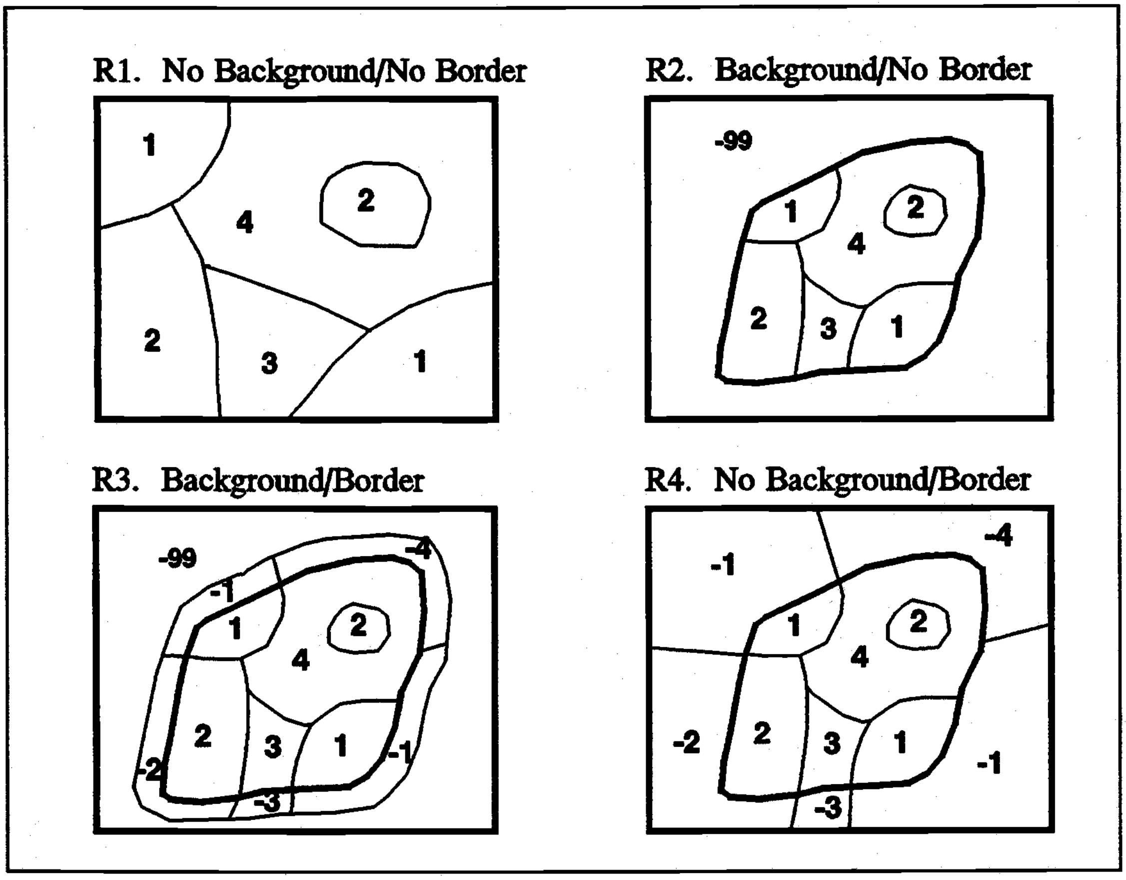


Figure 3.3. Alternative image formats accepted in the raster version of FRAGSTATS. Landscape boundary and border are defined in the text.

For example, if a border patch is a patch type of code 34, then its label must be -34. The border also must be contiguous around the landscape, yet can be any width. If an image does not contain a landscape border, the user must designate whether the landscape boundary should be treated as an edge or not (default is no). If so, the boundary is treated as maximum-contrast edge; that is, an edge consisting of maximum contrast between adjacent patch types (i.e., contrast weight = 1). If not, the boundary is ignored for all edge calculations or treated as a no-contrast edge (i.e., contrast weight = 0). This decision effects several metrics based on edge lengths and edge types and should be considered very carefully because it can have profound effects on these metrics depending on the landscape.

FRAGSTATS accepts vector images within Arc/Info in 2 formats and raster images in 4 formats, as follows:

Vector Format 1.--The simplest vector format consists of an image containing no border (Fig. 3.2a); recall that Arc/Info handles the background automatically. In this case, the entire digital image consists of defined patches contained within the landscape boundary. In this format, the user must designate whether the landscape boundary should be treated as a maximum-contrast edge or ignored. Regardless of whether the boundary is treated as edge or not, the user still has the option to specify a weight file, as this will determine whether those metrics requiring the contrast information are computed or not. If a weight file is specified, the boundary segments will receive a contrast weight of 1 or 0, depending on whether the boundary is specified as edge or not.

Vector Format 2.--The other vector format consists of an image containing a border (Fig. 3.2b). In this case, the digital image consists of a landscape mosaic containing defined patches surrounded by patches that are explicitly defined as belonging to the landscape border. Note that border patches must be set to the negative of the appropriate patch type code. In this format, the user must specify a weight file and there is no need to specify whether the landscape boundary should be treated as edge or not, since the weight file specifies the exact level of contrast for each edge segment, including boundary segments.

Raster Format 1.--The simplest raster format is analogous to vector format 1 and consists of an image containing no background and no border (Fig. 3.3a). In this case, the entire raster image consists of defined patches contained within the landscape of interest. In this format, the user must designate whether the landscape boundary should be treated as a maximum-contrast edge or ignored. Regardless of whether the boundary is treated as edge or not, the user still has the option to specify a weight file, because this will determine whether metrics requiring the contrast information are computed. If a weight file is specified, the boundary segments will receive a contrast weight of 1 or 0, depending on whether the boundary was specified as edge or not.

Raster Format 2.--The second raster format consists of an image containing a background but no border (Fig. 3.3b). In this case, the raster image consists of the landscape mosaic containing defined patches surrounded by an undefined background. Note that the background value can be any non-patch code, although it typically is set to a negative integer, and does not effect any landscape metric. As in raster format 1, the user must designate whether the landscape boundary should be treated as an edge or not and the user has the option to specify a weight file.

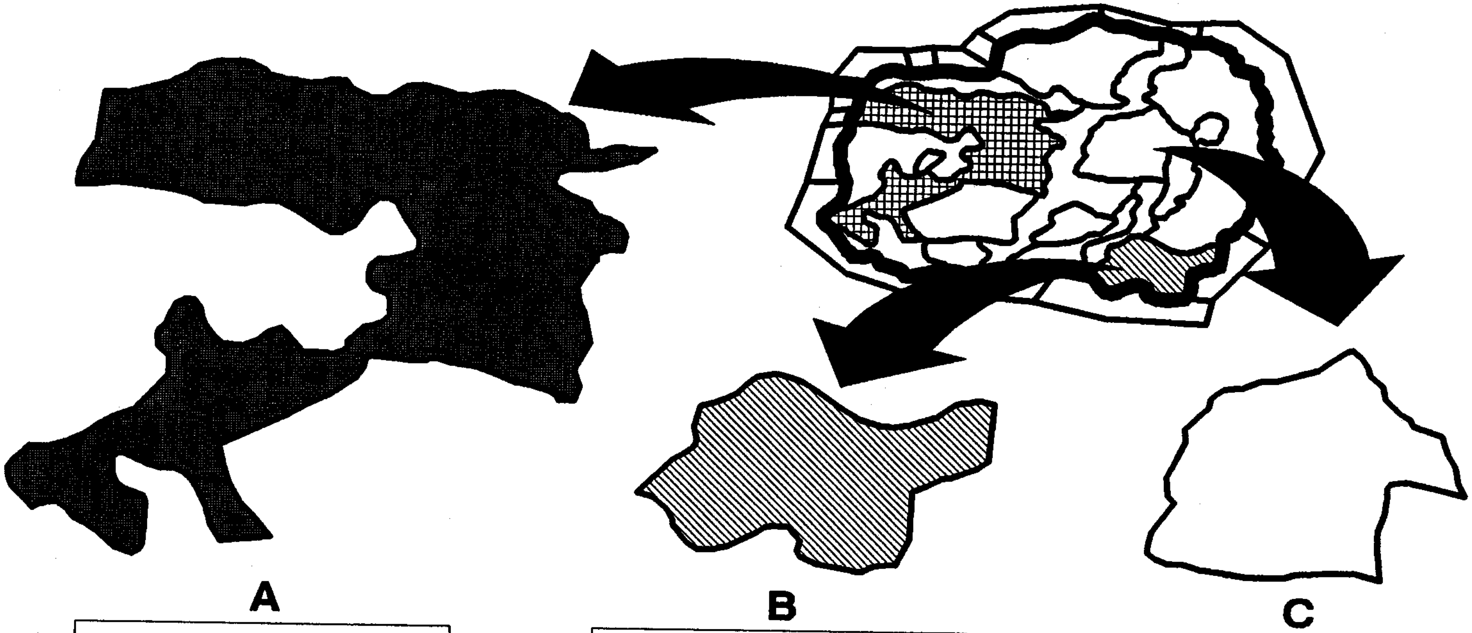
Raster Format 3.--The third raster format consists of an image containing a background and a border (Fig. 3.3c). In this case, the digital image consists of the landscape mosaic containing defined patches surrounded by defined patches that are explicitly defined as belonging to the landscape border surrounded by an undefined background. Note that the background value can be any non-patch code, although it typically is set to a negative integer, and does not effect any landscape metric, and that border patches must be set to the negative of the appropriate patch type code. In this format, the user must specify a weight file and there is no need to specify whether the landscape boundary should be treated as edge or not, since the weight file specifies that exact level of contrast for each edge segment, including boundary segments.

Raster Format 4.--The fourth raster format consists of an image containing a border but no background (Fig. 3.3d). In this case, the digital image consists of the landscape mosaic containing defined patches surrounded by defined patches that extend to the edge of the image and that are explicitly defined as belonging to the landscape border. Note that border patches must be set to the negative of the appropriate patch type code. As in raster format 3, the user must specify a weight file and there is no need to specify whether the landscape boundary should be treated as edge or not.

Often the user does not have control over the choice in formats. Should an option exist, I recommend including a landscape border if edge contrast is deemed important. If a border is defined, the user does not have to decide whether the landscape boundary should be treated as an edge or not. In most cases, some portions of the landscape boundary will constitute true edge and others will not. Thus, the decision to treat the entire landscape boundary as a maximum-contrast edge or to ignore it will not accurately represent the landscape. In the absence of a landscape border, the effect of designating the boundary as edge or not will vary as a function of landscape extent and heterogeneity. Larger and more heterogeneous landscapes will have greater internal edge-to-boundary ratio and therefore the boundary will have less influence on the landscape metric. Of course, only those metrics based on edge lengths and types are effected by the presence of a landscape border and the decision on how to treat the landscape boundary. When edge-based metrics are of particular importance to the investigation and the landscapes are small in extent and relatively homogeneous, the inclusion of a landscape border and the decision regarding the landscape boundary should be considered carefully.

FRAGSTATS computes 3 groups of metrics. For a given landscape mosaic, FRAGSTATS computes several statistics for (1) each patch in the mosaic (Fig. 3.4); (2) each patch type (class) in the mosaic (Fig. 3.5); and (3) the landscape mosaic as a whole (Fig. 3.6). In the assessment of landscape structure, patch characteristics serve primarily as the computational basis for several of the landscape metrics; the individual patch indices themselves may not have any interpretive value. However, sometimes the patch indices can be important and informative. For example, many vertebrates require suitable habitat patches larger than some minimum size (e.g., Robbins et al. 1989), so it would be useful to know the size of each patch in the landscape. Similarly, some species are adversely affected by edges and are more closely associated with patch interiors (e.g., Temple 1986), so it would be useful to know the size

Figure 3.4. Example of FRAGSTATS patch indices for 3 sample patches drawn from a landscape. See Appendix C for a mathematical definition of each metric.



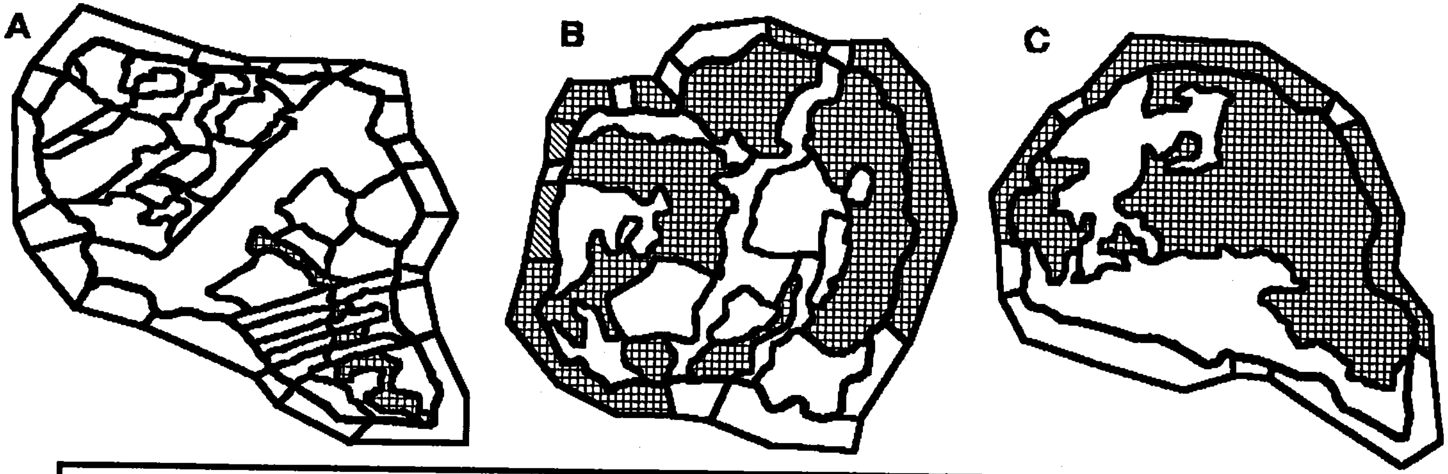
LID	----
PID	104
TYPE	MLS
AREA	51.33
PERIM	6230
SHAPE	2.45
FRACT	1.33
CORE	8.46
NCORE	2
CAI	16.48
LSIM	48.80
NEAR	25.00
EDGECON	16.96

LID	----
PID	400
TYPE	COS
AREA	16.83
PERIM	1922
SHAPE	1.32
FRACT	1.26
CORE	2.35
NCORE	1
CAI	13.94
LSIM	7.62
NEAR	155.10
EDGECON	42.02

LID	----
PID	200
TYPE	MGF
AREA	18.59
PERIM	1907
SHAPE	1.25
FRACT	1.25
CORE	4.62
NCORE	1
CAI	24.87
LSIM	8.41
NEAR	216.90
EDGECON	80.05

Figure 3.4

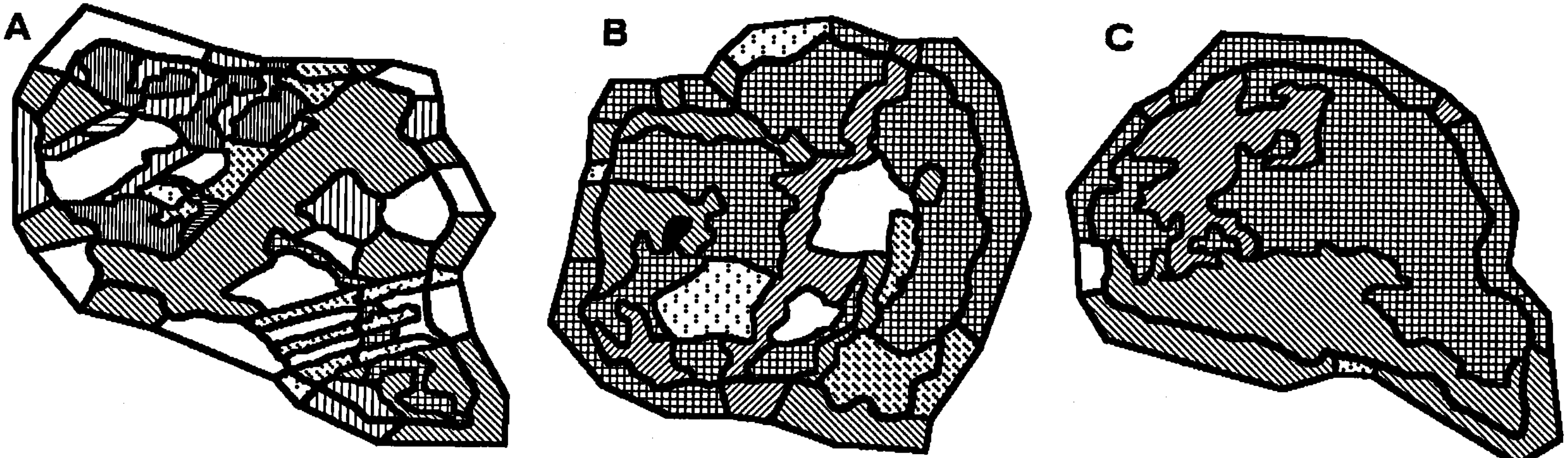
Figure 3.5. Example of FRAGSTATS class indices for the 'MLS' patch type in 3 sample landscapes. See Appendix C for a mathematical definition of each metric.



	A	B	C		A	B	C
LID	FN	NC	TC	TCAI	0	20.47	42.82
TYPE	MLS	MLS	MLS	MCAI	0	14.34	17.09
TA	284.74	296.07	279.78	MSI	1.59	1.70	1.78
CA	13.35	144.49	149.65	AWMSI	1.83	1.91	2.02
NP	4	5	3	LSI	1.93	3.22	2.62
PD	1.40	1.69	1.07	MPFD	1.34	1.29	1.31
MPS	3.34	28.90	49.88	DLFD	1.52	1.52	1.15
PSSD	2.86	22.29	70.53	LPI	2.50	17.34	46.79
PSCV	85.79	77.14	141.40	TE	4137	15198	9192
LSIM	4.69	48.80	53.49	ED	14.53	51.33	32.86
TCA	0	29.57	64.08	CWED	5.85	11.37	1.85
NCA	0	7	2	MECI	53.18	21.33	4.83
CAD	0	2.36	0.71	AWMECI	35.98	20.60	3.82
MCA	0	5.91	21.36	TECI	40.27	19.31	4.21
CASD	0	5.61	36.62	CONTAG1	47.80	75.67	49.99
CACV	0	94.78	171.42	MNN	NA	53.85	67.87
LCAS	0	9.99	22.90	NNSD	NA	30.09	3.67
				NNCV	NA	56.00	5.00

Figure 3.5

Figure 3.6. Example of FRAGSTATS landscape indices for 3 sample landscapes. See Appendix C for a mathematical definition of each metric.



■	Water
⁘	Grassland
□	Mixed Grass/Forb
⁚	Mixed Shrub
▩	Mixed Open Sapling
▧	Conifer Open Sapling
▤	Mixed Open Pole
▥	Conifer Open Pole
▤	Mixed Closed Pole
▥	Conifer Closed Pole
▦	Mixed Large Sawtimber
▧	Conifer Large Sawtimber
▨	Hardwood Large Sawtimber

	A	B	C
LID	FN	NC	TC
TA	284.74	296.07	279.78
NP	43	17	5
PD	15.10	5.74	1.79
MPS	6.62	17.42	55.96
PSSD	10.72	15.51	51.58
PSCV	161.86	89.06	92.17
TCA	27.69	42.86	95.58
NCA	11	14	7
CAD	3.86	4.73	2.50
MCA	0.64	2.52	19.12
CASD	3.26	7.14	27.09
CACV	506.63	283.35	141.71
TCAI	9.73	14.48	34.16
MCAI	2.24	8.47	19.16
MSI	1.47	1.64	2.02
AWMSI	1.60	1.86	2.17
LSI	5.01	3.88	2.73
MPFD	1.31	1.28	1.31
DLFD	1.26	1.49	1.22

	A	B	C
PR	10	7	3
PRD	3.51	2.36	1.07
RPR	37.04	25.93	11.11
SHDI	1.79	1.50	1.00
SIDI	0.79	0.70	0.60
MSIDI	1.56	1.22	0.92
SHEI	0.78	0.77	0.91
SIEI	0.88	0.82	0.90
MSIEI	0.68	0.63	0.84
LPI	25.08	17.34	46.79
TE	26313	19822	10334
ED	92.41	66.95	36.94
CWED	37.19	21.17	3.69
MECI	37.57	31.87	5.91
AWMECI	40.52	30.28	5.77
TECI	35.31	26.50	6.38
CONTAG1	74.03	64.71	46.52
CONTAG2	NA	NA	NA
MNN	NA	155.36	67.87
NNSD	NA	93.65	3.67
NNCV	NA	60.28	5.40

Figure 3.6

of the core area for each patch in the landscape. The probability of occupancy and persistence of an organism in a patch may be related to patch insularity (sensu Kareiva 1990), so it would be useful to know the nearest neighbor of each patch and the degree of contrast between the patch and its neighborhood. The utility of the patch characteristic information will ultimately depend on the objectives of the investigation.

FRAGSTATS computes several statistics for each patch in the landscape (Fig. 3.4). An ASCII data file with the filename "basename.patch" is generated containing the patch indices. The basename must be supplied by the user as an argument in the command line (see Appendix B, FRAGSTATS user guidelines). The ASCII file contains 1 record for each patch in the landscape; fields (columns) correspond to the patch metrics described below. The patch indices also are written to a second file with the filename "basename.full" formatted for display purposes (Appendix A).

In many landscape ecological applications, the primary interest is in the amount and distribution of a particular patch type (class). A good example is in the study of forest fragmentation. Forest fragmentation is a landscape-level process in which forest tracts are progressively sub-divided into smaller, geometrically more complex, and more isolated forest fragments as a result of both natural processes and human land use activities (Harris 1984). This process involves changes in landscape composition, structure, and function and occurs on a backdrop of a natural patch mosaic created by changing landforms and natural disturbances. Forest fragmentation is the prevalent trajectory of landscape change in several human-dominated forest regions of the world, and is increasingly becoming recognized as a major cause of declining biodiversity (Whitcomb et al. 1981, Terborgh 1989). Class indices quantify the amount and distribution of each patch type in the landscape separately and thus can be considered indices of fragmentation for each patch type.

FRAGSTATS computes several statistics for each patch type (class) in the landscape (Fig. 3.5) and generates an ASCII data file with the filename "basename.class" containing the class indices. The basename must be supplied by the user as an argument in the command line (see Appendix B, FRAGSTATS user guidelines). The ASCII file contains 1 record for each class in the landscape; fields (columns) correspond to the class metrics described below. The class indices also are written to a second file with the filename "basename.full" formatted for display purposes (Appendix A).

In many landscape ecological applications, the primary interest is in the structure (i.e., composition and pattern) of the entire landscape(s). A good example is in the study of landscape diversity. Aldo Leopold (1933) noted that wildlife diversity was greater in more diverse landscapes. Thus, the quantification of landscape diversity has assumed a preeminent role in landscape ecology. A major focus of landscape ecology is on quantifying the relationships between landscape structure and ecological processes. Consequently, much emphasis has been placed on developing methods to quantify landscape structure (e.g., O'Neill et al. 1988, Li 1990, Turner 1990a, Turner and Gardner 1991) and a great variety of landscape structural indices have been developed for this purpose. Many of these published indices have been incorporated into FRAGSTATS, although sometimes in modified form.

FRAGSTATS computes several statistics for the entire landscape mosaic (Fig. 3.6) and generates an ASCII data file with the filename "basename.land" containing the landscape indices. The basename must be supplied by the user as an argument in the command line (see Appendix B, FRAGSTATS user guidelines). The ASCII file contains 1 record for each landscape; fields (columns) correspond to the landscape metrics described below. The landscape indices also are written to a second file with the filename "basename.full" formatted for display purposes (Appendix A).

FRAGSTATS METRICS

In this section, I provide a general overview and discussion of the various metrics computed in FRAGSTATS; a detailed mathematical definition and description of each metric, including the units and range in values, is provided in Appendix C. Metrics are grouped in logical fashion according to the aspect of landscape structure measured. For example, the core area metrics (i.e., those based on core area measurements) available at the patch, class, and landscape levels are grouped together. For each group, I discuss the general applicability of the metrics to landscape ecological investigations and some of their limitations. The results presented in Figures 3.4-3.6 may be useful as a visual aid in interpreting each metric.

General Considerations

Metrics involving standard deviation employ the population standard deviation formula, not the sample formula, because all patches in the landscape (or class) are included in the calculations. In other words, the landscape is considered a population of patches and every patch is counted. Thus, FRAGSTATS does not sample patches from the landscape, it censuses the entire landscape. Even if each landscape represents a sample from a larger region, it is still more appropriate to compute the standard deviation for each landscape using the population formula, because for each landscape every patch is included in the calculations. In this case it would be appropriate to use the sample formula when calculating the variation among landscapes using the FRAGSTATS output for each landscape. The difference between the population and sample formulas is insignificant when sample sizes (i.e., number of patches) are large (e.g., >20). However, when quantifying landscapes with a small number of patches the differences can be significant.

FRAGSTATS computes several statistics for each patch and class in the landscape and the landscape as a whole. At the class and landscape level, some of the metrics quantify landscape composition, while others quantify landscape pattern. As previously discussed, composition and pattern can affect ecological processes independently and interactively. Thus, it is especially important to understand for each metric what aspect of landscape structure is being quantified. In addition, many of the metrics are partially or completely redundant; that is, they quantify a similar or identical aspect of landscape structure. In most cases, redundant metrics will be very highly or even perfectly correlated. For example, at the landscape level patch density (PD) and mean patch size (MPS) will be perfectly correlated because they represent the same information. These redundant metrics are alternative ways of representing the same information. I included many such redundant metrics in FRAGSTATS because the preferred form of representing a particular aspect of landscape structure will differ among applications and users. For practical reasons, I did not include every possible alternative formulation for each unique aspect of landscape structure. Instead, I included those forms most commonly used or the forms I deemed to be most meaningful and widely applicable. It behooves the user to understand these redundancies, because in most applications only 1 of each set of redundant metrics should be employed. It is important to note that in a particular application, some metrics may be empirically redundant; not because they measure the same aspect of landscape structure, but because for the particular landscapes under investigation, different aspects of landscape structure are statistically correlated. The distinction between this form of redundancy and the former is important, because little can be learned by interpreting metrics that are intentionally redundant, but much can be learned about landscapes by interpreting metrics that are empirically redundant.

Many of the patch indices have counterparts at the class and landscape levels. For example, many of the class indices (e.g., mean shape index) represent the same basic information as the corresponding patch indices (e.g., patch shape index), but instead of considering a single patch they consider all patches of a particular type simultaneously. Likewise, many of the landscape indices are derived from patch or class characteristics. Consequently, many of the class and landscape indices are computed from patch and class statistics by summing or averaging over all patches or classes. Even though many of the class and landscape indices represent the same fundamental information, naturally the algorithms differ slightly (see Appendix C). Class indices represent the spatial distribution and pattern within a landscape of a single patch type; whereas, landscape indices represent the spatial pattern of the entire landscape mosaic, considering all patch types simultaneously. Thus, even though many of the indices have counterparts at the class and landscape levels, their interpretations may be somewhat different. Most of the class indices can be interpreted as fragmentation indices because they measure the fragmentation of a particular patch type; whereas, most of the landscape indices can be interpreted more broadly as landscape heterogeneity indices because they measure the overall landscape structure. Hence, it is important to interpret each index in a manner appropriate to its scale (patch, class, or landscape).

Area Metrics

FRAGSTATS computes several simple statistics representing area at the patch, class, and landscape levels (Table 3.1). These metrics help to quantify landscape composition, not landscape pattern. The area of each patch (AREA) comprising a landscape mosaic is perhaps the single most important and useful piece of information contained in the landscape. Not only is this information the basis for many of the patch, class, and landscape indices, but patch area has a great deal of ecological utility in its own right. For example, there is considerable evidence that bird species richness and the occurrence and abundance of some species are strongly correlated with patch size (e.g., Robbins et al. 1989). Thus, patch size information alone could be used to model species richness, patch occupancy, and species distribution patterns in a landscape given the appropriate empirical relationships derived from field studies.

Table 3.1. Metrics computed in FRAGSTATS, grouped by subject area. See Appendix C for a mathematical definition of each metric.

Scale	Acronym	Metric (units)
Area metrics		
Patch	AREA	Patch area (ha)
Class	CA	Class area (ha)
Class/landscape	TA	Total landscape area (ha)
Patch/class	LSIM	Landscape similarity (%)
Class/landscape	LPI	Largest patch index (%)
Patch density, patch size and variability metrics		
Class/landscape	NP	Number of patches (#)
Class/landscape	PD	Patch density (#/100 ha)
Class/landscape	MPS	Mean patch size (ha)
Class/landscape	PSSD	Patch size standard deviation (ha)
Class/landscape	PSCV	Patch size coefficient of variation (%)
Edge metrics		
Patch	PERIM	Patch perimeter (m)
Class/landscape	TE	Total edge (m)
Class/landscape	ED	Edge density (m/ha)
Patch	EDCON	Patch edge contrast (%)
Class/landscape	MECI	Mean edge contrast index (%)
Class/landscape	AWMECI	Area-weighted mean edge contrast index (%)
Class/landscape	TECI	Total edge contrast index (%)
Class/landscape	CWED	Contrast-weighted edge density (m/ha)
Shape metrics		
Patch	SHAPE	Shape index
Patch	FRACT	Fractal dimension
Class/landscape	MSI	Mean shape index
Class/landscape	AWMSI	Area-weighted mean shape index
Class/landscape	LSI	Landscape shape index
Class/landscape	DLFD	Double log fractal dimension
Class/landscape	MPFD	Mean patch fractal dimension
Core area metrics		
Patch	CORE	Patch core area (ha)
Class/landscape	TCA	Total core area (ha)
Patch/class	LCAS	Landscape core area similarity (%)
Patch	NCORE	Number of core areas (#)
Class/landscape	NCA	Number of core areas (#)

Table 3.1. Continued.

Scale	Acronym	Metric (units)
Core area metrics--continued.		
Class/landscape	CAD	Core area density (#/100 ha)
Class/landscape	MCA	Mean core area (ha)
Patch	CAI	Core area index (%)
Class/landscape	MCAI	Mean core area index (%)
Class/landscape	TCAI	Total core area index (%)
Class/landscape	CASD	Core area standard deviation (ha)
Class/landscape	CACV	Core area coefficient of variation (%)
Nearest neighbor metrics		
Patch	NEAR	Nearest neighbor (m)
Class/landscape	MNN	Mean nearest neighbor (m)
Class/landscape	NNSD	Nearest neighbor standard deviation (m)
Class/landscape	NNCV	Nearest neighbor coefficient of variation (%)
Diversity metrics		
Landscape	SHDI	Shannon's diversity index
Landscape	SIDI	Simpson's diversity index
Landscape	MSIDI	Modified Simpson's diversity index
Landscape	PR	Patch richness (#)
Landscape	PRD	Patch richness density (#/100 ha)
Landscape	RPR	Relative patch richness (%)
Landscape	SHEI	Shannon's evenness index
Landscape	SIEI	Simpson's evenness index
Landscape	MSIEI	Modified Simpson's evenness index
Contagion metrics		
Class/landscape	CONTAG1	Contagion index 1 (%)
Landscape	CONTAG2	Contagion index 2 (%)

Class area (CA) is a measure of landscape composition; specifically, how much of the landscape is comprised of a particular patch type. This is an important measure in a number of ecological applications. For example, an important by-product of habitat fragmentation is habitat loss. In the study of forest fragmentation, therefore, it is important to know how much of the target patch type (habitat) exists within the landscape. In addition, although many vertebrate species that specialize on a particular habitat have minimum area requirements (e.g., Robbins et al. 1989), not all species require that suitable habitat to be present in 1 contiguous patch. For example, northern spotted owls have minimum area requirements for late-seral forest that varies geographically; yet, individual spotted owls use late-seral forest that may be distributed among many patches (Forsman et al. 1984). For this species, late-seral forest area (i.e., class area) might be a good index of habitat suitability within landscapes the size of spotted owl home ranges (Lehmkuhl and Raphael 1993). In addition to its direct interpretive value, class area is used in the computations for many of the class and landscape metrics.

Total landscape area (TA) often does not have a great deal of interpretive value with regards to evaluating landscape structure, but it is important because it defines the extent of the landscape. Moreover, total landscape area is used in the computations for many of the class and landscape metrics. Total area is included as both a class and landscape index (and included in the corresponding output files) because it is important regardless of whether the primary interest is in class or landscape indices.

Patch area, class area, and total landscape area quantify area in absolute terms (hectares). However, it is often desirable to quantify area in relative terms as a percentage of total landscape area. Therefore, at the patch and class levels, FRAGSTATS computes a landscape similarity (LSIM) index that quantifies class area as a percentage of total landscape area. It is included as a patch characteristic because some ecological properties of a patch can be influenced by the abundance of similar patches in the surrounding landscape. For example, island biogeographic theory predicts that the probability of patch occupancy for some species or species richness is a function of both patch size and isolation (MacArthur and Wilson 1967). One aspect of isolation is the amount of similar habitat within a specified distance. Thus, the dynamics of a local population contained within a patch are likely to be influenced by the size of the metapopulation occupying the entire landscape. Indeed, there is some evidence that regional habitat availability has a strong influence on local bird populations at the patch level (Askins and Philbrick 1987).

Area metrics have limitations imposed by the scale of investigation. Minimum patch size and landscape extent set the lower and upper limits of these area metrics, respectively. These are critical limits to recognize because they establish the lower and upper limits of resolution for the analysis of landscape composition and pattern. Otherwise, these area metrics are subject to few limitations.

Patch Density, Size and Variability Metrics

FRAGSTATS computes several simple statistics representing the number or density of patches, the average size of patches, and the variation in patch size at the class and landscape levels (Table 3.1). These metrics help to quantify landscape pattern. The number of patches (NP) of a particular habitat type may affect a number of ecological processes, depending on the landscape context. For example, the number of patches may determine the number of subpopulations in a spatially-structured population, or metapopulation, for species exclusively associated with that habitat type. The number of subpopulations could influence the dynamics and persistence of the metapopulation (Gilpin and Hanski 1991). The number of patches also can alter the stability of species interactions and opportunities for coexistence in both predator-prey and competitive systems (Kareiva 1990). In addition, habitat subdivision, as indexed by the number of patches, may affect the propagation of disturbances across a landscape (Franklin and Forman 1987). A patch type that is subdivided into a greater number of patches may be more resistent to the propagation of some disturbances (e.g., disease, fire, etc.), and thus more likely to persist in a landscape than a patch type that is contiguous; although habitat fragments may suffer higher rates of disturbance for some disturbance types (e.g. windthrow) than contiguous habitats. The number of patches in a landscape mosaic (pooled across patch types) can have the same ecological applicability, but more often serves as a index of spatial heterogeneity of the entire landscape mosaic. A landscape with a greater number patches has a finer grain; that is, the spatial heterogeneity occurs at a finer resolution. Although the number patches in a class or in the landscape may be fundamentally important to a number of ecological processes, often it does not have any interpretive value by itself because it conveys no information about area, distribution, or density of patches. Of course, if total landscape area and class area are held constant, then number of patches conveys the same information as patch density or mean patch size and it could be a useful index to interpret. Number of patches is probably most valuable, however, as the basis for computing other, more interpretable, metrics.

Patch density (PD) is a limited, but fundamental, aspect of landscape structure. Patch density has the same basic utility as number of patches as an index, except that it expresses number of patches on a per unit area basis that facilitates comparisons among landscapes of varying size. Of course, if total landscape area is held constant, then patch density and number of patches convey the same information. If numbers of patches, not their area or distribution, is particularly meaningful, then patch density of a particular patch type could serve as a good fragmentation index. Holding total class area constant, a landscape with a greater density of patches of a target patch type would be considered more fragmented than a landscape with a lower density of patches of that patch type. Similarly, the density of patches in the entire landscape mosaic could serve as a good heterogeneity index because a landscape with greater patch density would have more spatial heterogeneity.

Another class and landscape index based on the number of patches is mean patch size (MPS). As discussed previously, the area of each patch comprising a landscape mosaic is perhaps the single most important and useful piece of information contained in the landscape. The area comprised by each patch type (class) is equally important. For example, progressive reduction in the size of habitat fragments is a key component habitat fragmentation. Thus, a landscape with a smaller mean patch size for the target patch type than another landscape might be considered more fragmented. Similarly, within a single landscape, a patch type with a smaller mean patch size than another patch type might be considered more fragmented. Thus, mean patch size can serve as a habitat fragmentation index, although the limitations discussed below may reduce its utility in this respect. At the landscape level, mean patch size has the same utility as patch density because both indices are a function of the number of patches and total landscape area; they are completely redundant.

Like patch area, the range in mean patch size is ultimately constrained by the grain and extent of the image and minimum patch size; relationships cannot be detected beyond these lower and upper limits of resolution. Mean patch size at the class level is a function of the number patches in the class and total class area. In contrast, patch density is a function of total landscape area. Therefore, at the class level, these 2 indices represent slightly different aspects of class structure. For example, 2 landscapes could have the same number and sizes of patches of the corresponding class and thus have the same mean patch size; yet, if total landscape area differed, patch density could be very different between landscapes. Alternatively, 2 landscapes could have the same number of patches and total landscape area and thus have the same patch density; yet, if class area differed, mean patch size could be very different between landscapes. These differences should be kept in mind when selecting class metrics for a particular application. In addition, although mean patch size is derived from the number patches, it does not convey any information about how many patches are present. A mean patch size of 10 ha could represent 1 or 100 patches and the difference could have profound ecological implications. Furthermore, mean patch size represents the average condition. Variation in patch size may convey more useful information. For example, a mean patch size of 10 ha could represent a class with 5 10-ha patches or a class with 2-, 3-, 5-, 10-, and 30-ha patches, and this difference could be important ecologically.

For these reasons, mean patch size is probably best interpreted in conjunction with total class area, patch density (or number of patches), and patch size variability.

At the landscape level, mean patch size and patch density are both a function of number of patches and total landscape area. In contrast to the class level, these indices are completely redundant. Although both indices may be useful for "describing" 1 or more landscapes, they would never be used simultaneously in a statistical analysis of landscape structure. Including both of these indices in a discriminant analysis, for example, would cause a singularity in the correlation matrix and inhibit the eigenanalysis.

In many ecological applications, second-order statistics, such as the variation in patch size, may convey more useful information than first-order statistics, such as mean patch size. Variability in patch size measures a key aspect of landscape heterogeneity that is not captured by mean patch size and other first-order statistics. For example, consider 2 landscapes with the same patch density and mean patch size, but with very different levels of variation in patch size. Greater variability indicates greater spatial heterogeneity either at the class level or landscape level and may reflect differences in underlying processes affecting the landscapes. Variability is a difficult thing to summarize in a single metric. FRAGSTATS computes 2 of the simplest measures of variability--standard deviation and coefficient of variation.

Patch size standard deviation (PSSD) is a measure of absolute variation; it is a function of the mean patch size and variation in patch size among patches. Thus, although patch size standard deviation does convey information about patch size variability, it is a difficult parameter to interpret without doing so in conjunction with mean patch size because the absolute variation is dependent on mean patch size. For example, 2 landscapes may have the same patch size standard deviation, e.g., 10 ha; yet 1 landscape may have a mean patch size of 10 ha, while the other may have a MPS of 100 ha. In this case, the interpretations of landscape structure would be very different, even though absolute variation is the same. Specifically, the former landscape has greatly varying and smaller patch sizes, while the latter has more uniformly-sized and larger patches. For this reason, patch size coefficient of variation (PSCV) is generally preferable to standard deviation for comparing variability among landscapes. Patch size coefficient of variation measures relative variability about the mean (i.e., variability as a percentage of the mean), not absolute variability. Thus, it is not necessary to know mean patch size to interpret the coefficient of variation. Nevertheless, patch size coefficient of variation also can be misleading with regards to landscape structure in the absence of information on the number of patches or patch density and other structural characteristics. For example, 2 landscapes may have the same patch size coefficient of variation, e.g., 100%; yet 1 landscape may have 100 patches with a mean patch size of 10 ha, while the other may have 10 patches with a mean patch size of 100 ha. In this case, the interpretations of landscape structure could be very different, even though PSCV is the same. Ultimately, the choice between standard deviation and coefficient of variation will depend on whether absolute or relative variation is more meaningful in a particular application.

It is important to keep in mind that both standard deviation and coefficient of variation assume a normal distribution about the mean. In a real landscape, the distribution of patch sizes may be highly irregular. It may be more informative to inspect the actual distribution itself, rather than relying on summary statistics such as these that make assumptions about the distribution and therefore can be misleading. Also, note that patch size standard deviation and coefficient of variation can equal 0 under 2 different conditions: (1) when there is only 1 patch in the landscape; and (2) when there is more than 1 patch, but they are all the same size. In both cases, there is no variability in patch size, yet the ecological interpretations could be quite different.

Edge Metrics

FRAGSTATS computes several statistics representing the amount of edge or degree of edge contrast at the patch, class, and landscape levels (Table 3.1). These metrics help to quantify landscape pattern. Total amount of edge in a landscape is important to many ecological phenomena. In particular, a great deal of attention has been given to wildlife-edge relationships (Thomas et al. 1978 and 1979, Strelke and Dickson 1980, Morgan and Gates 1982, Logan et al. 1985). In landscape ecological investigations much of the presumed importance of spatial pattern is related to edge effects. The forest edge effect, for example, results primarily from differences in wind and light intensity and quality reaching a forest patch that effect changes in microclimate and disturbance rates (e.g., Gratkowski 1956, Ranney et al. 1981, Chen and Franklin 1990). These changes, in combination with changes in seed dispersal and herbivory, can effect changes in vegetation composition and structure (Ranney et al. 1981). The proportion of a forest patch that is effected in this manner is dependent, therefore, upon patch shape and orientation, and by adjacent land cover. A large but convoluted patch, for example, could be entirely edge habitat. It is now widely accepted that edge effects must be viewed from an organism-centered perspective; that edge effects influence organisms differently. Some species have an affinity for edges, some are unaffected, and others are negatively influenced.

Early wildlife management efforts were focussed on maximizing edge habitat because it was believed that most species favored habitat conditions created by edges and that the juxtaposition of different habitats would increase species diversity (Leopold 1933). Indeed this concept of edge as a positive influence has guided land management practices until recently. Recent studies, however, have suggested that changes in vegetation, invertebrate populations, predation, brood parasitism, and competition along forest edges has resulted in the population declines of several vertebrate species associated with forest interior conditions (e.g., Strelke and Dickson 1980, Kroodsma 1982, Brittingham and Temple 1983, Wilcove 1985, Temple 1986, Noss 1988, Yahner and Scott 1988, Robbins et al. 1989). Forest interior species, therefore, may be sensitive to patch shape because for a given patch size, the more complex the shape, the larger the edge-to-interior ratio. Most of the adverse effects of forest fragmentation on organisms seem to be directly or indirectly related to edge effects. Total class edge in a landscape, therefore, often is the most critical piece information in the study of fragmentation, and many of the class indices directly or indirectly index the amount of class edge. Similarly, the total amount of edge in a landscape is directly related to the degree of spatial heterogeneity in that landscape.

At the patch level, edge is a function of patch perimeter (PERIM). The edge effect on a patch can be indexed using the perimeter-to-area ratio employed in the shape indices discussed below. At the class and landscape levels, edge can be quantified in other ways. Total edge (TE) is an absolute measure of total edge length (m). In applications that involve comparing landscapes of varying size, this index may not facilitate those comparisons. Edge density (ED) standardizes edge to a per unit area basis that facilitates comparisons among landscapes of varying size. However, when comparing landscapes of identical size, total edge and edge density are completely redundant.

These edge indices are effected by the resolution of the image. Generally, the finer the resolution (i.e., the greater the detail with which edges are delineated), the greater the edge length. At coarse resolutions, edges may appear as relatively straight lines; whereas, at finer resolutions, edges may appear as highly convoluted lines. Thus, comparing edge calculations among images with different resolutions should be avoided. In addition, vector and raster images portray lines differently. Patch perimeter and the length of edges will be biased upward in raster images because of the stair-step patch outline, and this will effect these edge indices. The magnitude of this bias will vary in relation to the grain or resolution of the image, and the consequences of this bias with regards to the use and interpretation of these indices must be weighed relative to the phenomenon under investigation.

The contrast between a patch and its neighborhood can influence a number of important ecological processes (Forman and Godron 1986). The "edge effects" described previously are influenced by the degree of contrast between patches. For example, microclimatic changes (e.g., wind, light intensity and quality, etc.) are likely to extend farther into a patch along an edge with high structural contrast than an edge with low structural contrast (Ranney et al. 1981). Similarly, the adverse effects of brown-headed cowbird nest parasitism on some forest-dwelling neotropical migratory bird species are likely to be greatest along high-contrast forest edges (e.g., between mature forest patches and grassland), because cowbirds prefer to forage in early-seral habitats and parasitize nests in late-seral habitats (Brittingham and Temple 1983). Because of the edge effects described previously, the boundaries between some patch types can have distinctive enough characteristics to be considered a separate edge habitat (Reese and Ratti 1988).

Patch insularity is a function of many things, including distance between the patch and its nearest neighbor, age of the patch or its duration of isolation, connectivity of the patch with neighbors (e.g., through corridors), and the character of the intervening landscape. The permeability of a landscape for some organisms may depend on the character of the intervening landscape. The degree of contrast between the focal habitat patch and the surrounding landscape may influence dispersal patterns and survival and thus indirectly affect the degree of patch isolation. Similarly, an organism's ability to use the resources in adjacent patches, as in the process of landscape supplementation (Dunning et al. 1992), depends on the nature of the boundary between the patches. The boundary between patches can function as a barrier to movement, a differentially-permeable membrane that facilitates some ecological flows but impedes others, or as a semipermeable membrane that partially impairs flows (Wiens et al. 1985, Hansen and Castri 1992). For example, high-contrast edges may prohibit or inhibit some organism's from seeking supplementary resources in surrounding patches. Conversely, some species (e.g., great horned owl, Bubo virginianus) seem to prefer the juxtaposition of patch types with high contrast, as in the process of landscape complementation (Dunning et al. 1992).

Clearly, edge contrast can assume a variety of meanings for different ecological processes. Therefore, contrast can be defined in a variety of ways, but generally always reflects the magnitude of difference between patches in 1 or more ecological attributes at a given scale that are important to the phenomenon under investigation (Kotliar and Wiens 1990, Wiens et al. 1985). Like Romme (1982), FRAGSTATS employs weights to represent the magnitude of edge contrast between adjacent patch types; weights must range between 0 (no contrast) and 1 (maximum contrast). Under most circumstances, it is probably not valid to assume that all edges function the same. Often there will not be a strong empirical basis for establishing a weighting scheme, but a reasoned guess based on a theoretical understanding of the phenomenon is probably better than assuming all edges are alike. For example, from an avian habitat use standpoint, we might weight edges somewhat subjectively according to the degree of structural and floristic contrast because a number of studies have shown these features to be important to many bird species (Thomas et al. 1978 and 1979, Logan et al. 1985).

FRAGSTATS computes several indices based on edge contrast at the patch, class, and landscape levels (Table 3.1). At the patch level, EDGECON indexes the degree of contrast between a patch and its immediate neighborhood. Each segment of the patch perimeter is weighted by the degree of contrast with the adjacent patch. Total patch perimeter is reduced proportionate to the degree of contrast in the perimeter and reported as a percentage of the total perimeter. Thus, a patch with a 10% edge contrast index has very little contrast with its neighborhood; it has the equivalent of 10% of its perimeter in maximum-contrast edge. Conversely, a patch with a

90% edge contrast index has high contrast with its neighborhood. Mean edge contrast index (MECI) quantifies the average edge contrast (EDGECON) for patches of a particular patch type (class level) or for all patches in the landscape. FRAGSTATS also computes an area-weighted mean edge contrast index (AWMECI) by weighting patches according to their size. Thus, larger patches are weighted more heavily than smaller patches in calculating the average patch edge contrast for the class or landscape. This area-weighted index may be more appropriate than the simple mean index in cases where larger patches play a dominant role in the landscape dynamics relative to the phenomenon under consideration. In such cases, it may make sense to weight larger patches more heavily when characterizing landscape structure. Otherwise, small patches will have an equal effect on the average edge contrast index, when in fact they play a disproportionately small role in the overall landscape function. At the class and landscape levels, FRAGSTATS also computes a total edge contrast index (TECI). Like its patch-level counterpart (EDGECON), this index quantifies edge contrast as a percentage of maximum possible. However, this index ignores patch distinctions; it quantifies edge contrast for the landscape as a whole, thereby focussing on the landscape condition, not the average patch condition, as do the previous indices.

These edge contrast indices are relative measures. Given any amount or density of edge, they measure the degree of contrast in that edge. For this reason, these indices are probably best interpreted in conjunction with total edge or edge density. High values of these indices mean that the edge present, regardless of whether there is 10 m or 1,000 m, is of high contrast, and vice versa. Note that these indices consider landscape boundary segments even if they have a contrast of zero (i.e., the patch extends beyond the landscape boundary). These zero-contrast boundary segments are included in the calculation of these indices because I believe that boundary segments should be treated equal to internal edge segments in determining the degree of contrast in the patch, class, or landscape. Therefore, if a landscape border is absent, the choice of whether to treat the landscape boundary as maximum-contrast edge or no-contrast edge could have significant effects on these indices, depending on the size and heterogeneity of the landscape.

The edge contrast indices discussed thus far all measure edge contrast in relative terms; they are unaffected by the total amount of edge or edge density. FRAGSTATS computes an index that incorporates edge density and edge contrast together into a single index. Contrast-weighted edge density (CWED) standardizes edge to a per unit area basis that facilitates comparison among landscapes of varying size. However, this index reduces the length of each edge segment proportionate to the degree of contrast. Thus, 100 m/ha of maximum-contrast edge (i.e., weight=1) is unaffected; but 100 m/ha of edge with a contrast weight of 0.2 is reduced by 80% to 20 m/ha of contrast-weighted edge. This index measures the equivalent maximum-contrast edge density. For example, an edge density of 100 means that there are 100 meters of edge per hectare in the landscape. A contrast-weighted edge density of 80 for the same landscape means that there are 80 meters of maximum-contrast edge per hectare in the landscape. A landscape with 100 m/ha of edge and an average contrast weight of 0.8 would have twice the contrast-weighted edge density (80 m/ha) as a landscape with only 50 m/ha of edge but with the same average contrast weight (40 m/ha). Thus, both edge density and edge contrast are reflected in this index. For many ecological phenomena, edge types function differently. Consequently, comparing total edge density among landscapes may be misleading because of differences in edge types. This contrast-weighted edge density index attempts to quantify edge from the perspective of its functional significance. Thus, landscapes with the same contrast-weighted edge density have the same total magnitude of edge effects from a functional perspective.

These edge contrast indices are limited by the same considerations discussed previously for total edge metrics. These indices are only calculated if an edge contrast weight file is specified. Otherwise, these indices are not reported in the display output file and are left blank in the ASCII output files. The usefulness of any of these edge contrast indices is directly related to the meaningfulness of the weighting scheme used to quantify edge contrast. Careful consideration should be given to devising weights that reflect the empirical and theoretical knowledge and understanding of the phenomenon under consideration. If the weighting scheme does not accurately represent the phenomenon under investigation, then the results will be spurious.

Shape Metrics

FRAGSTATS computes several statistics representing the complexity of patch shape at the patch, class, and landscape levels (Table 3.1). These metrics help to quantify landscape pattern. The interaction of patch shape and size can influence a number of important ecological processes. Patch shape has been shown to influence inter-patch processes such as small mammal migration (Buechner 1989) and woody plant colonization (Hardt and Forman 1989), and may influence animal foraging strategies (Forman and Godron 1986). However, the primary significance of shape in determining the nature of patches in a landscape seems to be related to the "edge effect" (see discussion of edge effects for edge metrics).

Shape is a difficult parameter to quantify concisely in a metric. FRAGSTATS computes 2 types of shape indices; both are based on perimeter-area relationships. Patton (1975) proposed a diversity index based on shape for quantifying habitat edge for wildlife species and as a means for comparing alternative habitat improvement efforts (e.g., wildlife clearings). This shape index (SHAPE) measures the complexity of patch shape compared to a standard shape. In the vector version of FRAGSTATS, patch shape is evaluated with a circular standard; SHAPE is minimum for circular patches and increases as patches become increasingly noncircular. Similarly, in the raster version of FRAGSTATS, patch shape is evaluated with a square standard. While there are other means of quantifying patch shape (e.g., Lee and Sallee

1970), SHAPE is a widely applicable index used in landscape ecological research (Forman and Godron 1986). This shape index can be applied at the class and landscape levels as well. Mean shape index (MSI) measures the average patch shape, or the average perimeter-to-area ratio, for a particular patch type (class level) or for all patches in the landscape. FRAGSTATS also computes an area-weighted mean shape index (AWMSI) of patches at the class and landscape levels by weighting patches according to their size. Thus, larger patches are weighted more heavily than smaller patches in calculating the average patch shape for the class or landscape. This index may be more appropriate than the simple mean shape index in cases where larger patches play a dominant role in the landscape function relative to the phenomenon under consideration, similar to the area-weighted mean edge contrast index. The difference between MSI and AWMSI can be particularly noticeable when sample sizes are small (i.e., few patches).

An alternative to these patch shape indices at the class and landscape levels that are based on the "average" patch condition is the landscape shape index (LSI). The landscape shape index measures the perimeter-to-area ratio for the landscape as a whole. This index is identical to the habitat diversity index proposed by Patton (1975), except that I apply the index at the class level as well. This index quantifies the amount of edge present in a landscape relative to what would be present in a landscape of the same size but with a simple geometric shape (circle in vector, square in raster) and no internal edge (i.e., landscape comprised of a single circular or square patch). Landscape shape index is identical to the shape index at the patch level (SHAPE), except that LSI treats the entire landscape as if it were 1 patch and any patch edges (or class edges) as though they belong to the perimeter. The landscape boundary must be included as edge in the calculation in order to use the circle or square as a standard for comparison. Unfortunately, this may not be meaningful in cases where the landscape boundary does not represent true edge and/or the actual shape of the landscape is of no particular interest. In this case, the total amount of true edge, or some other index based on edge, would probably be more meaningful. If the landscape boundary represents true edge or the shape of the landscape is particularly meaningful, then LSI can be a meaningful index, especially when comparing among landscapes of varying sizes.

These shape indices have important limitations. First, vector and raster images use different shapes as standards. Thus, the absolute value of these indices differs between vector and raster images. The implications of this difference should be considered relative to the phenomenon under investigation. Second, these shape indices are limited in the same manner as the edge indices discussed above with regards to the differences between how lines are portrayed in vector and raster images. Perimeter length will be biased upward in raster images because of the stair-stepping pattern of line segments and the magnitude of this bias will vary in relation to the grain or resolution of the image. Third, as an index of "shape", the perimeter-to-area ratio method is relatively insensitive to differences in patch morphology. Thus, although patches may possess very different shapes, they may have identical areas and perimeters and SHAPE indexes. For this reason, these shape indices are not useful as measures of patch morphology; they are best considered as measures of overall shape complexity. Finally, the mean shape index and area-weighted mean shape index are subject to the limitations of first-order statistics. For example, the average patch shape for a class or the landscape may not be very meaningful if the distribution of patch shapes is complex.

The other basic type of shape index computed by FRAGSTATS is the fractal dimension. In landscape ecological research, patch shapes are increasingly characterized with the fractal dimension (Krummel et al. 1987, Milne 1988, Turner and Ruscher 1988, Iverson 1989, Ripple et al. 1991). The appeal of fractal analysis is that it can be applied to spatial features over a wide variety of scales. Mandelbrot (1977, 1982) introduced the concept of fractal, a geometric form that exhibits structure at all spatial scales and proposed a perimeter-area method to calculate the fractal dimension of natural planar shapes. The perimeter-area method quantifies the degree of complexity of the planar shapes. The degree of complexity of a polygon is characterized by the fractal dimension (D), such that the perimeter (P) of a patch is related to the area (A) of the same patch by $P \approx \sqrt{A}^D$ (i.e., $\log P \approx \frac{1}{2} D \log A$). For simple Euclidean shapes (e.g., circles and rectangles), $P \approx \sqrt{A}$ and $D = 1$ (the dimension of a line). As the polygons become more complex, the perimeter becomes increasingly plane-filling and $P \approx A$ with $D \rightarrow 2$. Although fractal analysis typically has not been used to characterize individual patches in landscape ecological research, I use this relationship to calculate the fractal dimension of each patch separately (FRACT).

Fractal analysis usually is applied to the entire landscape mosaic using the perimeter-area relationship $A = k\ P^{2/D}$, where k is a constant (Burrough 1986). If sufficient data are available, the slope of the line obtained by regressing log(P) on log(A) is equal to 2/D (Burrough 1986). Note, fractal dimension using this perimeter-area method is equal to 2 divided by the slope; D is not equal to the slope (Krummel et al. 1987) nor is it equal to 2 times the slope (e.g., O'Neill et al. 1988, Gustafson and Parker 1992) as reported by some authors. I refer to this index as the double log fractal dimension (DLFD) in FRAGSTATS. Because this index employs regression analysis, it is subject to spurious results when sample sizes are small. In landscapes with only a few patches, it is not unusual to get values that greatly exceed the theoretical limits of DLFD. Thus, this index is probably only useful if sample sizes are large (e.g., $n > 20$). If insufficient data area available, an alternative to the regression approach is to calculate the mean patch fractal dimension (MPFD) based on the fractal dimension of each patch (FRACT). This index may be particularly meaningful if the focus of the analysis is on patch characteristics; that is, when patch-level phenomena are deemed most important and patch shape is particularly meaningful.

Because the method used to calculate these fractal indices involves perimeter-area calculations, these fractal indices are subject to some of the same limitations as the previous shape indices discussed above. Perhaps the greatest limitation of the fractal indices is the difficulty in conceptualizing fractal dimension. Even though fractal dimension is increasingly being used in landscape ecological research, it remains an abstract concept to many.

Core Area Metrics

FRAGSTATS computes several statistics based on core area at the patch, class, and landscape levels (Table 3.1). Core area is defined as the area within a patch or patches greater than some specified edge distance or buffer width. These core area metrics help to quantify both landscape composition and landscape pattern. Most of the indices dealing with number or density of patches, size of patches, and variability in patch size have corresponding core area-based indices computed in the same manner after eliminating the edge or buffer from all patches. Like patch shape, the primary significance of core area in determining the nature of patches in a landscape appears to be related to the "edge effect." As discussed previously, "edge effects" result from a combination of biotic and abiotic factors that alter environmental conditions along patch edges compared to patch interiors. The nature of the edge effect differs among organisms and ecological processes (Hansen and Castri 1992). For example, some bird species are adversely affected by predation, competition, brood parasitism, and perhaps other factors along forest edges (see discussion of edge metrics for citations). Core area has been found to be a much better predictor of habitat quality than patch area for these forest interior specialists (Temple 1986). Unlike patch area, core area is affected by patch shape. Thus, while a patch may be large enough to support a given species, it still may not contain enough suitable core area to support the species.

For ecological processes or organisms adversely affected by edge, it seems likely that core area would better characterize a patch than total area. In addition, it seems likely that edge effects would vary in relation to the type and nature of the edge (e.g., the degree of floristic and structural contrast and orientation). Unfortunately, in most cases, there is insufficient empirical support (or none) for designating separate edge widths for each unique edge type. An educated guess may be better than no guess at all. FRAGSTATS allows the user to specify separate edge distances for each unique edge type. When it is too difficult to estimate unique edge widths for each edge type, a single edge width for all edge types may still be better than none at all.

Patch area (AREA), class area (CA), total landscape area (TA), and landscape similarity (LSIM) all have counterparts computed after eliminating edge area defined by the specified edge widths; these are core area (CORE) at the patch level, total core area (TCA) at the class and landscape levels, and landscape core area similarity (LCAS) at the patch and class levels. The landscape core area similarity index quantifies the core area in each patch type as a percentage of total landscape area. For organisms strongly associated with patch interiors, LCAS provides a better index of habitat availability than its counterpart LSIM. In contrast to their counterparts, these core area indices integrate into a single measure the effects of patch area, patch shape, and edge effect distance. Therefore, although in absolute terms they quantify landscape composition, they are affected by landscape pattern. For this reason, these metrics at the class level may be useful in the study of habitat fragmentation, because fragmentation effects both habitat area and pattern. On the other hand, these indices confound the effects of habitat area and pattern. For example, a small landscape core area similarity index indicates that very little core area is available, but it does not discriminate between a small amount of the patch type (area effect) and a large amount of the patch type in a highly fragmented state (pattern effect). Thus, like many indices that summarize more than 1 feature (e.g., diversity indices), these indices are best interpreted in conjunction with other indices to provide a more complete description of landscape structure.

From an organism-centered perspective, a single patch may actually contain several patches of suitable interior habitat, and it may be more appropriate to consider disjunct core areas as separate patches. For this reason, FRAGSTATS computes the number of disjunct core areas in each patch (NCORE), as well as the number in each class and the landscape as a whole (NCA). If core area is deemed more important than total area, then these indices may be more applicable than their counterparts, but they are subject to the same limitations as their counterpart with respect to not being standardized to a per unit area basis. Thus, although these metrics are not particularly useful in most cases, they are used to compute other landscape metrics based on core area.

Number of core areas can be reported on a per unit area basis (core area density, CAD) that has the same ecological applicability as its counterpart (patch density, PD), except that all edge habitat (as defined by the specified edge widths) is eliminated from consideration. Similarly, the number of core areas is represented as a function of total core area in the mean core area index (MCA). Like their counterparts, note the difference between core area density and mean core area at the class level. Specifically, core area density is based on total 'landscape' area; whereas, mean core area is based on total 'core' area for the class. In contrast, at the landscape level, they are both based on total landscape area and are therefore completely redundant. Furthermore, mean core area, as I have defined it, represents the mean amount of core area per patch, not the mean area per individual core area. Thus, patches with no core area are included in the average, and the total core area in a patch (CORE) is considered together as 1 observation, regardless of whether the core area is contiguous or divided into 2 or more disjunct areas within the patch. The mean size of individual core areas is not included in FRAGSTATS. The distinction between these 2 ways of defining mean core area should be noted.

FRAGSTATS also computes several relative core area indices that quantify core area as a percentage of total area. The core area index at the patch level (CAI) quantifies the percentage of the patch that is comprised of core area. Similarly, the total core area index (TCAI) at the class and landscape levels quantifies core area for the entire class or landscape as a percentage of total class or landscape area, respectively. At the class and landscape levels, FRAGSTATS also computes the mean core area index (MCAI) and area-weighted mean core area index (AWMCAI) of patches comprising the class or landscape. The latter index weights patches according to their size. Thus, larger patches are weighted more heavily than smaller patches in calculating the average core area index for the class or landscape. This index may be more appropriate than the simple mean core area index in cases where larger patches play a dominant role in the landscape function relative to the phenomenon under consideration, similar to the area-weighted mean edge contrast and shape indices.

Note that these core area indices are basically edge-to-interior ratios like the shape indices discussed previously, the main difference being that the core area indices treat edge as an area of varying width and not as a line (perimeter) around each patch. In addition, these core area indices are relative measures; they are not affected by patch size, class area, or total landscape area. These indices quantify the percentage of available area, regardless of whether it is 10 ha or 1,000 ha, comprised of core. They do not confound area and pattern like the previous core area indices; rather, they isolate the pattern effect. For this reason, these core area indices are probably best interpreted in conjunction with total area at the corresponding scale. In conjunction with total class area (CA), for example, the core area index (MCAI, AWMCAI, or TCAI) for a particular class could serve as an effective fragmentation index.

Variation in core area size may convey more useful information than mean core area. Like variation in patch size, FRAGSTATS computes corresponding measures of variability among patches in core area size. Core area standard deviation (CASD) and core area coefficient of variation (CACV) have the same ecological applicability as patch size standard deviation (PSSD) and patch size coefficient of variation (PSCV), except that all edge habitat (as defined by the specified edge widths) is eliminated from consideration. In contrast to their counterparts, these core area metrics reflect the interaction of patch size and shape and edge width, and therefore may serve as better heterogeneity indices when edge width can be meaningfully specified and edge effects are of particular interest. Standard deviation can be difficult to interpret without doing so in conjunction with other statistics (e.g., mean patch size or mean core area). For this reason, core area coefficient of variation usually is preferable to core area standard deviation. Also, note that core area standard deviation and coefficient of variation can equal 0 under 3 conditions: (1) when there is only 1 core area in the landscape; (2) when there is more than 1 core area greater than 0 in size, but they are all the same size; and (3) when there is more than 1 patch, but none have any core area (CORE=0). In all 3 cases, there is no variability in core area size, yet the ecological interpretations could be quite different.

All of the core area indices are affected by the interaction of patch size, patch shape, and the specified edge widths. In particular, increasing edge widths will decrease core area, and vice versa. Therefore, these indices are meaningful only if the specified edge widths are relevant and meaningful to the phenomenon under investigation. Unfortunately, in many cases there is no empirical basis for specifying specific edge widths and they must be chosen somewhat arbitrarily. The usefulness of these metrics is directly related to the arbitrariness in the specified edge widths and this should be clearly when using these metrics. Moreover, the utility of core area indices compared to their area-based counterparts depends on the resolution, minimum patch dimensions, and edge widths employed. For example, given a landscape with a resolution of 1 m^2 and minimum patch dimensions of 100 x 100 m; if an edge width of 1 m is specified, then the core area indices and their counterparts will be nearly identical and the core area indices will be relatively insensitive to changes in patch size and shape. In this case, core area indices will offer little in terms of unique characterization of landscape structure.

Nearest-Neighbor Metrics

FRAGSTATS computes a few statistics based on nearest-neighbor distance at the patch, class, and landscape levels (Table 3.1). Nearest-neighbor distance is defined as the distance from a patch to the nearest neighboring patch of the same type, based on edge-to-edge distance. Nearest-neighbor metrics help to quantify landscape pattern. Nearest-neighbor distance can influence a number of important ecological processes. For example, there has been a proliferation of mathematical models on population dynamics and species interactions in spatially subdivided populations (Kareiva 1990), and results suggest that the dynamics of local plant and animal populations in a patch are influenced by their proximity to other subpopulations of the same or competing species. Several authors have claimed, for example, that patch isolation is a causal factor for why fragmented habitats often contain fewer bird species than contiguous habitats (Moore and Hooper 1975, Forman et al. 1976, Helliwell 1976, Whitcomb et al. 1981, Hayden et al. 1985, Dickman 1987). Opdam (1991) reviewed a number of studies that empirically demonstrated an isolation effect on bird communities in various habitat patches. Interpatch distance plays a critical role in island biogeographic theory (MacArthur and Wilson 1967) and metapopulation theory (Levins 1970, Gilpin and Hanski 1991) and has been discussed in the context of conservation biology (e.g., Burkey 1989). The role of interpatch distance in metapopulations has had a preeminent role in recent conservation efforts for endangered species (e.g., Lamberson et al. 1992, McKelvey et al. 1992). Clearly, nearest-neighbor distance can be an important characteristic of the landscape depending on the phenomenon under investigation.

FRAGSTATS computes the nearest-neighbor distance for each patch (NEAR). At the class and landscape levels, FRAGSTATS computes the mean nearest-neighbor (MNN) distance for patches comprising the class or for all patches in the landscape. Mean nearest-neighbor distance can only be computed for a class if there are at least 2 patches. At the landscape level, mean nearest-neighbor distance considers only patches that have neighbors. Thus, there could be 10 patches in the landscape, but 8 of them might belong to separate patch types and therefore have no neighbor within the landscape. In this case, mean nearest-neighbor distance would be based on the distance between the remaining 2 patches of the same type. These 2 patches could be close together or far apart. In either case, the mean nearest-neighbor distance for this landscape would not necessarily characterize the entire landscape very well. For this reason, this index should be interpreted carefully when landscapes contain rare patch types.

Mean nearest-neighbor distance is a first-order statistic and may not be meaningful if the distribution is complex. Variability in nearest-neighbor distance measures a key aspect of landscape heterogeneity that is not captured by mean nearest-neighbor distance. Nearest-neighbor standard deviation (NNSD) is a measure of patch dispersion; a small standard deviation implies a fairly uniform or regular distribution of patches across landscapes, whereas a large standard deviation implies a more irregular or uneven distribution of patches. The degree of regularity in the distribution of patches may reflect underlying natural processes or human-caused disturbance patterns. In absolute terms, the magnitude of nearest-neighbor standard deviation is a function of the mean nearest-neighbor distance (MNN) and variation in nearest-neighbor distance (NEAR) among patches. Thus, while the standard deviation does convey information about nearest neighbor variability, it is a difficult parameter to interpret without doing so in conjunction with the mean nearest-neighbor distance. For example, 2 landscapes may have the same nearest-neighbor standard deviation, e.g., 100 m; yet 1 landscape may have a mean nearest-neighbor distance of 100 m, while the other may have a mean nearest-neighbor distance of 1,000 m. In this case, the interpretations of landscape structure would be very different, even though the absolute variation is the same. Specifically, the former landscape has a more irregular but concentrated pattern of patches, while the latter has a more regular but dispersed pattern of patches. In addition, standard deviation assumes a normal distribution about the mean. In a real landscape, nearest-neighbor distribution may be highly irregular. In this case, it may be more informative to inspect the actual distribution itself, rather than relying on summary statistics such as standard deviation that make assumptions about the distribution and therefore can be misleading.

Coefficient of variation often is preferable to standard deviation for comparing variability among landscapes. Nearest-neighbor coefficient of variation (NNCV) measures relative variability about the mean (i.e., variability as a percentage of the mean), not absolute variability. Thus, it is not necessary to know the mean nearest-neighbor distance to interpret this metric. Even so, nearest-neighbor coefficient of variation can be misleading with regards to landscape structure without also knowing the number of patches or patch density and other structural characteristics. For example, 2 landscapes may have the same nearest-neighbor coefficient of variation, e.g., 100%; yet 1 landscape may have 100 patches with a mean nearest-neighbor distance of 100 m, while the other may have 10 patches with a mean nearest-neighbor distance of 1,000 m. In this case, the interpretations of overall landscape structure could be very different, even though nearest-neighbor coefficient of variation is the same; although the identical coefficients of variation values indicate that both landscapes have the same regularity or uniformity in patch distribution.

FRAGSTATS rasterizes vector images to compute nearest-neighbor distance because of limitations in Arc/Info. During the rasterization process, depending on the cell size selected, it is possible for polygons to merge and divide. When this happens, there is no longer 1-to-1 correspondence between polygons on the vector image and polygons on the raster image. As a result, the nearest-neighbor information computed for the raster polygons cannot be merged with the vector image and FRAGSTATS reports 'N/A' for these metrics. If nearest-neighbor information is critical, then there are at least 2 options. First, the entire image can be rasterized first and FRAGSTATS run on the raster image. Second, the offending polygons can be modified so that they do not merge or divide during the rasterization process.

The most important limitation of these nearest-neighbor indices is that nearest-neighbor distances are computed from patches contained within the landscape boundary. If the landscape extent is small relative to scale of the organism or ecological processes under consideration and the landscape is an "open" system relative to that organism or process, then nearest-neighbor results can be misleading. For example, consider a small subpopulation of a bird species occupying a patch near the boundary of a somewhat arbitrarily (from a bird's perspective) defined landscape. The nearest neighbor within the landscape boundary may be quite far away, yet in reality the closest patch might be very close, but just outside the boundary. The magnitude of this problem is a function of scale. Increasing the size of the landscape relative to the scale at which the organism under investigation perceives and responds to the environment will decrease the severity of this problem. Although this issue of scale is a critical consideration for all landscape metrics, it is particularly problematic for nearest-neighbor indices.

Diversity Metrics

FRAGSTATS computes several statistics that quantify diversity at the landscape level (Table 3.1). These metrics help to quantify landscape composition. Diversity measures have been used extensively in a variety of ecological applications. They originally gained popularity as measures of plant and animal species diversity. There has been a proliferation of diversity indices and I will make no attempt to review them here. FRAGSTATS computes 3 diversity indices. These diversity measures are influenced by 2 components--richness and evenness. Richness refers to the number of patch types present; evenness refers to the distribution of area or abundance among types. Richness and evenness are generally referred to as the compositional and structural components of diversity, respectively. Some indices, like the Shannon Index, are more sensitive to richness than evenness. Thus, rare types have a disproportionately large influence on the magnitude of the index. Other indices, like the Simpson's Index, are relatively less sensitive to richness and thus place more weight on the common species. These diversity indices have been applied by landscape ecologists to measure 1 aspect of landscape structure--landscape composition (e.g., Romme 1982, O'Neill et al. 1988, Turner 1990a).

The most popular diversity index is the Shannon and Weaver (1949) diversity index based on information theory (SHDI). The magnitude of SHDI represents the amount of "information" per individual (or patch, in this case). Information is a somewhat abstract mathematical concept that I will not attempt to define. The absolute magnitude of SHDI is not particularly meaningful; therefore, SHDI is used as a relative index for comparing landscapes or the same landscape at different times. Simpson's diversity index (1949) is another popular diversity measure (SIDI); it is not based on information theory. Simpson's index is less sensitive to the presence of rare types than SHDI and has an interpretation that is much more intuitive than Shannon's index. Specifically, the value of SIDI represents the probability that any types selected at random would be different types. Thus, the higher the SIDI the greater the likelihood that any 2 randomly drawn patches would be different patch types (i.e., greater diversity). Because Simpson's index is a probability, it can be interpreted in both absolute and relative terms. FRAGSTATS also computes Pielou's (1975) modification of Simpson's (1949) diversity index; this index was used by Romme (1982). The modification eliminates the intuitive interpretation of Simpson's index as a probability, but transforms the index into one that belongs to a general class of diversity indices to which Shannon's diversity index belongs (Pielou 1975). Thus, the modified Simpson's and Shannon's diversity indices are similar in many respects and have the same applicability.

The use of diversity measures in community ecology has been heavily criticized because diversity convey's no information on the actual species composition of a community. Species diversity is a community summary measure that does not take into account the uniqueness or potential ecological, social, or economical importance of individual species. A community may have high species diversity yet be comprised largely of common or undesirable species. Conversely, a community may have low species diversity yet be comprised of especially unique, rare, or highly desired species. Although these criticisms have not been discussed explicitly with regards to the landscape ecological application of diversity measures, these criticisms are equally valid when diversity measures are applied to patch types instead of species. In addition, these diversity indices combine richness and evenness components into a single measure, even though it is usually more informative to evaluate richness and evenness independently.

Patch richness measures the number of patch types present; it is not affected by the relative abundance of each patch type or the spatial arrangement of patches. Therefore, 2 landscapes may have very different structure yet have the same richness. For example, 1 landscape may be comprised of 96% patch type A and 1% each of patch types B-E, whereas another landscape may be comprised of 20% each of patch types A-E. Although, patch richness would be the same, the functioning of these landscapes and the structure of the animal and plant communities would likely be greatly different. Because richness does not account for the relative abundance of each patch type, rare patch types and common patch types contribute equally to richness. Nevertheless, patch richness is a key element of landscape structure because the variety of landscape elements present in a landscape can have an important influence on a variety of ecological processes. Because many organisms are associated with a single patch type, patch richness usually may correlate well with species richness (McGarigal and McComb, unpubl. data).

Richness is generally a function of scale. Larger areas are generally richer because there is generally greater heterogeneity over larger areas than over comparable smaller areas. This contributes to the species-area relationship predicted by island biogeographic theory (MacArthur and Wilson 1967). Therefore, comparing richness among landscapes that vary in size can be problematic. Patch richness density (PRD) standardizes richness to a per area basis that facilitates comparison among landscapes, although it does not correct for this problem of scale. FRAGSTATS also computes a relative richness index. Relative patch richness (RPR) is similar to patch richness, but it represents richness as a percentage of the maximum potential richness (Romme 1982). This form may have more interpretive value than absolute richness or richness density in some applications. Note that relative patch richness and patch richness are completely redundant and would not be used simultaneously in any subsequent statistical analysis.

Evenness measures the other aspect of landscape composition--the distribution of area among patch types. There are numerous ways to quantify evenness and most diversity indices have a corresponding evenness index derived from them. In addition, evenness can be express as its compliment--dominance (i.e., evenness = 1 - dominance). Indeed, dominance has often been the chosen form in landscape ecological investigations (e.g., O'Neill et al. 1988, Turner et al. 1989, Turner 1990a), although I prefer evenness because larger values imply greater landscape diversity. FRAGSTATS computes 3 evenness indices (SHEI, SIEI, MSIEI), corresponding to the 3 diversity indices. Each evenness index isolates the evenness component of diversity by controlling for the contribution of richness to the diversity index. Evenness is expressed as the observed level of diversity divided by the maximum diversity for a given patch richness. Maximum diversity for any level of richness is based on an equal distribution among patch types. Therefore, the observed diversity divided by the maximum diversity (i.e., equal distribution) for a given number of patch types represents the proportional reduction in the diversity index attributed to lack of perfect evenness. As the evenness index approaches 1, the observed diversity approaches perfect evenness.

Because evenness is represented as a proportion of maximum evenness, Shannon's evenness index does not suffer from the limitation of Shannon's diversity index with respect to interpretability. Nevertheless, it is important to note that evenness, like richness and diversity, does not convey any information about which patch types are most or least abundant which may be of more ecological significance.

Contagion Metrics

FRAGSTATS computes 2 contagion indices for the class and landscape levels; although 1 index applies only to the landscape level (Table 3.1). These metrics help to quantify landscape pattern. A contagion index was proposed first by O'Neill et al. (1988) and subsequently it has been widely used (Turner and Ruscher 1988, Turner 1989, Turner et al. 1989, Turner 1990a and b, Graham et al. 1991, Gustafson and Parker 1992). Li and Reynolds (1993) showed that the original formula was incorrect; they introduced 2 forms of an alternative contagion index that corrects this error and has improved performance. Both contagion indices are designed for raster images in which each pixel is individually evaluated for adjacency, and like-adjacencies (cells not on a patch perimeter) are considered. Moreover, both indices have been applied at the landscape level to measure landscape structure. According to the previous authors, contagion measures the extent to which landscape elements (patch types) are aggregated or clumped; higher values of contagion may result from landscapes with a few large, contiguous patches, whereas lower values generally characterize landscapes with many small patches.

I present a new contagion index (CONTAG1) that is compatible with both vector and raster images. Unlike the previous indices that are based on raster "cell" adjacencies, CONTAG1 is based on "patch" adjacencies. Each patch is evaluated for adjacency with all other patch types; like adjacencies are not possible because a patch can never be adjacent to a patch of the same type. For raster images, internal cells are ignored; only the patch perimeters are considered in determining the total length of each unique edge type. Because this index is a measure of "patch" adjacency and not "cell" adjacency, the interpretation is somewhat different than the earlier contagion indices. My contagion index measures patch type adjacency or juxtaposition relative to a given number of patch types; it is not directly affected by the number, size, contiguity, or dispersion of patches as are the earlier indices. Consequently, a landscape containing 4 large, contiguous patches of patch types and a landscape of the same extent containing 100 small patches of 4 patch types will have the same value of CONTAG1 if the patch types are equally adjacent (based on the proportion total edge length in each edge type) to each other. In addition, I apply my contagion index at both the class level and landscape level. At the class level, CONTAG1 measures the juxtapositioning of a focal patch type with all others. At the landscape level, CONTAG1 measures the juxtapositioning of all patch types. At the class level, CONTAG1 is not directly affected by the dispersion of the focal patch type; the focal patch type can be aggregated in 1 portion of the landscape or maximally dispersed and CONTAG1 will be the same if the proportion of total edge length involving the focal patch and each other patch type is the same. In contrast to the original contagion index O'Neill et al. (1988), and like the alternative contagion index of Li and Reynolds (1993), my index represents the observed level of contagion (or juxtaposition) as a percentage of the maximum possible given the total number of patch types. Although CONTAG1 is really a measure of interspersion and juxtaposition of patch types, I continue to use the term "contagion" in order to be consistent with the growing number of published applications using the earlier contagion index.

FRAGSTATS computes a second contagion index at the landscape level (CONTAG2). This contagion index was proposed by Li and Reynolds (1993) for raster images in which each cell is individually evaluated for adjacency, and like adjacencies (cells not on a patch perimeter) are considered. This index is applicable to raster images only and measures raster "cell" adjacencies, not "patch" adjacencies. This contagion index consists of the sum, over patch types, of the product of 2 probabilities: (1) the probability that a randomly chosen pixel belongs to patch type i (estimated by the proportional abundance of patch type i), and (2) the conditional probability that given a pixel is of patch type i, one of its neighboring pixels belongs to patch type j (estimated by the proportional abundance of patch type i adjacencies involving patch type j). The product of these probabilities equals the probability that 2 randomly chosen adjacent pixels belong to patch type i and j. This contagion index is appealing because of the straightforward and intuitive interpretation of this probability. According to the previous authors, CONTAG2 measures the extent to which landscape elements (patch types) are aggregated or clumped; higher values of contagion may result from landscapes with a few large, contiguous patches, whereas lower values generally characterize landscapes with many small patches. CONTAG2 measures dispersion as much as patch type adjacency because pixels, not patches, are evaluated for adjacency. Landscapes consisting of large, contiguous patches have a majority of internal cells with like adjacencies. In this case, contagion is low because the proportion of total pixel adjacencies comprised of like adjacencies is very large and distribution of adjacencies among edge types is very uneven. Like CONTAG1, CONTAG2 also represents the observed level of contagion as a percentage of the maximum possible given the total number of patch types.

This second contagion index is strongly affected by the grain size or resolution of the image. Given a particular patch mosaic, a smaller grain size will result in lower contagion because of the proportional increase in like adjacencies from internal cells. This scale effect should be carefully considered when attempting to compare results from different studies. In addition, it is important to note the differences between CONTAG1 and CONTAG2. CONTAG1 is affected by patch type juxtaposition and not necessarily by the size, contiguity, or dispersion of patches as is CONTAG2. Moreover, CONTAG1 measures "patch" juxtapositioning, not raster "cell" adjacency like CONTAG2. These differences should be kept in mind when attempting to compare the results of CONTAG1 with published accounts using the earlier contagion indices (CONTAG2).

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CHAPTER 4

RELATIONSHIP BETWEEN HABITAT AREA AND PATTERN AND BREEDING BIRDS IN THE OREGON COAST RANGE

INTRODUCTION

Landscapes are characterized by spatial heterogeneity at a variety of scales (Forman and Godron 1986). Habitats are distributed heterogeneously within landscapes and the spatial patterns supposedly exert a strong influence on the abundance, distribution, and dynamics of vertebrate populations inhabiting those landscapes (Wiens 1976, 1989a,b). Habitat subdivision, in particular, can lead to population subdivision and the creation of a metapopulation structure, which can affect population stability or persistence (Gilpin and Hanski 1991). Habitat subdivision also can alter the stability of species interactions and opportunities for coexistence in both predator-prey and competitive systems (Kareiva 1990). Habitat patterning and habitat fragmentation affect populations by altering movement patterns of individuals, intra- and interspecific interactions among individuals, and exposure to factors associated with the juxtapositioning of habitats (e.g., edge effects). This conceptualization of populations in spatially heterogeneous environments is embodied in the field of landscape ecology (Forman and Godron 1986, Urban et al. 1987, Turner 1989) and stems from a variety of sources, including island biogeography (MacArthur and Wilson 1967), metapopulation theory (Gilpin and Hanski 1991), patch dynamic theory (Pickett and White 1985), a vast and complex array of mathematical models on dispersal and spatially distributed populations (Kareiva 1990), and field studies on habitat fragmentation (Saunders et al. 1991).

However, the idea that landscape pattern (i.e., the spatial distribution of habitats) plays an important role in the regulation of populations has not been rigorously challenged empirically (Kareiva 1990, Wiens 1992). The basis for this conceptual framework is almost entirely theoretical. There are few observational studies (e.g., Pokki 1981, Jennersten 1988, Quinn and Harrison 1988, Solbreck and Sillen-Tullberg 1990) and even fewer experimental studies (e.g., Hanski 1987, Quinn and Robinson 1987, Kareiva 1987, Quinn et al. 1989, Crist et al. 1992, Kadmon 1993) that demonstrate population responses to habitat patterning at the landscape scale. Moreover, these empirical studies have focussed largely on plants and invertebrates in artificial laboratory systems or in small natural systems; it is unclear whether these empirical findings extend to vertebrates or to the large and spatially complex landscapes in which many vertebrates live. I am aware of few studies on vertebrates (e.g., Wiens and Rotenberry 1985, Wiens et al. 1986 and 1987).

This conceptual model is supported, in part, from field studies on forest fragmentation (Saunders et al. 1991). Studies primarily from the eastern deciduous forest of North America indicate that vertebrate species associated with forest interiors generally decline while those specializing on forest edges increase in abundance in response to forest fragmentation caused by agricultural development and urbanization (Whitcomb et al. 1981, Robbins et al. 1989, Terborgh 1989). Changes in vegetation, food resources (e.g., invertebrates), predation, brood parasitism, and competition have been suggested as possible causes of the observed vertebrate declines (Strelke and Dickson 1980, Kroodsma 1982, Brittingham and Temple 1983, Wilcove 1985, Noss 1988, Yahner and Scott 1988). However, the process of forest fragmentation is not limited to urbanization and agricultural expansion; commercial timber management is the major cause of forest fragmentation in several regions of North America, including the Pacific Northwest (PNW)(Lehmkuhl and Ruggiero 1991). It is unclear whether the empirical findings on forest fragmentation from urban and agricultural landscapes extend to the spatially and temporally dynamic forest landscapes of the PNW. Furthermore, almost all of the studies on fragmentation have employed a patch-centered sampling scheme in which independent patches, not landscapes, were sampled (e.g., Rosenberg and Raphael 1986, Lehmkuhl et al. 1991).

Based on the derived relationship between species richness or abundance and a variety of 'patch' characteristics, such as patch size and isolation, inferences often were made about how 'landscape' structure effects wildlife populations. It is unclear whether relationships derived at the patch level can be extrapolated to the landscape level (Wiens 1989a,b, Wiens et al. 1993).

Finally, although landscape ecology has provided a strong conceptual basis for considering how populations may function in spatially heterogeneous landscapes, it has not provided a corresponding level of empirical evidence to support this theoretical framework (Wiens 1992). Landscape ecology is largely founded on the notion that the patterning of landscape elements (patches) strongly influences ecological processes and vertebrate populations. The ability to quantify landscape structure is prerequisite to the study of landscape function and change. For this reason, much emphasis has been placed on developing methods to quantify landscape structure (e.g., O'Neill et al. 1988, Li 1990, Turner 1990, Turner and Gardner 1991). Unfortunately, while a number of investigators have quantified landscape structure (in terms of composition and pattern) in a variety of natural and human-altered systems (e.g., Krummel et al 1987, Turner and Ruscher 1988, Gustafson and Parker 1992), few have quantified the relationship between this structure and ecological processes.

I investigated the relationship between landscape structure and breeding bird abundance in the central Oregon Coast Range. This study was designed as part of a broader research program. The ultimate goal of this research program is to determine how changes in landscape structure (both composition and pattern) affect bird populations in the spatially and temporally dynamic forest landscape of the Oregon Coast Range, with the aim of providing land managers information on the likely consequences to bird populations of their landscape management decisions. To accomplish this goal, we must identify and understand the ecological processes (e.g., competition, predation, dispersal, etc.) acting upon individuals and populations that are affected by landscape structure (e.g. habitat area, edge effects, insularity, etc.). However, as described above, it is unclear whether existing theories apply to the spatially and temporally dynamic forest landscape in the Oregon Coast Range. To test specific process hypotheses in this unstudied system would be premature. I chose to initiate this research program with a comparative mensurative experiment (Hurlbert 1984) designed to explore patterns in the relationship between landscape structure and bird populations. Specifically, I quantified the relationship between habitat area and habitat pattern and the abundances of several species associated with selected habitats in subbasins representing landscape structural gradients. This paper represents the first of several exploratory analyses on multiscale bird-habitat associations in this system that in combination will provide the observational foundation from which to select and test specific process hypotheses.

STUDY AREA

The study was conducted in the central Oregon Coast Range in Lobster Creek basin and immediate vicinity (latitude 44° 11' to 44° 22'; longitude 123° 31' to 123° 52'), Drift Creek basin (latitude 44° 24' to 44° 34'; longitude 123° 44' to 123° 58'), and Nestucca River basins (latitude 45° 8' to 45° 22'; longitude 123° 27' to 123° 58'). Drift Creek and Lobster Creek basins are located predominantly in Lincoln and Benton Counties and drain into the Alsea River east of the Pacific Ocean near Waldport, Oregon. Nestucca River is located predominantly in Tillamook County and drains directly into the Pacific Ocean near Pacific City. Elevation ranges from sea level to 968 m. Climate is Pacific Northwest Maritime and is characterized by mild, wet winters (Oct-Jun) and cool, dry summers (Jul-Sep). Annual precipitation ranges from 150 to 300 cm and occurs primarily during the winter months in the form of rain with some snow at high elevations; temperatures during January and July average 2.4 and 16.6 C, respectively (Franklin and Dyrness 1973:71-72).

The study area is characterized by steep slopes and deeply-cut drainages. The area is almost entirely forested and lies almost exclusively within the western hemlock (Tsuga heterophylla) vegetation zone (Franklin and Dyrness 1973:70-108). The natural forest overstory is dominated by Douglas-fir (Pseudotsuga menziesii), western hemlock, and red alder (Alnus rubra); western redcedar (Thuja plicata) and bigleaf maple (Acer macrophyllum) also are common. Understory vegetation is variable in composition and patchy in distribution; common species include salmonberry (Rubus spectabilis), vine maple (Acer circinatum), salal (Gaultheria shallon), Oregon grapes (Berberis spp.), huckleberries (Vaccinium spp.), and swordfern (Polystichum munitum). Franklin and Dyrness (1973:70-108) provide a more complete description of the vegetation.

The entire area experienced a catastrophic, stand-replacement fire in the mid-1800's and regenerated naturally. Over the past 40 years federal land managers have used the dispersed-patch or staggered-setting system of clearcutting which maximizes fragmentation of the late-seral forest (Franklin and Forman 1987); 10- to 20-ha patch cuts are interspersed with uncut forest areas of at least equal size (Smith 1986). As a result, the area currently possesses a bimodal age distribution. Mid-aged (40-100 years) and older (> 140 years) forest is poorly represented in the study area. For the purpose of this study, I defined late-seral forest as large sawtimber (> 20% overstory cover comprised of trees with a mean dbh > 53.3 cm, predominantly 120-140 years old); remnant old-growth (>20% overstory cover comprised of trees with a mean dbh > 81.3 cm and multistory canopy, predominantly > 200 years old) trees and patches are scattered irregularly throughout the late-seral forest. Late-seral and large sawtimber are used interchangeably hereafter (see Appendix E for a definition of patch types). The study area contains a mixture of public and private lands (primarily industrial forestland), but is dominated by public lands administered by the Forest Service and Bureau of Land Management. In portions of the study area dominated by private ownership, the landscape consists largely of extensive, young (0-40 years), even-aged, Douglas-fir plantations; although some portions contain fragmented stands of late-seral forest. In portions of the Coast Range dominated by public ownership, the landscape consists of a matrix of late-seral, unmanaged forest dominated by Douglas-fir and red alder embedded with numerous small (8-25 ha), young, even-aged, Douglas-fir plantations. Consequently, a wide range of landscape structural conditions exist within the study area, particularly with respect to the amount and distribution of late-seral forest.

METHODS

Study Design

I selected 10 subbasins in each of 3 basins (i.e., 3 replicates, $\underline{n} = 30$ subbasins) based on the proportion of subbasin in a late-seral condition and the spatial distribution pattern (i.e., relative fragmentation) of late-seral forest within the subbasin (Fig. 4.1). This 2-dimensional design ensured that I sampled a wide range of landscape structural conditions with respect to late-seral forest. Moreover, this design allowed me to separate the potentially confounding effects of habitat area and habitat pattern on the bird community. I sampled 1 basin (block) each year between 1990-1992. Consequently, year and basin (replicates) were confounded. To estimate the potential significance of this confounding, I resampled a selection of late-seral forest patches in Drift Creek each year (see below).

I defined subbasins as 250- to 300-ha, third- or fourth-order watersheds. Subbasins of this size represented a compromise between landscape size and sample size. From a functional perspective, larger landscapes would have been more appropriate to the organisms under investigation; but because of a number of constraints (e.g., time and money), I only would have been able to sample a few landscapes and the analysis would have been limited to a case study. I chose the largest landscape size that still provided sufficient sample size for multivariate analyses. I chose subbasins as the means for initially delineating landscapes because much of the land managment planning in the study area is conducted on a watershed basis. Initial selection of subbasins was

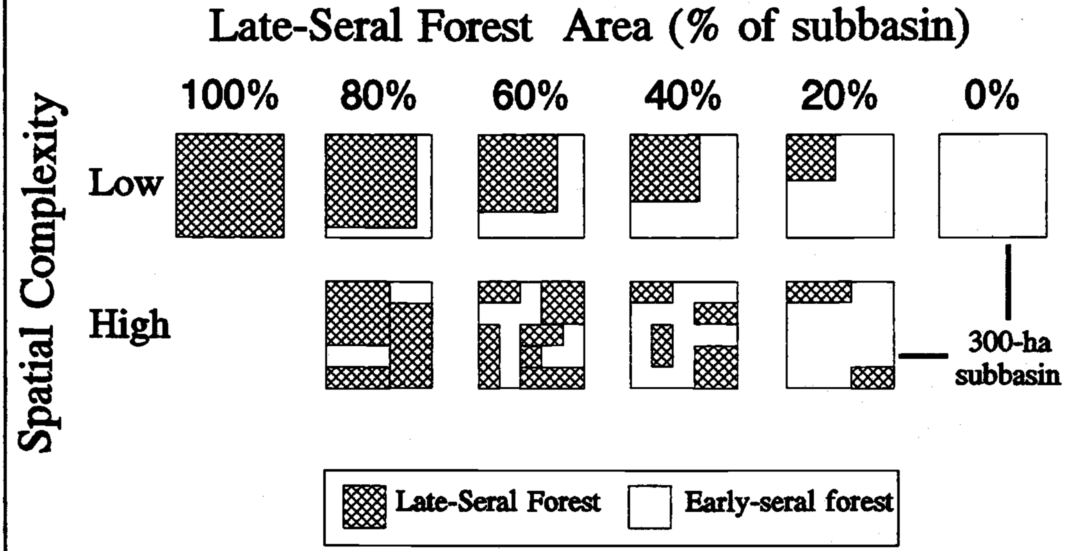


Figure 4.1. Schematic of study design, representing 1 of 3 replicates, with each replicate in a separate basin.

based on measurements of late-seral forest area and density of edge involving late-seral forest (as an index of spatial heterogeneity) from aerial photos (1988 and 1989 Color Infrared, 1:20,000). Priority was given to choosing subbasins that were of the proper extent (250-300 ha) and contained the necessary amount and distribution of late-seral forest (Fig. 4.1). However, because many subbasins did not meet these study design requirements, I usually (21 of 30 subbasins) delineated portions of subbasins or combined portions of more than 1 watershed into landscapes for my purposes. In addition, it is important to note that I did not take a random sample of landscapes from the study area. Rather, I subjectively selected landscapes to represent gradients in late-seral forest area and pattern (Fig. 4.1). Thus, although I gained power to evaluate the effects of habitat area and pattern on bird abundance, I forfeited some ability to directly characterize the entire study area on the basis of the empirical findings.

Bird Sampling

I systematically sampled each subbasin for diurnal breeding birds using a grid layout of sampling points and standard point count methodology for breeding birds. Specifically, I systematically located sample points in a uniform, grid-like fashion at 200-m intervals along transects spaced 400-m apart in each subbasin. I located the first transect and sample point randomly in each subbasin. Based on an assumed effective bird detection distance of 50 m, each sample point corresponded to an effective survey area of 0.785 ha, and the 200- x 400-m grid provided approximately a 10% sample of the subbasin area. At this sampling intensity, 32-38 sample points per subbasin were required, depending on subbasin size, for a total of 1,046 sampling points. Because most species had greater effective detection distances (Appendix D), sampling intensity was actually much greater for most species (Fig. 4.2). As a simple estimate of effective detection distance, for each species I calculated the distance at which ≥ 75% of all detections were made. Given this estimate of effective detection distance, the graph in figure 4.2 can be used to determine the approximate sampling intensity for each species.

I sampled diurnal breeding birds in the Drift Creek, Lobster Creek, and Nestucca River subbasins in 1990, 1991, and 1992, respectively. During each year, I sampled diurnal birds in each of the 10 subbasins 4 times at nearly regular intervals between 1 May and 12 July. Samples were spaced evenly throughout this period to account for differences in breeding phenologies among bird species. I varied the order in which sampling points within a subbasin were visited so that each point was surveyed at different times during the morning. Surveys were not conducted under conditions of dense, low-lying and widespread fog, winds exceeding 15 km/h, or rain heavier than a light drizzle. During each sample, observers visited all sampling points within the

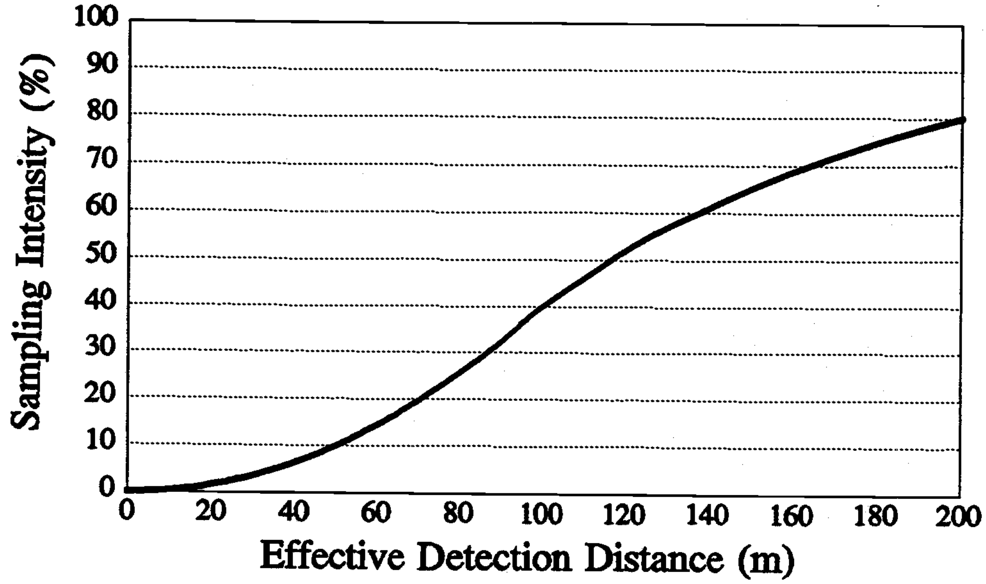


Figure 4.2. Relationship between effective bird detection distance and sampling intensity (% of landscape area sampled). The relationship is curvilinear because a circular effective detection area was assumed (i.e., area does not increase linearly with increasing radius) and because effective detection areas overlap when effective detection distance increases beyond 100 m, given the 200- x 400- m grid-like spacing of sample points.

subbasin on the same day. Surveys began 15-20 minutes before sunrise and ended within 4 hours after sunrise. On each visit to a sample point, the observer waited 2 minutes to allow birds to resume normal activity and then recorded all birds detected (90.2% aurally, 1.0% visually, 8.8% both aurally and visually) at any distance during an 8-minute sampling period. Whenever possible (71.6% of total detections), observers noted the distance between bird and sample point when a bird was first detected. Although the same bird often was heard at more than 1 station along a transect, observers noted for each detection whether the individual was a new or repeat detection. Only new detections during the sample of a subbasin were included in the analysis. My goal was to accurately estimate relative bird abundance at the subbasin level; therefore, subbasins were considered the independent observations for purposes of analysis.

Visits were made by 4 observers in 1990 and 1992 and 3 observers in 1991; 2 observers were the same during all 3 years and 3 others were involved for 1 or 2 years each. During each year, each observer's effort was distributed equally among sample points over the 4 visits to eliminate any systematic observer bias. However, in 1991 because there were only 3 observers, yet 4 visits, each observer visited some sampling points twice. I attempted to minimize observer variability by subjecting observers to a 3-4 week training period prior to the start of each breeding season.

Vegetation Mapping

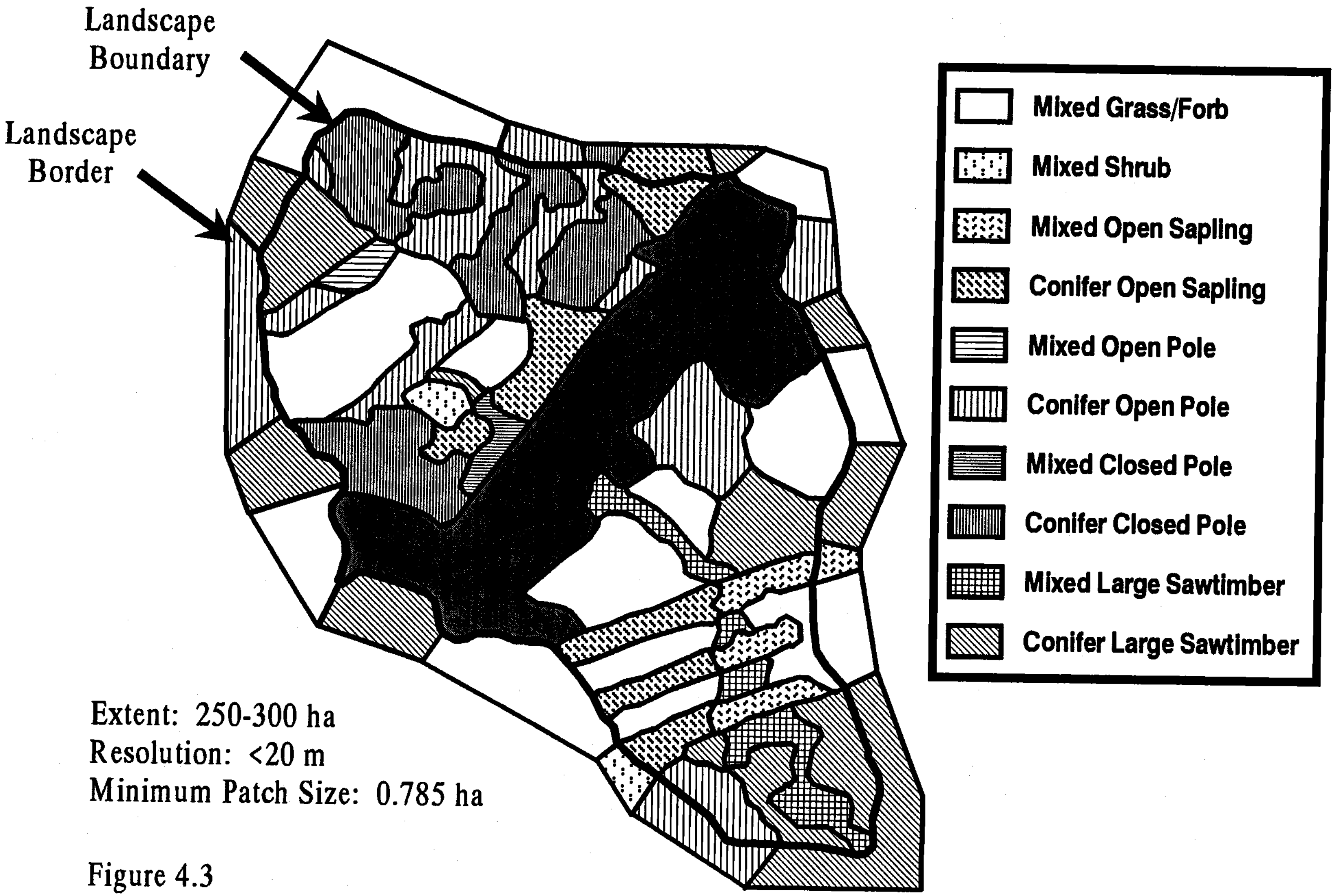
I modified an existing vegetation classification scheme developed and widely used in western Oregon and Washington for wildlife-habitat relationships (Hall et al. 1985). I defined 27 patch types (see Appendix E for complete definitions), including 5 nonforested patch types and 22 forested patch types; the latter varied on the basis of plant community (conifer, hardwood, mixed), seral condition (grass/forb, shrub, sapling, pole, small sawtimber, large sawtimber), and canopy closure (open, closed). These patch types correspond to broad habitat types that are widely recognized to be meaningful to a wide variety of wildlife in western Oregon and Washington (Bruce et al. 1985). I defined minimum patch size as 0.785 ha and ≥50 m wide in the narrowest dimension. This minimum area corresponds to a 50-m radius circle and minimum effective bird survey area surrounding each sampling point, and also roughly to the smallest estimated home range size of any bird species found in the study area (Brown 1985). The minimum width represents a somewhat arbitrary decision based on a practical consideration to avoid mapping the numerous narrow stringers of discrete vegetation along small streams and roads. The implications of this choice of minimum patch size is discussed below under Scope and limitations.

Initially, I mapped vegetation patches in each subbasin on aerial photos (1988-1989 color infrared, 1:20,000) using a stereoscope and then verified or remapped 100 percent of each subbasin in the field. Vegetation cover maps of each subbasin were then transformed into digital coverages using a second-order analytical stereoplotter (Carto AP190) with 6-power magnification binocular attachments (Fig. 4.3). With these aerial photos, the analytical stereoplotter offered a potential resolution of < 1 m; although, given the error in interpreting the exact location of "fuzzy" patch boundaries, I assumed a maximum resolution of 20 m.

Data Analysis

Bird Abundance Patterns.--For each species, I calculated an index of abundance for each subbasin to serve as the dependent variable in the analyses of bird-habitat relationships described below. Specifically, I calculated the average number of bird detections per visit per station (sampling point within subbasin) for each species, including detections of new individuals (males and females) at any distance from the station. I included detections of birds flying through or over the stand (5.2% of total detections) as well because I felt that these birds were probably using habitat within the subbasin; excluding these detections did not change the results. The larger the effective detection area for a species (Appendix D), the more closely this index represents an estimate of actual population size because of the corresponding increase in sampling intensity (Fig. 4.2). I did not attempt to estimate numbers of breeding pairs. Furthermore, I did not adjust for potential differences in detection distances among patch types because birds were detected in more than 1 patch type from most stations, and it would have been impossible to adjust estimates for those stations. However, I felt confident that detectabilities within 50 m of the station did not vary among patch types. Thus, I also calculated the average

Figure 4.3. Landscape patch mosaic for the Fan Creek subbasin in Nestucca River basin, Tillamook County, Oregon, 1992.



Extent: 250-300 ha
Resolution: <20 m
Minimum Patch Size: 0.785 ha

Figure 4.3

number of bird detections per visit per area, including only detections within 50 m of the station. Preliminary analyses indicated that both abundance indices produced similar results, so I report only the results of analyses based on detections at any distance.

To evaluate potential annual changes in the abundance of bird species associated with late-seral forest patches, I resampled a portion (referred to as sites) of 3 subbasins in the Drift Creek basin each year during the 3-year study. I selected well-separated subbasins to better assess basin-level or more regional-level changes in the abundance of species associated with late-seral forest. The 3 sites represented different locations within the late-seral forest matrix present in this portion of the study area and represented a range of plant community conditions from conifer-dominated to hardwood-dominated. At each site, I resampled 12 consecutive stations along transects within contiguous late-seral forest. The transects were designed to sample patch interiors, although 1 station at each of 2 sites was approximately 50 m from young forest edge. I calculated an index of abundance for each species and site (as described above) for species with ≥ 30 total detections across sites and years and analyzed the data using 2-way Analysis of Variance (ANOVA) with site as a block (3 years, 3 sites, $\underline{n} = 9$). I used the overall error term to test the year effect which, in this case, was equivalent to the site-by-year interaction term. This procedure controlled for differences among sites and, in effect, was similar to a repeated measures ANOVA (T. Sabin, pers. commun.). The index of abundance for each species served as the dependent variable in separate ANOVA's. Based on an analysis of the residuals, I log-transformed all dependent variables; although, means and standard errors are reported in original units. Mean separation tests were conducted using the conservative Bonferroni method.

In my study design, basin served as a complete block because the 10 subbasins within a basin were geographically separated from the other 2 basins, and all 10 landscape structural conditions were represented within each basin. Blocking factors cannot be tested in ANOVA, yet I wished to assess the potential difference in bird abundances among the 3 geographic areas (basins). Therefore, I selected a portion of 3 subbasins in each basin comparable in plant community composition and other aspects to the resurvey sites in Drift Creek basin. At each site, I selected 12 consecutive stations along transects within the contiguous late-seral forest matrix. I calculated an index of abundance for each species and site (as described above) for species with ≥30 total detections within a basin and analyzed the data using 1-way ANOVA (3 basins, $\underline{n} = 9$). The index of abundance for each species served as the dependent variable in separate ANOVA's. Again, I log-transformed all dependent variables and used the Bonferroni mean separation test. Note that the samples from each basin were taken in different years; thus, basin and year are still confounded in this analysis and I cannot conclude among-basin differences from these results alone. Therefore, if the among-basin ANOVA indicated significant differences among basins and the among-year ANOVA within Drift Creek indicated no differences among years, I interpreted this as evidence of among-basin differences in bird abundance. I supported this conclusion by comparing bird abundance between the Drift Creek basin resurvey sites and the selected sites in each of the other 2 basins during the same year. For example, if the among-basin ANOVA indicated that abundance differed between the Nestucca River and Drift Creek basins, I compared abundance at the 3 Nestucca River sites sampled in 1992 with the 3 Drift Creek resurvey sites sampled in the same year.

From these analyses, I hoped to gain an indication of the potential significance of the basin (i.e., replicate) and year confounding. A significant year effect does not necessarily introduce any systematic bias into the analysis because all landscape structural conditions were sampled each year; however, it does increase experimental error and therefore reduce the power to detect area and/or pattern effects. In addition, I hoped to gain some indication of the appropriateness of treating all 30 subbasins as independent observations in the correlational analyses described below. A significant year and/or basin effect indicates some level of autocorrelation in the data set that would violate the assumptions of regression analysis.

Vegetation Patterns.--I quantified the landscape structure of each subbasin using the program FRAGSTATS (see Chapter 3). Specifically, I imported the digital vegetation map coverages into the Arc/Info Geographic Information System (GIS) and used FRAGSTATS to calculate the area and pattern of each patch type. FRAGSTATS computes the absolute area of each patch type as well as the percentage of the landscape comprised by each patch type. Because my landscapes were similar in size, these metrics are largely redundant. I used the proportional abundance of each patch type (LSIM) in all analyses.

For each patch type, I used FRAGSTATS to compute 25 indices of pattern that were suitable for these landscapes (Table 4.1); nearest-neighbor and contagion indices were not appropriate given the small extent and limited number of patches contained within these landscapes. The 25 indices quantify different aspects of pattern, although many are redundant and simply represent alternative formulations of the same information (see Chapter 3 for a complete description of each index).

I used FRAGSTATS to compute several core area indices based on a specified edge width. For the purposes of this study, I defined edge as a 100-m-wide buffer along the perimeter of each patch; all edges were treated similarly. Because I had no local empirical basis from which to estimate edge widths for each edge type individually, the 100-m width represents a somewhat arbitrary decision based, in part, on avian studies by Temple (1986) and local studies of microclimatic gradients along forest edges (Chen and Franklin 1990).

I used FRAGSTATS to compute several indices based on edge contrast. Edge contrast is defined using weights that range between 0 and 1, with increasing weights representing greater edge contrast. For the purposes of this study, I defined edge contrast on the basis of floristic and structural differences between adjacent patch types. Specifically, each change in seral condition along the sequence from grass/forb through large sawtimber (Appendix E) received a

Table 4.1. Indices used to quantify the area (1) and spatial pattern (25) of patch types in 30 300-ha subbasins in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92.

Acronym	Index Name (units)	Description[a]
LSIM	Landscape similarity (%)	Percentage of the landscape comprised of the corresponding patch type
LPI	Largest patch index (%)	Percent of total landscape in the largest patch of the corresponding patch type.
NP	Number of patches (#)	Number of patches.
PD	Patch density (#/100 ha)	Density of patches.
MPS	Mean patch size (ha)	Average size of patch.
PSSD	Patch size standard deviation (ha)	Absolute measure of patch size variability.
PSCV	Patch size coefficient of variation (%)	Relative measure of patch size variability.
TE	Total edge (m)	Total length of edge involving the corresponding patch type.
ED	Edge density (m/ha)	Density of edge involving the corresponding patch type.
CWED	Contrast-weighted edge density (m/ha)	Density of edge, weighted by the degree of structural and floristic contrast between adjacent patches, involving the corresponding patch type; equals ED when all edge is maximum contrast and approaches 0 when all edge is minimum contrast
MECI	Mean edge contrast index (%)	Mean patch edge contrast, as a percent of maximum contrast; equals 100% when all edge is maximum contrast and approaches 0 when all edge is minimum contrast.
AWMECI	Area-weighted mean edge contrast index (%)	Similar to mean patch edge contrast, but patch edge contrast weighted by patch area.
TECI	Total edge contrast index (%)	Total edge contrast as a percent of maximum contrast; equals 100% when all edge is maximum contrast and approaches 0 when all edge is minimum contrast.

Table 4.1. Continued.

Acronym	Index Name (units)	Description[a]
MSI	Mean shape index	Mean patch shape complexity; equals 1 when all patches area circular and increases as patches become noncircular.
AWMSI	Area-weighted mean shape index	Similar to mean shape index, but patch shape index weighted by patch area.
LSI	Landscape shape index	Landscape shape complexity; equals 1 when the landscape consists of a single circular patch and increases as landscape shape becomes noncircular and the amount of internal edge increases.
MPFD	Mean patch fractal dimension	Mean patch shape complexity; approaches 1 for simple geometric shapes (e.g., circle) and 2 for complex shapes.
TCA	Total core area (ha)	Total amount of core area of the corresponding patch type; core areas were defined by eliminating a 100-m wide buffer along the perimeter of each patch.
LCAS	Landscape core area similarity (%)	Percent of total landscape comprised of core area (as defined above) of the corresponding patch type.
NCA	Number of core areas (#)	Number of core areas, as defined above.
CAD	Core area density (#/100 ha)	Density of core areas, as defined above.
MCA	Mean core area (ha)	Average size of core area per patch, as defined above.
MCAI	Mean core area index (%)	Average percentage of a patch that is core area, as defined above.
TCAI	Total core area index (%)	Total percentage of the landscape that is core area, as defined above.
CASD	Core area standard deviation (ha)	Absolute measure of core area variability, as defined above.
CACV	Core area coefficient of variation (%)	Relative measure of core area variability, as defined above.

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[a] See Appendix C for a mathematical definition of each index.

weight of 0.2. Thus, a sapling-pole edge received a weight of 0.2; whereas, a sapling-large sawtimber edge received a weight of 0.6. In addition, each change in plant community along the sequence from hardwood to mixed to conifer received a weight of 0.05. Thus, a hardwood-conifer edge received a weight of 0.1; whereas, a hardwood-mixed edge received a weighted of 0.05. Finally, a change from an open- to closed-canopy condition received a weight of 0.05. Grass-forb and shrub conditions were always defined as open-canopy and small and large sawtimber conditions were always defined as closed canopy. Sapling and pole conditions were either open- or closed-canopy. Thus, a change from a closed-pole to a small sawtimber condition received a weight of 0.2 (1 seral condition change); whereas, a change from an open-pole to a small sawtimber condition received a weight of 0.25 (1 seral condition change plus a change from open- to closed-canopy). Nonforest patch types were always considered a full plant community change and open-canopied. Seral condition change among nonforested patch types or between nonforested and forested patch types depended on the height of the dominant vegetation in the nonforest patch type. For example, the brush patch type was considered equivalent in seral condition to the forest shrub types and thus there was no weight attributed to seral condition change between them. The sum of seral condition, plant community, and canopy closure weights determined the overall weight for a particular edge. The decision to weight seral condition differences more than plant community and canopy closure differences was based partly on ecological considerations, but also on differences in the arbitrariness in delineating patch edges. Most seral condition differences represent induced edges (i.e., created through management activities); these edges were very discrete and thus objectively delineated. On the other hand, most plant community and canopy closure differences represent inherent edges (i.e., created through natural processes); these ecotones were usually "fuzzy" and thus difficult to objectively delineate.

As expected, changes in habitat area and pattern were highly confounded in my 30 subbasins. In order to evaluate the independent relationships between habitat area and pattern and bird abundances, I used regression analysis to remove any significant empirical relationship between patch type area (LSIM) and each pattern index (Table 4.1) for each patch type. Specifically, I regressed LSIM on each of the pattern indices using general linear and nonlinear (quadratic polynomials) models. Based on an analysis of the residuals, when necessary, I used appropriate dependent variable transformations ($\log_{10}$ or square root) to ensure that regression assumptions were adequately met. No-intercept models were used for pattern indices that logically must pass through the origin when patch type area is 0. For each patch type, I included only subbasins in which the patch type was present. Thus, sample sizes for the regression analyses varied among patch types ($\underline{n} \geq 25$ for 4 of 5 patch types and $\underline{n} = 13$ for 1 patch type addressed in this paper). I constructed models for each pattern index and patch type separately and selected the logical model exhibiting the largest and most significant R^2 and best residual distribution. The residuals from each model represented the variation in pattern unrelated to, or independent from, changes in habitat area. Thus, using this process, I transformed the 25 original pattern indices computed using FRAGSTATS into 25 new residual pattern indices for each patch type representing gradients in pattern independent of area.

To eliminate redundant indices and summarize the set of 25 residual pattern indices for each patch type into a smaller and more parsimonious set of variables, I used a combination of techniques, including: (1) Pearson product-moment correlations between each pair of indices; (2) multiple correlations between each index and all others; (3) cluster analysis using the Unweighted Pair-Group Average fusion strategy based on Pearson product-moment correlations between each pair of indices; and (4) principal components analysis (PCA). Again, for all techniques, I included only subbasins in which the corresponding patch type was present. I used the first 3 procedures to eliminate redundant variables; cluster analysis was particularly effective in this respect. The choice of an index within a group of redundant indices was based on personal preference and interpretability. I reduced the set of 25 residual pattern indices for each patch type to 5-10 final variables depending on the patch type. The final number of variables, in part, reflected my desire to maintain roughly a 3:1 ratio of observations-to-variables in the PCA. These final variables represented, for each patch type, a set of residual pattern indices that quantified somewhat different aspects of pattern. I used PCA to summarize the 5-10 final residual pattern indices into 2-4 new principal components representing independent gradients in pattern for each patch type. The final 2-4 principal components retained for interpretation were rotated using the Varimax method and were interpreted using the component loadings (i.e., correlations between the principal component and each original variable). I judged the usefulness of the final principal components using the relative percent variance criterion and final communalities for each variable. Relative percent variance represents the percent of variation in the original data set accounted for by each principal component. Final communalities represent the percent of variation in each original variable accounted by the retained principal components.

Bird-Habitat Relationships.--In figure 4.4, I provide a schematic outline of the sequence of procedures employed in the analysis of bird-habitat relationships described below. To determine patch type associations for each bird species, I compared the distribution of detections among patch types to that expected based on the distribution of sampling effort among patch types. I focused on identifying species strongly associated with large sawtimber. First, I compared observed and expected distributions among seral condition classes (grass/forb, shrub, sapling, pole, and large sawtimber); there were not enough small sawtimber patches to include this patch type. I considered all bird detections ≤ 50 m from a station; I excluded detections at greater distances because of the subjectivity in estimating exact bird locations and patch

Figure 4.4. Schematic outline of the sequence of procedures used to assess bird-habitat relationships (see text for details of procedures).

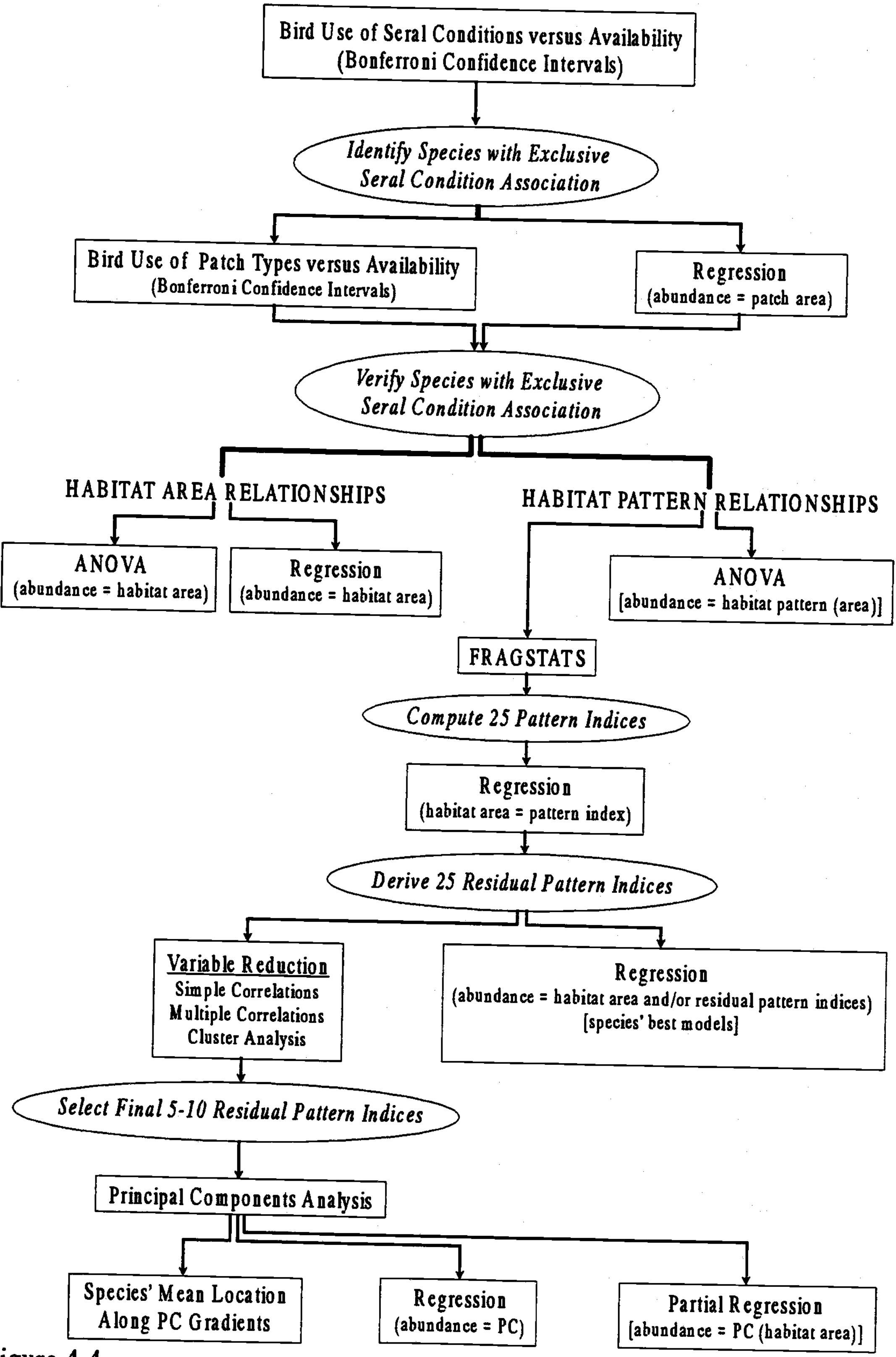
Bird Use of Seral Conditions versus Availability
(Bonferroni Confidence Intervals)
Identify Species with Exclusive Seral Condition Association
Bird Use of Patch Types versus Availability
(Bonferroni Confidence Intervals)
Regression
(abundance = patch area)
Verify Species with Exclusive Seral Condition Association
HABITAT AREA RELATIONSHIPS
HABITAT PATTERN RELATIONSHIPS
ANOVA
(abundance = habitat area)
Regression
(abundance = habitat area)
ANOVA
[abundance = habitat pattern (area)]
FRAGSTATS
Compute 25 Pattern Indices
Regression
(habitat area = pattern index)
Derive 25 Residual Pattern Indices
Variable Reduction
Simple Correlations
Multiple Correlations
Cluster Analysis
Regression
(abundance = habitat area and/or residual pattern indices)
[species' best models]
Select Final 5-10 Residual Pattern Indices
Principal Components Analysis
Species' Mean Location Along PC Gradients
Regression
(abundance = PC)
Partial Regression
[abundance = PC (habitat area)]

Figure 4.4

associations at distances > 50 m. For each detection within 50 m, I recorded the seral condition of the bird's location; birds within 10 m of a seral condition edge were recorded as such (i.e., they were not associated with either patch type). For each species, I summed the number of detections in each seral condition class across all sampling points ($\underline{n} = 1046$) and calculated the proportion in each type, as well as the percentage of total observations in induced edge habitat (i.e., ≤ 10 m from seral condition edge). Note, I did not record each detection to 1 of the 27 specific patch types because I was not confident that all bird observers could consistently differentiate among patch types. However, I was confident that seral conditions could be consistently and objectively differentiated. To determine the expected distribution, I calculated the area of each patch type within a 50-m radius circle around each sampling point. Thus, a sampling point located ≥ 50 m from a patch edge contributed 0.785 ha of the corresponding patch type; whereas, a sampling point located < 50 m from a patch edge contributed area to each patch type proportional to its representation on the plot. I summed the area of each patch type across all sampling points ($\underline{n} = 1046$) and calculated the proportion of the total area sampled (815.17 ha, excluding small sawtimber and nonforested patch types) in each seral condition (by pooling patch types with seral condition class). I did not account for seral condition edges in these area calculations, but this should not bias the proportional abundance of each patch type. Indeed, results were similar when I excluded all sampling points containing a seral condition edge within 50 m.

I compared observed and expected distributions both graphically and objectively using 95% simultaneous Bonferroni Confidence intervals (Neu et al. 1974, Byers and Steinhorst 1984). However, because the individual bird detections used to calculate the observed distribution did not represent independent observations (e.g., the same birds were likely detected on subsequent visits to sample points), the significance tests associated with the confidence intervals are not valid. Thus, I used the confidence intervals as an aid and not to suggest statistical rigor. Adequate expected cell values (> 1) were achieved for species with > 48 total detections, although I evaluated species with as few as 20 detections.

Second, because associations with seral conditions may mask stronger associations with specific plant communities (e.g., conifer-dominated habitats versus hardwood-dominated habitats), I also compared observed and expected distributions among specific patch types. Because bird detections within 50 m were not recorded to specific patch type, for the reasons discussed above, I included only sampling points ≥ 50 m from a patch edge. Thus, each 50-m radius plot consisted of a single patch type and all detections within 50 m could be associated with a specific patch type. Fifty-nine percent (613/1046) of the sampling points representing 12 forested patch types were included in the analysis; the 3 shrub types were combined into a single class and the remaining 8 forested patch types were not adequately sampled. I compared observed and expected distributions as described above. Because I was interested in identifying species exclusively associated with large sawtimber or a specific plant community within large sawtimber, I used this analysis to filter out species that seemed, on first examination, to exclusively select the large sawtimber seral condition, but upon scrutiny actually selected a specific plant community type in both the pole and sawtimber seral conditions; although, the detailed results of this analysis are not included in this paper.

In addition, for species strongly associated with large sawtimber, I regressed LSIM of each patch type (conifer large sawtimber, hardwood large sawtimber, and mixed large sawtimber) on the abundance index for each species separately using general linear and nonlinear (quadratic polynomials) models. I included all 30 subbasins in the analysis, regardless of whether the corresponding patch type was present or absent from the subbasin. I ignored the blocking of subbasins by basin and treated all 30 subbasins as independent observations. All dependent variables were log-transformed to improve the distribution of the residuals and ensure that regression assumptions were adequately met.

From these analyses, I identified several species strongly associated with large sawtimber. For these species, I assessed the effects of habitat area and pattern on abundance using 3-way ANOVA (3 basins by 6 levels of area by 1 or 2 levels of pattern depending on area, $\underline{n} = 30$) with basin as a block and pattern nested within area (see study design). The index of abundance for each species served as the dependent variable in separate ANOVA's. Based on an analysis of the residuals, I log-transformed all dependent variables. Although I arbitrarily categorized both area and pattern variables for purposes of this ANOVA study design (Fig. 4.1), I did this in part to ensure representation of the full range of these inherently continuous gradients in landscape structure. Moreover, the ANOVA design treated pattern as a simple dichotomous variable defined on the basis of edge density (i.e., high or low density), yet I recognized that pattern consists of many aspects. Therefore, I also assessed the relationship between habitat area and pattern and bird abundance using correlational procedures, as follows.

To determine the strength and nature of the relationship between habitat area and bird abundance for each species strongly associated with a single seral condition (e.g., large sawtimber) or specific patch type (e.g., conifer large sawtimber), I used regression analysis. Specifically, I regressed LSIM of the corresponding patch type on the abundance index for each species separately using general linear and nonlinear (quadratic polynomials) models. I included all 30 subbasins in the analysis, regardless of whether the corresponding patch type was present or absent from the subbasin. I ignored the blocking of subbasins by basin and treated all 30 subbasins as independent observations. All dependent variables were log-transformed to improve the distribution of the residuals and ensure that regression assumptions were adequately met. However, the grass/forb patch type was present in only 13 subbasins; thus, the large number of zeros in the independent variable (LSIM) prohibited meeting the assumptions well. The results were similar when only subbasins with non-zero values of the independent variable were included in the analysis.

To determine the strength and nature of the relationship between habitat pattern and bird abundance for each species strongly associated with a single seral condition class or patch type, I used 4 techniques. For all techniques, I included only subbasins in which the corresponding patch type was present and treated those subbasins as independent observations (i.e., I ignored the blocking of subbasins by basin). First, for each species, I calculated its weighted average location along each of the retained corresponding standardized principal components (i.e., each principal component has a mean=0 and standard deviation=1). Specifically, I used the index of abundance to weight each subbasin's standardized principal component score (i.e., location along the standardized gradient). The weighted average location, therefore, represents the species' average association or location along the landscape pattern gradient represented by the principal component. I also constructed a 95% confidence interval (CI) about the mean. If the CI did not include zero (i.e., the average landscape condition), I concluded that the species' was associated with landscape patterns significantly different from the average landscape pattern along the corresponding principal component gradient. It is important to recall that the area effect was removed from the pattern indices. Thus, a species with a location significantly different from the average used landscapes in which the corresponding patch type was distributed more or less heterogeneously (depending on the direction of the difference) than the average distribution pattern, regardless of whether the patch type comprised 20% or 80% of the landscape.

Second, for each species, I determined the relationship between each corresponding principal component and the species' abundance using simple linear regression. Specifically, I regressed the principal component scores for the corresponding patch type on the abundance index for each species and principal component separately using general linear and nonlinear (quadratic polynomials) models. I detected few significant nonlinear relationships; moreover, they were difficult to interpret. Therefore, I report the results of the linear models only.

Third, for each species, I determined the relationship between each corresponding principal component and the species' abundance after accounting for any relationship with habitat area using partial regression analysis. Specifically, I regressed the principal component scores and LSIM for the corresponding patch type on the abundance index for each species and principal component separately. The partial-F statistic and associated partial R^2 for the principal component variable measure the additional explanatory contribution of the pattern gradient after habitat area has been taken into account. Note, even though the empirical relationship between area and pattern was removed from each pattern index separately, the principal component variables were still correlated with habitat area because they represented simple linear combinations of all the original variables. I conducted partial regression analyses only for species with significant habitat area relationships.

Last, for each species, I evaluated the relationship between each species' abundance and a combination of habitat area (LSIM) and individual residual pattern indices using multiple linear regression. Specifically, I used stepwise, maximum R^2, and other variable selection methods to identify the "best" simple or multiple linear regression model. In general, I identified the model with the largest R^2 in which all component variables had significant partial-F statistics.

RESULTS

Bird Abundance Patterns

I detected 82,704 birds representing 89 species during 4 visits to 1,046 sampling stations distributed among the 30 subbasins (see Appendix D for scientific names). Ninety percent (74,427/82,704) of the detections were of new individuals and 35% (28,718/82,704) were detected within 50 m of a station (Appendix D). Forty-five of the species had ≥ 20 detections within 50 m of a station and were therefore suitable for analysis of patch-type associations.

I recorded enough detections (≥ 30) for 11 species strongly associated with large sawtimber (see below) on the 3 resurvey sites in Drift Creek basin to assess among-year and among-basin differences. Only 1 species (winter wren) showed a strong ($\underline{P} = 0.003$) among-year difference in abundance; 2 other species (chestnut-backed chickadee and brown creeper) showed mild ($\underline{P} < 0.098$) differences (Table 4.2). For all 3 species, abundances were lowest the first year of the study and greatest the second year. Nevertheless, for most species there was little indication that abundance in the Drift Creek basin varied significantly among the 3 years of the study.

Five species exhibited a difference in abundance among basins ($\underline{P} < 0.071$, Table 4.3). Winter wren and chestnut-backed chickadee differences corresponded to the among-year differences; that is, abundances were lowest the first year of study in Drift Creek, highest the second year in both Lobster Creek and Drift Creek basins, and intermediate the third year in both Nestucca River and Drift Creek basin. Furthermore, abundances of these 2 species did not differ between Lobster Creek and Drift Creek basins during the second year ($\underline{P} > 0.254$) or between Nestucca River and Drift Creek during the third year ($\underline{P} > 0.166$). These patterns reflect either widespread annual population fluctuations in these 2 species or improvements in observer skill during the second and third years of the study. The 3 remaining species (red-breasted nuthatch, varied thrush, and red crossbill) exhibited geographic differences in abundance that seem to be unrelated to annual population fluctuations or improved observer skill. None of these species showed among-year differences on the resurvey sites (Table 4.2). Red-breasted nuthatch abundance was greater in Drift Creek and Lobster Creek basins than in Nestucca River basin and these geographic differences were supported by the between-basin comparisons within the same year (1991 Drift vs. Lobster, $\underline{P} = 0.698$; 1992

Table 4.2. Effect of year (1990, 1991, 1992) on breeding bird species abundance in Lincoln County, Oregon. Data represent birds detected at any distance during 4 visits/year to 12 consecutive sampling points in large sawtimber in each of 3 subbasins, including only detections of new individuals from separate sampling points within a subbasin during a visit. Only species strongly associated with large sawtimber at the patch level and with ≥ 30 detections are included. Species are listed in order of decreasing significance of the test statistic. Years connected by solid lines were not significantly different (P > 0.05) based on Bonferroni means separation test.

Species[a]	N[b]	F[c]	P	Year	mean[d]	SE
Winter wren	1069	35.50	0.003	1991	35.17	1.50
				1992	31.08	1.34
				*1990	22.83	1.92
Chestnut-backed chickadee	378	5.38	0.074	1991	14.25	2.25
				1992	11.75	0.66
				1990	5.50	1.66
Brown creeper	249	4.40	0.098	1991	8.92	1.42
				1992	6.17	1.12
				1990	5.67	1.94
Red-breasted nuthatch	65	2.60	0.189	1990	2.17	0.46
				1992	2.00	0.29
				1991	1.25	0.63
Pileated woodpecker	41	1.91	0.262	1990	1.50	0.38
				1992	1.25	0.25
				1991	0.67	0.22
Evening grosbeak	362	1.48	0.331	1992	15.50	6.87
				1990	7.92	0.94
				1991	6.75	1.39
Varied thrush	583	0.93	0.466	1991	18.33	2.92
				1992	15.25	2.27
				1990	15.00	0.90
Hammond's flycatcher	181	0.76	0.525	1992	5.67	1.54
				1991	4.83	0.58
				1990	4.58	1.06
Red crossbill	336	0.73	0.536	1992	11.42	4.76
				1990	11.33	4.95
				1991	5.25	3.33
Gray jay	57	0.31	0.750	1991	1.83	0.33
				1992	1.50	0.25
				1990	1.42	0.44

Table 4.2. Continued.

Species[a]	N[b]	F[c]	P	Year	mean[d]	SE
Western tanager	112	0.22	0.811	1992	3.50	1.77
				1990	3.50	2.77
				1991	2.33	1.26

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[a] Scientific names in Appendix D.

[b] N = Total number of detections during 4 visits/year to 3 subbasins (12 sampling points each) over 3 years.

[c] 2-way ANOVA [model: $\log_{10}$(abundance) = subbasin + year] with subbasin as a block; $n = 9$ sample observations; 2,4 degrees of freedom.

[d] Mean number of detections/visit/subbasin ($n = 3$ subbasins).

Drift vs. Nestucca, $P = 0.001$). Varied thrush abundance was greatest in Nestucca River basin, intermediate in Drift Creek basin, and lowest in Lobster Creek basin; although the between-basin comparisons within the same year were consistent with this trend, only the Nestucca River-Drift Creek comparison was mildly significant ($P = 0.076$). Red crossbill abundance patterns were similar to the varied thrush, although the between-basin comparisons were not significant ($P > 0.462$).

Based on these results, the confounding of basin (replicate) and year did not seem to be a problem for most species associated with late-seral forest. Two species (winter wren and chestnut-backed chickadee) may have experienced significant annual population fluctuations during the period of study which, if true, would have increased the experimental error and reduced the statistical power to detect area and/or pattern effects. Three species (red-breasted nuthatch, varied thrush, and red crossbill) demonstrated significant geographic variation in abundance. Therefore, for these species, treating all 30 subbasins as independent observations violates certain assumptions of regression analysis and the significance tests reported below are not strictly valid; I used the test statistics simply as aids in this exploratory analysis and not to suggest statistical rigor.

Table 4.3. Effect of basin (Drift Creek, Lobster Creek, Nestucca River) on breeding bird species abundance in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92. Data represent birds detected at any distance during 4 visits in 1 year to 12 consecutive sampling points in large sawtimber in each of 3 subbasins, including only detections of new individuals from separate sampling points within a subbasin during a visit. Each basin was sampled during a separate year. Only species strongly associated with large sawtimber at the patch level and with ≥ 30 detections are included. Species are listed in order of decreasing significance of the test statistic. Basins connected by solid lines were not significantly different ($P > 0.05$) based on Bonferroni means separation test.

Species[a]	N[b]	F[c]	P	Basin[d]	mean[e]	SE
Red-breasted nuthatch	44	16.25	0.004	D	2.16	0.46
				L	1.42	0.08
				* N	0.08	0.08
Chestnut-backed chickadee	337	8.18	0.019	L	13.50	0.58
				N	9.08	1.46
				D	5.50	1.66
Winter wren	1024	8.08	0.020	L	32.42	1.42
				N	30.08	1.80
				D	22.83	1.92
Varied thrush	594	4.97	0.053	N	21.17	0.74
				D	15.00	0.90
				L	13.33	2.72
Red crossbill	350	4.26	0.071	N	14.83	0.55
				D	11.33	4.95
				L	3.00	0.29
Hammond's flycatcher	149	2.78	0.140	L	6.00	1.01
				D	4.58	1.06
				N	1.83	1.71
Pileated woodpecker	49	2.32	0.180	L	1.92	0.30
				D	1.50	0.38
				N	0.67	0.55
Brown creeper	229	1.43	0.311	L	8.50	1.91
				D	5.67	1.94
				N	4.92	0.58
Western tanager	71	1.04	0.410	D	3.50	2.77
				L	2.17	0.83
				N	0.25	0.14
Evening grosbeak	447	0.95	0.438	L	15.83	3.67
				N	13.35	5.63
				D	7.92	0.94

Table 4.3. Continued.

Species[a]	N[b]	F[c]	P	Basin[d]	mean[e]	SE
Gray jay	60	0.14	0.872	L N D	1.92 1.67 1.42	0.65 0.79 0.44

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[a] Scientific names in Appendix D.

[b] N = Total number of detections during 4 visits to 3 subbasins (12 sampling points each) in each of 3 basins.

[c] 1-way ANOVA [model: $\log_{10}$(abundance) = basin]; n = 9 sample observations; 2,6 degrees of freedom.

[d] D = Drift Creek; L = Lobster Creek; N = Nestucca River.

[e] Mean number of detections/visit/subbasin (n = 3 subbasins).

Vegetation Patterns

Based on the analysis of patch type associations (see below), I focused the analysis of landscape patterns on 5 patch types. I focused primarily on late-seral forest. First, I assessed large sawtimber as a class, ignoring plant community (i.e., conifer, mixed, hardwood) differences, because most bird species associated with late-seral forest (see below) showed strongest associations at this resolution. Second, I assessed conifer large sawtimber and mixed large sawtimber patch types separately because a few bird species exhibited greatest association at this finer resolution. Finally, I assessed pole and grass/forb seral conditions as separate classes for comparative purposes.

By design, landscape structure relative to late-seral forest varied greatly among the 30 subbasins (Table 4.4). Most indices of large sawtimber pattern had coefficients of variation (CV) > 50% (mean = 76%), indicating that gradients in many aspects of pattern were represented in these landscapes. By default, landscape structural gradients relative to other patch types also were well represented, but they were generally shorter, as might be expected because they were not sampled by design. For example, the grass/forb patch type comprised between 0 and 21% of the landscapes; thus, my ability to assess the relationship between habitat area and bird abundance for species associated

Table 4.4. Summary statistics for indices used to quantify area and spatial pattern of 3 patch types (seral condition classes) in 30 300-ha subbasins in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92. Only indices included in the final principal components analysis for at least 1 patch type (Table 4.5) are included.

Patch Type[a] Index[b]	Units	min	max	mean[c]	CV
Large sawtimber					
Landscape similarity	%	0.7	100.0	51.9	56
Patch density	#/100 ha	0.3	2.1	0.6	74
Mean patch size	ha	2.1	281.3	124.6	73
Patch size coefficient of variation	%	0.0	172.0	31.0	174
Mean patch fractal dimension	none	1.19	1.37	1.27	3
Core area density	#/100 ha	0.0	1.7	0.7	65
Core area coefficient of variation	%	0.0	195.4	37.7	171
Mean core area index	%	0.0	76.6	40.7	58
Total core area index	%	0.0	76.6	44.0	48
Landscape core area similarity	%	0.0	76.6	28.0	83
Largest patch index	%	0.7	100.0	49.6	61
Edge density	m/ha	1.1	39.3	19.5	58
Contrast-weighted edge density	m/ha	0.6	25.4	10.8	65
Total edge contrast index	%	2.3	92.6	36.3	51
Pole					
Landscape similarity	%	1.9	93.6	44.4	57
Patch density	#/100 ha	0.3	2.3	0.8	67
Mean patch size	ha	2.5	273.5	83.5	92
Patch size coefficient of variation	%	0.0	139.7	50.0	110
Mean patch fractal dimension	none	1.22	1.36	1.27	3
Core area density	#/100 ha	0.0	2.1	0.8	65

Table 4.4. Continued.

Patch Type[a] Index[b]	Units	min	max	mean[c]	CV
Core area coefficient of variation	%	0.0	189.7	66.6	104
Mean core area index	%	0.0	68.8	32.8	59
Total core area index	%	0.0	68.8	39.9	48
Landscape core area similarity	%	0.0	62.3	21.8	90
Largest patch index	%	1.2	93.6	38.3	73
Edge density	m/ha	8.2	46.4	22.0	47
Contrast-weighted edge density	m/ha	3.2	19.5	8.3	63
Total edge contrast index	%	12.2	40.8	26.7	32
Grass/forb					
Landscape similarity	%	2.0	20.6	9.0	55
Patch density	#/100 ha	0.4	2.8	0.9	74
Mean patch size	ha	2.9	28.7	12.0	58
Patch size coefficient of variation	%	0.0	115.6	43.9	94
Mean patch fractal dimension	none	1.25	1.38	1.27	3
Core area density	#/100 ha	0.0	1.5	0.6	74
Core area coefficient of variation	%	0.0	200.0	92.8	76
Mean core area index	%	0.0	29.2	9.3	84
Total core area index	%	0.0	29.2	11.4	75
Landscape core area similarity	%	0.0	3.3	1.2	85
Largest patch index	%	1.1	11.2	5.9	46
Edge density	m/ha	8.0	37.8	13.6	60
Contrast-weighted edge density	m/ha	4.7	26.0	10.1	56
Total edge contrast index	%	49.5	96.0	72.9	20

[a] See Appendix E for definition of each seral condition class.
[b] See Table 4.1 for description of each index.
[c] Large sawtimber, n = 29 subbasins; pole, n = 25 subbasins; grass/forb, n = 13 subbasins.

with grass/forb conditions was limited to a relatively narrow range along this gradient.

I summarized the final 10 residual pattern indices for large sawtimber (see methods for procedure) into 3 principal components that accounted for 78% of the variation in the original data set (Table 4.5). The first principal component (PC1) captured 33% of the variance and represented a gradient patch shape and edge contrast. Landscapes positively associated with PC1 contained large sawtimber distributed in patches with more complex shapes, greater edge density, less core area, and greater edge contrast than the average landscape for the particular amount of large sawtimber present. The second principal component (PC2) captured an additional 23% of the variance and represented an independent gradient in patch density. Landscapes positively associated with PC2 contained large sawtimber fragmented into more patches than the average landscape for the particular amount of large sawtimber present. The third principal component (PC3) captured an additional 22% of the variance and represented an independent gradient in patch size. Landscapes positively associated with PC3 contained large sawtimber distributed in smaller patches than the average landscape for the particular amount of large sawtimber present. These 3 PC's represent dominant gradients of variation in the pattern of large sawtimber distribution among the 29 subbasins containing large sawtimber; they represent gradients in large sawtimber fragmentation. The gradients defined by the PC's are intuitively appealing because they have a straightforward interpretation. Final communalities (Table 4.5) indicate that most of the residual pattern indices were well accounted for by the 3 PC's; total edge contrast index and patch size variability had ≤ 65% of their variability accounted for. Note, the relative percent variance criterion indicates that landscape pattern cannot be described adequately by a single gradient; each gradient alone accounts for only 20-30% of the variance.

Table 4.5. Principal components derived from a final set of residual pattern indices (i.e., correlation with habitat area has been removed, see text) for large sawtimber habitats in 30 300-ha subbasins in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92.

Patch Type[a]	Principal Components				
Summary Statistics	PC1	PC2	PC3	PC4	Final Commun[b]
Large sawtimber[c]					
Eigenvalue	3.32	2.33	2.18		
% variance	33.2%	23.3%	21.8%		
Cum. % variance	33.2%	56.5%	78.3%		
Component loadings[d]					
TCAI	**-0.855**	-0.162	-0.360		88.7%
MPFD	**0.849**	-0.050	0.045		72.6%
ED	**0.806**	0.343	0.050		77.0%
TECI	**0.756**	-0.124	0.170		61.6%
MCAI	-0.637	-0.458	-0.546		91.5%
PD	-0.036	**0.885**	0.093		79.4%
CAD	0.256	**0.843**	0.008		77.6%
PSCV	-0.115	0.577	0.551		65.0%
MPS	-0.165	-0.285	**-0.843**		82.0%
LPI	-0.359	0.227	**-0.835**		87.7%
Conifer large sawtimber[c]					
Eigenvalue	2.95	2.62	1.80		
% variance	29.5%	26.2%	18.0%		
Cum. % variance	29.5%	55.7%	73.7%		
Component loadings[d]					
PSCV	**0.904**	0.011	0.095		82.7%
ED	**0.811**	0.460	0.006		86.9%
PD	**0.792**	0.026	0.089		63.6%
MPS	-0.627	-0.519	-0.142		68.3%
LCAS	-0.388	**-0.878**	0.098		93.1%
TCAI	-0.124	**-0.854**	0.032		74.6%
MPFD	-0.219	**0.687**	0.334		63.1%
CAD	0.338	0.394	-0.120		28.5%
TECI	-0.071	0.075	**0.947**		90.7%
CWED	0.348	-0.065	**0.855**		85.7%

Table 4.5. Continued.

Patch Type[a]	Principal Components				
Summary Statistics	PC1	PC2	PC3	PC4	Final Commun[b]
Mixed large sawtimber[c]					
Eigenvalue	2.26	2.05	2.04	1.85	
% variance	22.6%	20.5%	20.4%	18.5%	
Cum. % variance	22.6%	43.1%	63.5%	82.0%	
Component loadings[d]					
CWED	**0.950**	0.080	-0.018	0.062	91.3%
TECI	**0.848**	-0.358	0.004	0.063	85.1%
ED	0.095	**0.887**	0.229	0.143	86.9%
TCAI	0.463	**-0.739**	-0.092	0.122	78.4%
PSCV	0.014	0.157	**0.889**	0.230	86.9%
PD	0.154	0.295	**0.791**	0.009	73.7%
CAD	0.422	0.316	**-0.732**	0.057	81.8%
MPS	0.177	-0.123	-0.043	**-0.896**	85.2%
CACV	0.383	-0.056	0.112	**0.749**	72.4%
MPFD	-0.175	0.593	-0.098	-0.622	77.8%
Pole[c]					
Eigenvalue	3.38	3.04	1.63		
% variance	33.8%	30.4%	16.3%		
Cum. % variance	33.8%	64.2%	80.5%		
Component loadings[d]					
PSCV	**0.884**	0.003	0.165		80.9%
PD	**0.817**	0.187	-0.108		71.5%
MPS	**-0.812**	-0.192	-0.285		77.8%
CAD	**0.746**	0.376	-0.259		76.5%
LPI	-0.557	-0.395	-0.163		49.3%
TECI	0.090	**0.940**	-0.165		91.9%
CWED	0.286	**0.931**	0.140		96.7%
ED	0.250	**0.887**	0.295		93.7%
MPFD	-0.059	-0.009	**0.915**		84.1%
TCAI	-0.499	-0.357	**-0.665**		81.8%

Table 4.5. Continued.

Patch Type[a] Summary Statistics	Principal Components PC1	 PC2	 PC3	 PC4	Final Commun[b]
Grass/forb[c]					
Eigenvalue	2.81	1.17			
% variance	56.2%	23.4%			
Cum. % variance	56.2%	79.6%			
Component loadings[d]					
PD	**0.954**	0.003			91.0%
MPFD	**0.845**	-0.267			78.5%
TCAI	**-0.804**	-0.228			69.8%
PSCV	**0.733**	0.377			67.9%
TECI	0.036	**0.952**			90.8%

[a] See Appendix E for definition of each patch type.

[b] Final communalities equal the percent of variation in each variable accounted for by the retained principal components.

[c] Large sawtimber, n = 29 subbasins; conifer large sawtimber, n = 27 subbasins; mixed large sawtimber, n = 27 subbasins; pole, n = 25 subbasins; grass/forb, n = 13 subbasins.

[d] Component loadings equal the correlations between each variable and the principal component; see Table 4.1 for description of each index and appropriate units.

The results of PCA for the conifer and mixed large sawtimber patch types were comparable (Table 4.5). In both cases, the interpretations of the retained PC's are slightly different as judged by the component loadings. Edge contrast was separated out as a distinct and independent gradient for both patch types, indicating that the degree of structural and floristic contrast between conifer and mixed large sawtimber and the surrounding landscape varies strongly among subbasins. The other PC's represent gradients in other aspects of pattern, each representing a gradient in which the corresponding large sawtimber patch type is distributed more or less heterogeneously than the average landscape for the amount of sawtimber present. Otherwise, the performance of PCA for the 2 patch types as judged by the relative percent variance criterion and final communalities was similar to that described above for large sawtimber.

Although I did not intentionally sample a wide range of landscape structural conditions relative to the young forest patch types, the results of PCA for the pole and grass/forb patch types are surprisingly similar to the sawtimber results and are straightforward in interpretation (Table 4.5). Edge contrast was again separated out as a distinct and independent gradient for both young forest patch types, indicating that edge contrast is an important aspect of landscape pattern that may prove useful for discriminating among landscapes. The PC's derived for the 2 young forest patch types are nearly identical to those derived for the conifer large sawtimber type (Table 4.5), except that 2 of the gradients have been combined into 1 for the grass/forb patch type because of the smaller sample size. Otherwise, the performance of PCA for the 2 young forest patch types was similar to that described above for large sawtimber.

Bird-Habitat Relationships

Twelve bird species exhibited strong and exclusive "selection" for large sawtimber based on the analyses of patch type use versus availability (Table 4.6); although all of these species were detected in 2 or more seral conditions. In addition to these 12 species, 3 other less common but widely distributed species (olive-sided flycatcher, red-tailed hawk and western wood-pewee) seemed to be associated with large sawtimber, yet were detected too infrequently within 50 m of a station (< 20 times) to analyze (Appendix D). Nevertheless, the limited detections within 50 m for these species coupled with field observations indicated an association with large sawtimber. Of 540 olive-sided flycatcher detections, only 33 were within 50 m; however, 14 of these detections were within 10 m of a large sawtimber edge, while the remaining 19 were in early-seral, open-canopied patches adjacent to large sawtimber. Likewise, of 131 red-tailed hawk detections, only 14 were within 50 m; however, 9 of these detections were in large sawtimber or within 10 m of large sawtimber

Table 4.6. Distribution of bird detections (observed) and sampling effort (expected) among 5 seral condition classes in 30 300-ha subbasins in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92. Data represent total area in each patch type within 50 m of a sampling point ($\underline{n}$ = 1046 sampling points distributed among 30 subbasins) and birds detected within 50 m of a sampling point during 4 visits to each point, including new and repeat detections of individuals from separate sampling points within a subbasin during a visit. Only species with ≥ 20 detections were analyzed and only species demonstrating exclusive selection for large sawtimber included here. Seral conditions used significantly more or less than expected based on 95% simultaneous Bonferroni confidence intervals are highlighted in bold; although, note that any category with zero observed use is always found to be significantly different than expected. Also, observations were not independent and species with ≤ 48 total detections have at least 1 expected cell value < 1; thus, significance tests should be interpreted cautiously. Species are ordered relative to the strength of their selection for large sawtimber as judged by the magnitude of the standardized residuals.

	Seral Condition[b]					
Species[a]	Grass/Forb	Shrub	Sapling	Pole	Large Saw	Total
Expected distribution						
Area sampled (ha)	34.45	16.92	54.40	297.83	411.58	815.17
Percent	4.23	2.08	6.67	36.54	50.49	100.00
Observed distribution						
Large sawtimber associates						
Brown creeper						
# detections	1	0	1	7	786	795
Percent	0.13	0.00	0.13	0.88	98.87	100.00
Standard residuals[c]	**-5.63**	**-4.07**	**-7.14**	**-16.63**	**+19.20**	
Winter wren						
# detections	6	7	18	830	2297	3158
Percent	0.19	0.22	0.57	26.28	72.74	100.00
Standard residuals	**-11.04**	**-7.24**	**-13.27**	**-9.54**	**+17.59**	
Evening grosbeak						
# detections	1	0	1	22	417	441
Percent	0.23	0.00	0.23	4.99	94.56	100.00
Standard residuals	**-4.09**	**-3.03**	**-5.24**	**-10.96**	**+13.02**	

Table 4.6. Continued.

Species[a]	Seral Condition[b]					Total
	Grass/Forb	Shrub	Sapling	Pole	Large Saw	
Hammond's flycatcher						
# detections	1	0	1	8	320	330
Percent	0.30	0.00	0.30	2.42	96.97	100.00
Standard residuals	**-3.47**	**-2.62**	**-4.48**	**-10.25**	**+11.88**	
Chestnut-backed chickadee						
# detections	9	3	44	572	1386	2014
Percent	0.45	0.15	2.18	28.40	68.82	100.00
Standard residuals	**-8.25**	**-6.01**	**-7.79**	**-6.04**	**+11.58**	
Varied thrush						
# detections	0	0	1	76	420	497
Percent	0.00	0.00	0.20	15.29	84.51	100.00
Standard residuals	**-4.58**	**-3.22**	**-5.58**	**-7.84**	**+10.67**	
Red crossbill						
# detections	0	0	5	48	359	412
Percent	0.00	0.00	1.21	11.65	87.14	100.00
Standard residuals	**-4.17**	**-2.93**	**-4.29**	**-8.36**	**+10.47**	
Gray jay						
# detections	0	0	0	27	157	184
Percent	0.00	0.00	0.00	14.67	85.33	100.00
Standard residuals	**-2.79**	**-1.96**	**-3.50**	**-4.91**	**+6.65**	
Red-breasted nuthatch						
# detections	0	0	0	6	80	86
Percent	0.00	0.00	0.00	6.98	93.02	100.00
Standard residuals	**-1.91**	**-1.34**	**-2.40**	**-4.53**	**+5.55**	
Western tanager						
# detections	1	3	3	11	63	81
Percent	1.23	3.70	3.70	13.58	77.78	100.00
Standard residuals	-1.31	+1.02	-1.03	**-3.42**	**+3.46**	
Red-breasted sapsucker						
# detections	0	0	0	2	18	20
Percent	0.00	0.00	0.00	10.00	90.00	100.00
Standard residuals	**-0.92**	**-0.65**	**-1.15**	**-1.96**	**+2.49**	
Pileated woodpecker						
# detections	0	0	1	2	17	20
Percent	0.00	0.00	5.00	10.00	85.00	100.00
Standard residuals	**-0.92**	**-0.65**	-0.29	**-1.96**	**+2.17**	

Table 4.6. Continued.

	Seral Condition[b]					
Species[a]	Grass/Forb	Shrub	Sapling	Pole	Large Saw	Total
Pole associates						
Hutton's vireo						
# detections	0	3	4	110	14	131
Percent	0.00	2.29	3.05	83.97	10.69	100.00
Standard residuals	**-2.35**	**+0.17**	**-1.60**	**+8.98**	**-6.41**	
Black-throated gray warbler						
# detections	0	0	1	75	19	95
Percent	0.00	0.00	1.05	78.95	20.00	100.00
Standard residuals	**-2.00**	**-1.41**	**-2.12**	**+6.84**	**-4.18**	
Grass/forb associates						
Western bluebird						
# detections	20	1	1	0	0	22
Percent	90.91	4.55	4.55	0.00	0.00	100.00
Standard residuals	**+19.77**	**+0.80**	**-0.39**	**-2.84**	**-3.33**	
Violet-green swallow						
# detections	29	6	0	0	0	35
Percent	82.86	17.14	0.00	0.00	0.00	100.00
Standard residuals	**+22.62**	**+6.17**	**-1.53**	**-3.58**	**-4.20**	

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[a] Scientific names in Appendix D.
[b] See Appendix E for definition of seral conditions.
[c] Standardized residuals = (observed - expected)/$\sqrt{}$expected.

edge, while the remaining 5 were in early-seral patches adjacent to large sawtimber. Likewise, of 154 western wood-pewee detections, only 16 were within 50 m; 6 of these detections were in large sawtimber, while 9 of the remaining 10 were within 10 m of large sawtimber edge. These detections coupled with field observations suggested that these species were associated with the juxtaposition of large sawtimber and open-canopied, early-seral habitats. These 3 species were each present in more than 23 of the 30 subbasins. Therefore, I included these 3 species in all subsequent analyses.

Several additional species seemed to be strongly associated with large sawtimber habitats, but were detected too infrequently (e.g., spotted owl, Vaux's swift, bald eagle) to warrant conclusions regarding habitat associations (Appendix D), or were absent from too many (> 12) subbasins to analyze using ANOVA or regression (downy woodpecker, pine siskin, and ruffed grouse). In addition, 2 species (hermit warbler and Pacific-slope flycatcher) demonstrated exclusive "selection" for large sawtimber, but examination of patch type selection at a finer resolution (i.e., specific patch types) revealed that these species actually selected specific plant communities (hardwood and mixed) in both the pole and large sawtimber seral conditions. Similarly, 2 species (golden-crowned kinglet and hairy woodpecker) exhibited "selection" for large sawtimber, but showed "selection" for other seral conditions as well. These species were excluded from subsequent analyses.

Thus, I identified 15 species that were strongly associated with large sawtimber and sufficiently abundant and widely distributed for subsequent analyses. Variation in abundance among subbasins for 3 of these species was more strongly related to the abundance of a specific patch type than to the abundance of large sawtimber. Pileated woodpeckers and red-breasted nuthatches were more closely related to changes in conifer large sawtimber area and western tanagers were more closely related to changes in mixed large sawtimber. For comparative purposes, I also identified 2 species that were strongly and nearly exclusively associated with each of the pole and grass/forb seral conditions (Table 4.6). Several species were strongly associated with early-seral, open-canopied habitats, but they could not be clearly associated with a single seral condition or patch type as I defined them.

The relationship between large sawtimber area and species' abundances within subbasins varied dramatically among the 15 species clearly associated with large sawtimber, based on the analysis of variance (Table 4.7). Five species were strongly affected by changes in habitat area ($\underline{P} < 0.007$); 5 species were moderately affected ($\underline{P} < 0.092$); 5 species were virtually unaffected ($\underline{P} >$

Table 4.7. Effects of large sawtimber area (0, 20, 40, 60, 80, 100% of subbasin) and large sawtimber pattern (high vs. low fragmentation) on breeding bird species abundance in 30 300-ha subbasins in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92. Data represent birds detected at any distance during 4 visits to 32-38 sampling points within each subbasin, including only detections of new individuals from separate sampling points within a subbasin during a visit. Only species strongly associated with large sawtimber at the patch level are included. Species are listed in order of decreasing significance of the area effect.

	Area[b]		Pattern(Area)[b]	
Species[a]	F	P	F	P
Gray jay	14.24	<0.001	1.05	0.408
Brown creeper	13.40	<0.001	0.96	0.456
Winter wren	8.57	<0.001	1.17	0.357
Varied thrush	7.76	<0.001	0.28	0.888
Chestnut-backed chickadee	4.63	0.007	0.79	0.546
Evening grosbeak	4.14	0.011	0.54	0.708
Hammond's flycatcher	3.24	0.029	0.06	0.993
Pileated woodpecker	2.51	0.068	0.61	0.658
Western wood-pewee	2.42	0.076	3.07	0.043
Red-breasted nuthatch	2.26	0.092	2.02	0.134
Red crossbill	1.60	0.212	0.67	0.622
Red-breasted sapsucker	1.27	0.321	1.23	0.331
Western tanager	1.25	0.330	1.49	0.246
Olive-sided flycatcher	1.16	0.368	3.31	0.034
Red-tailed hawk	0.96	0.470	1.57	0.225

[a] Scientific names in Appendix D.

[b] 3-way ANOVA [model: $\log_{10}$(abundance) = basin + area + pattern(area)] with basin as a block; n = 30 subbasins; area effect 5,18 degrees of freedom; pattern(area) effect 4,18 degrees of freedom.

0.212). The percent of variation in species' abundances that was accounted for by changes in large sawtimber area ranged from 0 to 63% (Table 4.8). Species divided logically into 3 groups based on the strength of this relationship. Roughly 50-60% of the variation among subbasins in gray jay, brown creeper, winter wren, and varied thrush abundance was explained by the abundance of large sawtimber. Only the gray jay had a significantly nonlinear relationship (Fig. 4.5). Roughly 20-30% of the variation in pileated woodpecker, evening grosbeak, red-breasted nuthatch, Hammond's flycatcher, chestnut-backed chickadee, and western tanager abundance was explained by the abundance of large sawtimber. Virtually none of the variation in red crossbill, western woodpewee, olive-sided flycatcher, red-breasted sapsucker, and red-tailed hawk abundance was explained by large sawtimber area. Results were similar for the 2 species associated with each of pole and grass/forb seral conditions, in terms of the strength of the relationship between abundance and habitat area (Table 4.8).

Based on the analysis of variance, only 2 species (olive-sided flycatcher and western woodpewee) were affected by large sawtimber pattern when evaluated as a simple dichotomous variable nested within 4 levels of habitat area (20%, 40%, 60%, and 80% of subbasin area in large sawtimber; Table 4.7). Based on the correlational analyses, however, 8 of 15 species associated with large sawtimber habitats occupied landscape structural conditions that were different from the average landscape condition along the first principal component gradient ($\underline{P} < 0.059$, Figs. 4.6 and 4.7). The nature of the gradient (i.e., the specific aspects of habitat pattern represented) varied among patch types (Table 4.5), but all represented a gradient in landscape structural conditions from a relatively homogeneous distribution of habitat (i.e., less fragmented) to a relatively heterogeneous distribution of habitat (i.e., more fragmented). All 8 species were associated with a more heterogeneous or fragmented distribution of habitat. Abundances of the 4 species (red-breasted sapsucker, western woodpewee, olive-sided flycatcher, and red-tailed hawk)

Table 4.8. Relationship between habitat area and the abundance of breeding bird species associated with several patch types in 30 300-ha subbasins in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92. Data represent birds detected at any distance during 4 visits to 32-38 sampling points within each subbasin, including only detections of new individuals from separate sampling points within a subbasin during a visit. Only species strongly associated with each patch type are included. Species are listed in order of decreasing significance of the area effect by patch type.

Patch Type[a]	Intercept		Area[c]		
Species[b]	b_0	P	b_1	P	R^2
Large sawtimber					
Gray jay[d]	+	0.085	+	<0.001	63%
Brown creeper	+	0.081	+	<0.001	59%
Winter wren	+	<0.001	+	<0.001	53%
Varied thrush	+	<0.001	+	<0.001	52%
Evening grosbeak	+	0.002	+	0.001	31%
Hammond's flycatcher	+	0.075	+	0.003	28%
Chestnut-backed chickadee	+	<0.001	+	0.007	24%
Red crossbill	+	0.014	+	0.387	3%
Western wood-pewee	+	0.016	+	0.588	1%
Olive-sided flycatcher	+	0.026	+	0.904	0%
Red-tailed hawk	+	0.016	+	0.951	0%
Red-breasted sapsucker	+	0.039	+	0.993	0%
Conifer large sawtimber					
Pileated woodpecker	+	<0.001	+	0.001	34%
Red-breasted nuthatch	+	0.006	+	0.002	29%
Mixed large sawtimber					
Western tanager	+	0.003	+	0.019	18%

Table 4.8. Continued.

Patch Type[a] Species[b]	Intercept b_0	Intercept $\underline{P}$	Area[c] b_1	Area[c] $\underline{P}$	R^2
Pole					
Hutton's vireo	+	0.023	+	<0.001	56%
Black-throated gray warbler	+	0.509	+	0.002	29%
Grass/forb					
Western bluebird	+	0.805	+	<0.001	60%
Violet-green swallow[d]	+	0.267	+	<0.001	48%

[a] See Appendix E for definition of each patch type.
[b] Scientific names in Appendix D.
[c] Linear model: $\log_{10}(\text{abundance}) = b_0 + b_1(\text{area})$; $\underline{n} = 30$ subbasins.
[d] Quadratic polynomial model: $\log_{10}(\text{abundance}) = b_0 + b_1(\text{area}) + b_2(\text{area}^2)$; $\underline{n} = 30$ subbasins.

occupying the most heterogeneous landscapes were not related to habitat area ($\underline{P} > 0.588$, Table 4.8). Variation in abundance among subbasins for each of these species was related to variation along this pattern gradient based on simple linear regression analysis, although the percent of variation accounted for was low (R^2, 13-19%; $\underline{P} < 0.050$; Table 4.9). In contrast, abundances of the other 4 species (gray jay, pileated woodpecker, red-breasted nuthatch, and western tanager) associated with fragmented habitat patterns were affected by habitat area ($\underline{P} < 0.019$, Table 4.8), yet variation in abundance among subbasins was not related to variation along this pattern gradient alone ($\underline{P} > 0.131$, Table 4.9). However, variation along this pattern gradient was significant for 3 of these species (gray jay, pileated woodpecker, and western tanager) when habitat area relationships were taken into account first ($\underline{P} < 0.097$, Table 4.10). Thus, habitat area was of predominant importance with respect to this habitat pattern gradient for species with significant habitat area effects.

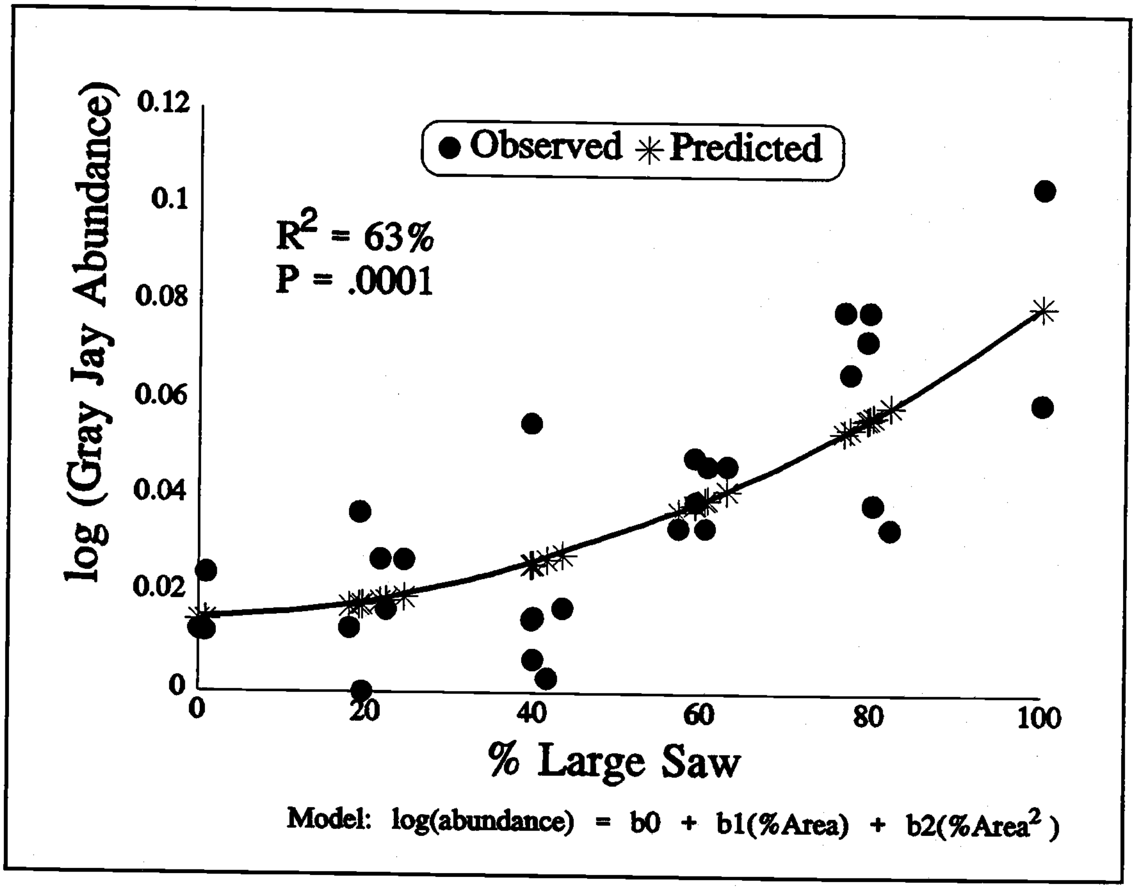

Figure 4.5. Relationship between gray jay abundance and large sawtimber area in 30 300-ha subbasins in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92.

Seven of 15 species associated with large sawtimber habitats occupied landscape structural conditions that were different from the average landscape condition along the second principal component gradient ($\underline{P} < 0.086$, Figs. 4.6 and 4.7). Again, the nature of the gradient varied among patch types (Table 4.5). Four species (western woodpewee, red-tailed hawk, pileated woodpecker, and red-breasted nuthatch) were associated with the more heterogeneous or fragmented distribution of habitat. However, only variation in the pileated woodpecker's abundance among subbasins was related to variation along this pattern gradient either with ($\underline{P} = 0.053$, Table 4.10) or without ($\underline{P} = 0.006$, Table 4.9) first taking habitat area into account, although the percent of variation accounted for was low in both cases (15% and 27%, respectively).

Figure 4.6. Weighted average location (and 95% confidence interval) of bird species strongly associated with large sawtimber along the first 3 principal component gradients representing the spatial pattern of large sawtimber in 29 300-ha subbasins in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92. Data represent birds detected at any distance during 4 visits to 32-38 sampling points within each subbasin, including only detections of new individuals from separate sampling points within a subbasin during a visit. Weighted averages were based on relative abundance in each subbasin. See Appendix D for the scientific names corresponding to bird acronyms, and see Table 4.5 for definition of each principal component (HAFL = Hammond's flycatcher; WIWR = winter wren; VATH = varied thrush; BRCR = brown creeper; EVGR = evening grosbeak; CBCH = chestnut-backed chickadee; GRJA = gray jay; RECR = red crossbill; RTHA = red-tailed hawk; OSFL = olive-sided flycatcher; WWPE = western wood-pewee; RBSA = red-breasted sapsucker).

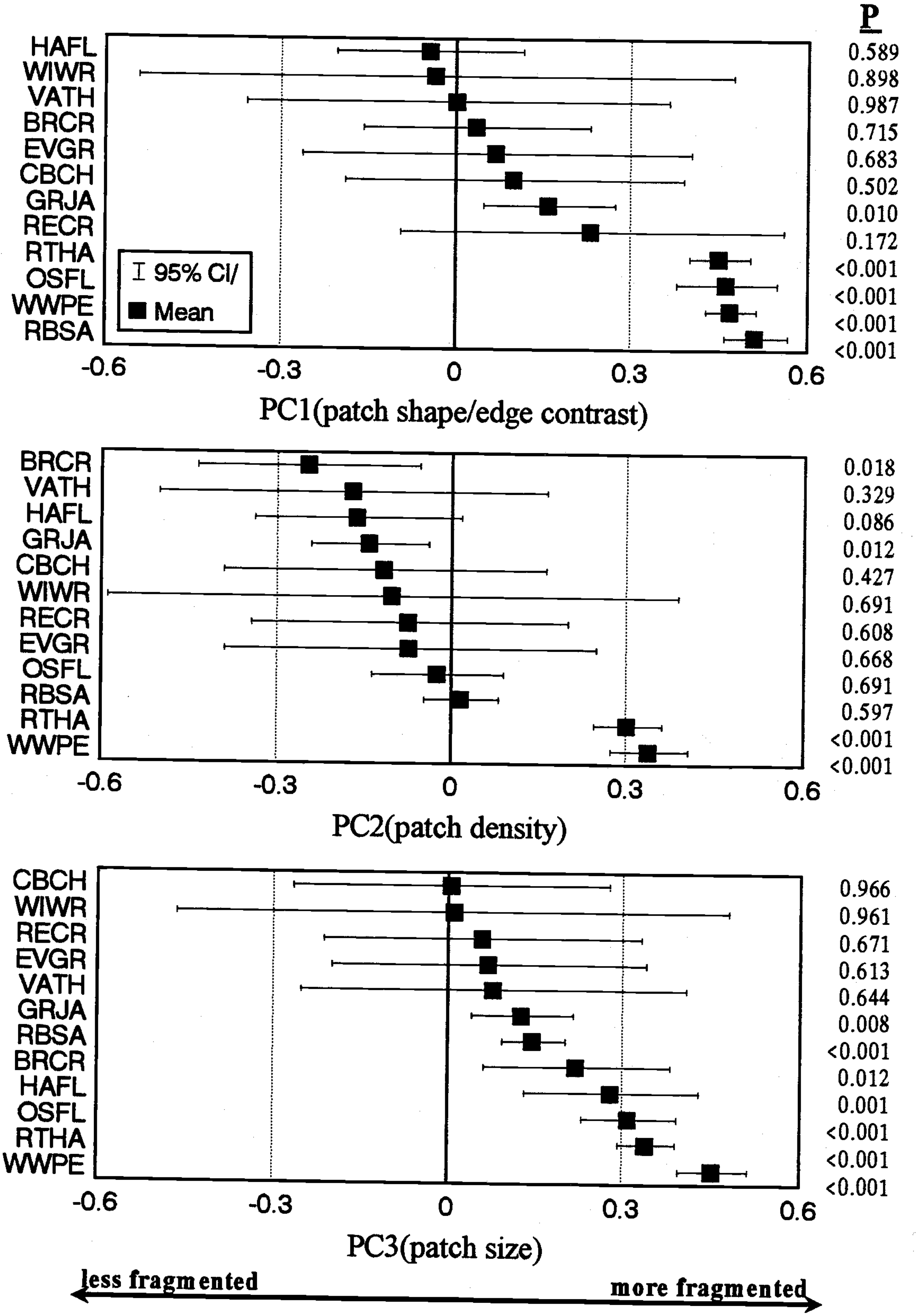
P
HAFL 0.589
WIWR 0.898
VATH 0.987
BRCR 0.715
EVGR 0.683
CBCH 0.502
GRJA 0.010
RECR 0.172
RTHA <0.001
OSFL <0.001
WWPE <0.001
RBSA <0.001
I 95% CI/
■ Mean
-0.6
-0.3
0
0.3
0.6
PC1(patch shape/edge contrast)
BRCR 0.018
VATH 0.329
HAFL 0.086
GRJA 0.012
CBCH 0.427
WIWR 0.691
RECR 0.608
EVGR 0.668
OSFL 0.691
RBSA 0.597
RTHA <0.001
WWPE <0.001
-0.6
-0.3
0
0.3
0.6
PC2(patch density)
CBCH 0.966
WIWR 0.961
RECR 0.671
EVGR 0.613
VATH 0.644
GRJA 0.008
RBSA <0.001
BRCR 0.012
HAFL 0.001
OSFL <0.001
RTHA <0.001
WWPE <0.001
-0.6
-0.3
0
0.3
0.6
PC3(patch size)
less fragmented
more fragmented

Figure 4.6

Figure 4.7. Weighted average location (and 95% confidence interval) of bird species strongly associated with conifer and mixed large sawtimber along the first 3-4 principal component gradients representing the spatial pattern of conifer (top) and mixed (bottom) large sawtimber in 27 300-ha subbasins in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92. Data represent birds detected at any distance during 4 visits to 32-38 sampling points within each subbasin, including only detections of new individuals from separate sampling points within a subbasin during a visit. Weighted averages were based on relative abundance in each subbasin. See Appendix D for the scientific names corresponding to bird acronyms, and see Table 4.5 for definition of each principal component (RBNU = red-breasted nuthatch; PIWO = pileated woodpecker; WETA = western tanager).

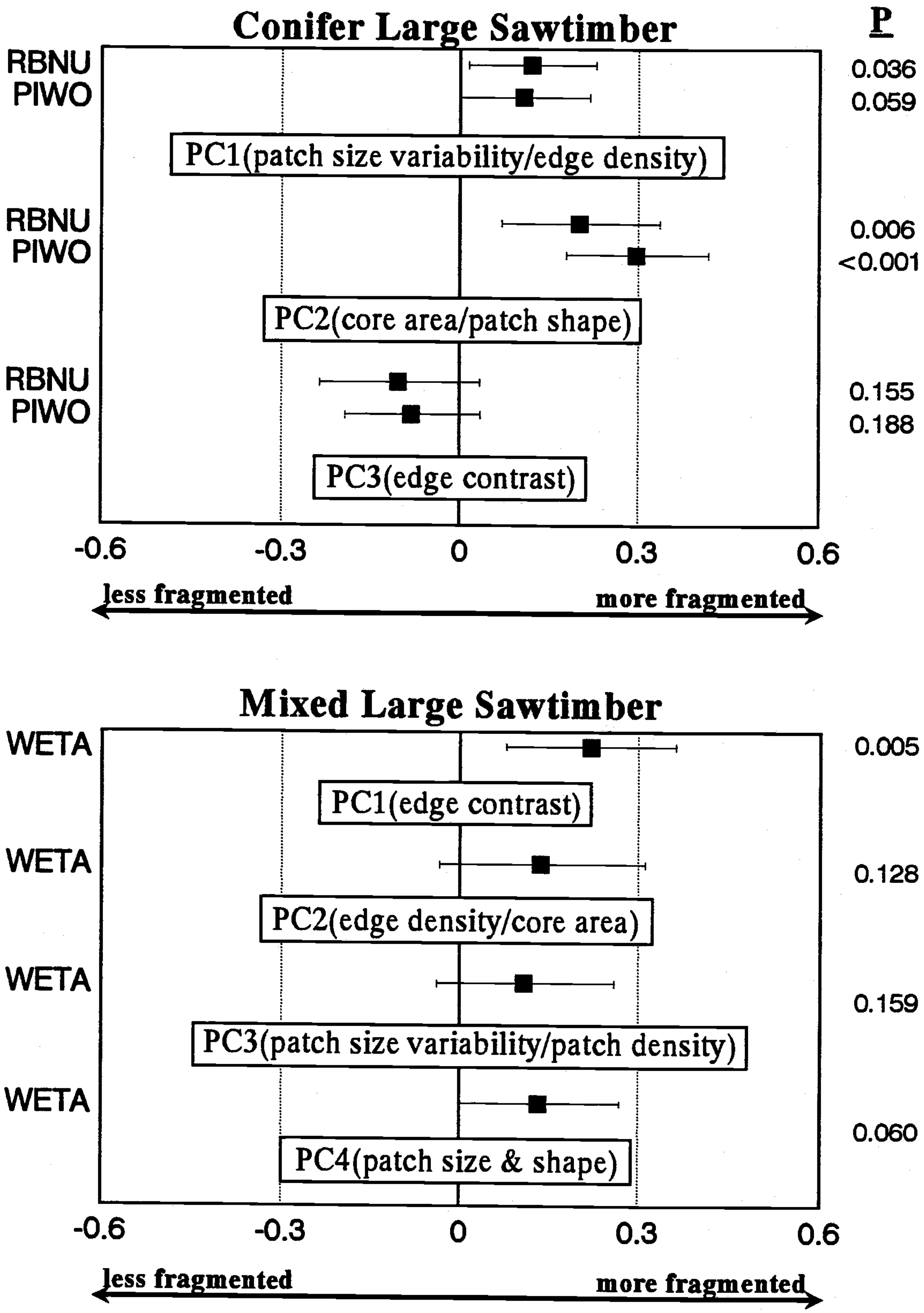
Conifer Large Sawtimber
P
RBNU
PIWO
0.036
0.059
PC1(patch size variability/edge density)
RBNU
PIWO
0.006
<0.001
PC2(core area/patch shape)
RBNU
PIWO
0.155
0.188
PC3(edge contrast)
-0.6
-0.3
0
0.3
0.6
less fragmented
more fragmented
Mixed Large Sawtimber
WETA
0.005
PC1(edge contrast)
WETA
0.128
PC2(edge density/core area)
WETA
0.159
PC3(patch size variability/patch density)
WETA
0.060
PC4(patch size & shape)
-0.6
-0.3
0
0.3
0.6
less fragmented
more fragmented

Figure 4.7

Figure 4.8. Weighted average location (and 95% confidence interval) of bird species strongly associated with pole and grass/forb habitats along the first 2-3 principal component gradients representing the spatial pattern of pole (top) and grass/forb (bottom) habitats in 25 and 13 300-ha subbasins, respectively, in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92. Data represent birds detected at any distance during 4 visits to 32-38 sampling points within each subbasin, including only detections of new individuals from separate sampling points within a subbasin during a visit. Weighted averages were based on relative abundance in each subbasin. See Appendix D for the scientific names corresponding to bird acronyms, and see Table 4.5 for definition of each principal component (HUVI = Hutton's vireo; BGWA = black-throated gray warbler; WEBL = western bluebird; VGSW = violet-green swallow).

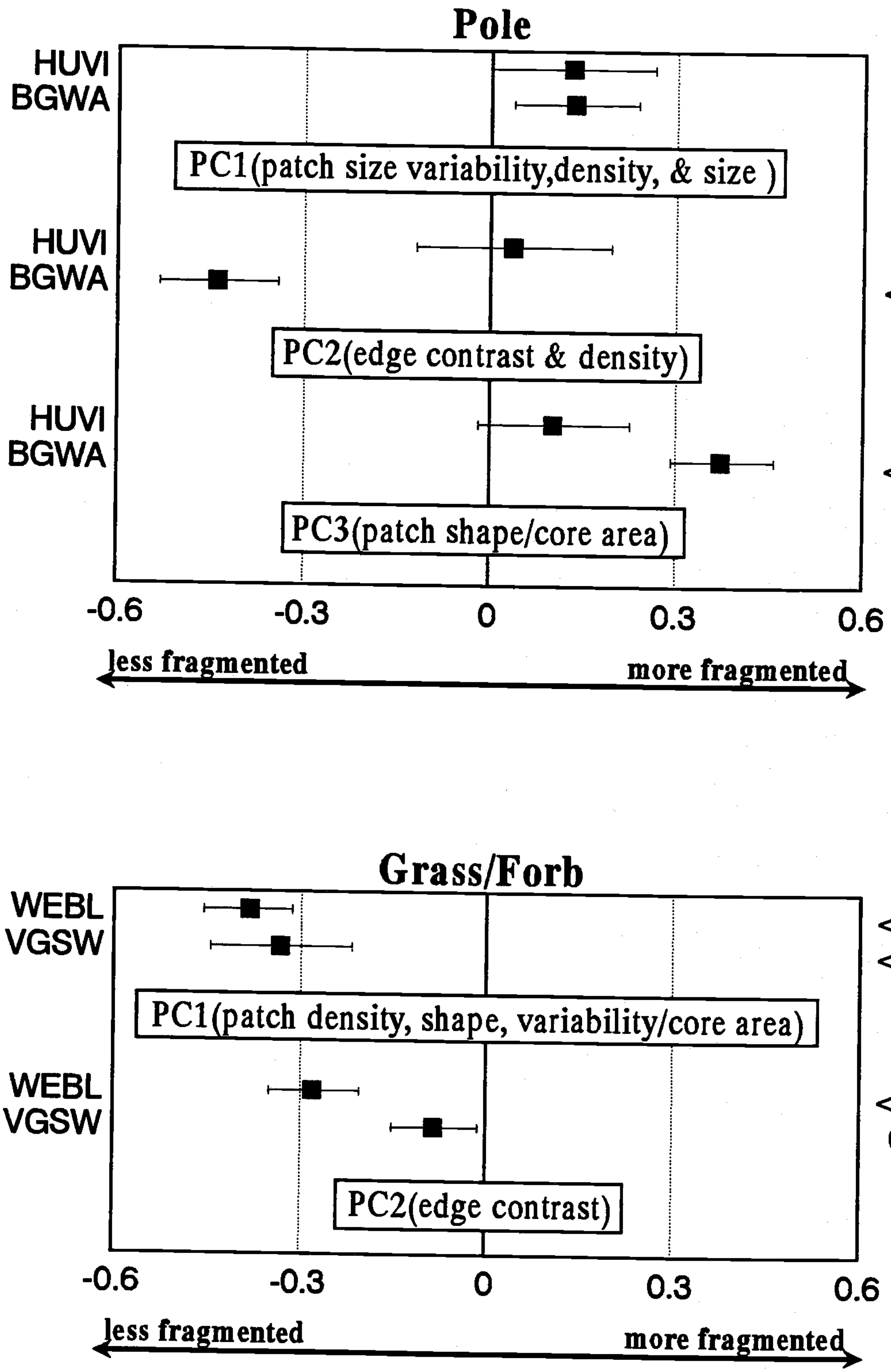
Pole
P
HUVI
BGWA
0.061
0.013
PC1(patch size variability,density, & size)
HUVI
BGWA
0.640
<0.001
PC2(edge contrast & density)
HUVI
BGWA
0.105
<0.001
PC3(patch shape/core area)
-0.6
-0.3
0
0.3
0.6
less fragmented
more fragmented
Grass/Forb
P
WEBL
VGSW
<0.001
<0.001
PC1(patch density, shape, variability/core area)
WEBL
VGSW
<0.001
0.039
PC2(edge contrast)
-0.6
-0.3
0
0.3
0.6
less fragmented
more fragmented

Figure 4.8

Table 4.9. Simple linear relationships between each principal component and the abundance of breeding bird species associated with several patch types in 30 300-ha subbasins in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92.[a] Data represent birds detected at any distance during 4 visits to 32-38 sampling points within each subbasin, including only detections of new individuals from separate sampling points within a subbasin during a visit. Only species strongly associated with each patch type are included.

Patch Type[b]	PC1[d]			PC2[d]			PC3[d]		
Species[c]	b_1	R^2	P	b_1	R^2	P	b_1	R^2	P
Large sawtimber									
Gray jay	+	6%	0.202	-	5%	0.265	+	4%	0.321
Brown creeper	+	0%	0.783	-	17%	0.026	+	15%	0.036
Winter wren	-	2%	0.432	-	21%	0.013	+	0%	0.822
Varied thrush	-	0%	0.990	-	22%	0.011	+	5%	0.253
Evening grosbeak	+	1%	0.536	-	1%	0.562	+	2%	0.474
Hammond's flycatcher	-	1%	0.701	-	6%	0.217	+	17%	0.025
Chestnut-backed chickadee	+	8%	0.141	-	9%	0.105	+	0%	0.869
Red crossbill	+	2%	0.422	-	0%	0.770	+	0%	0.724
Western wood-pewee	+	13%	0.050	+	7%	0.176	+	12%	0.065
Olive-sided flycatcher	+	17%	0.027	-	0%	0.882	+	7%	0.160
Red-tailed hawk	+	19%	0.019	+	8%	0.135	+	11%	0.086
Red-breasted sapsucker	+	16%	0.031	+	0%	0.938	+	1%	0.553
Conifer large sawtimber									
Pileated woodpecker	+	4%	0.317	+	27%	0.006	-	2%	0.483
Red-breasted nuthatch	+	4%	0.334	+	10%	0.108	-	2%	0.437
Mixed large sawtimber									
Western tanager[e]	+	9%	0.131	+	3%	0.359	+	2%	0.456

Table 4.9. Continued.

Patch Type[b]	PC1[d]			PC2[d]			PC3[d]		
Species[c]	b_1	R^2	P	b_1	R^2	P	b_1	R^2	P
Pole									
Hutton's vireo	+	5%	0.262	+	1%	0.726	+	4%	0.358
Black-throated gray warbler	+	1%	0.576	-	16%	0.051	+	13%	0.078
Grass/forb									
Western bluebird	-	15%	0.184	-	8%	0.353			
Violet-green swallow	-	8%	0.337	-	1%	0.810			

[a] Simple linear regression model: $\log_{10}(\text{abundance}) = b_0 + b_1(\text{principal component})$.

[b] See Appendix E for definition of each patch type. Large sawtimber, n = 29 subbasins; conifer large sawtimber, n = 27 subbasins; mixed large sawtimber, n = 27 subbasins; pole, n = 25 subbasins; grass/forb, n = 13 subbasins.

[c] Scientific names in Appendix D.

[d] See Table 4.5 for the definition of each principal component.

[e] PC4: coefficient, +; $R_2 = 4\%$; $P = 0.334$.

The other 3 species (gray jay, brown creeper, and Hammond's flycatcher) were associated with less fragmented habitat patterns, although only the brown creeper had a significant simple linear relationship between abundance and this principal component ($P = 0.026$, Table 4.9), and none had significant partial correlations ($P > 0.403$, Table 4.10). Thus, in contrast to the first principal component, habitat pattern defined by the second principal component did not have strong and consistent effects on the abundance of bird species associated with large sawtimber.

Seven of 15 species associated with large sawtimber habitats occupied landscape structural conditions that were more heterogeneous or fragmented than the average landscape condition as defined by the third principal component gradient ($P < 0.012$, Figs. 4.6 and 4.7). In this case, all 7 species were associated with landscapes in which large sawtimber was distributed in

Table 4.10. Partial linear relationships between each principal component and breeding bird species' abundances while controlling for any relationship between habitat area and bird abundance, for bird species associated with several patch types in 30 300-ha subbasins in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92.[a] Data represent birds detected at any distance during 4 visits to 32-38 sampling points within each subbasin, including only detections of new individuals from separate sampling points within a subbasin during a visit. Only species strongly associated with each patch type and with a significant relationship between abundance and habitat area (Table 4.8) are included.

Patch Type[b]	PC1[d]			PC2[d]			PC3[d]		
Species[c]	b_2	pR^2	P	b_2	pR^2	P	b_2	pR^2	P
Large sawtimber									
Gray jay[e]	+	11%	0.097	+	0%	0.818	-	1%	0.600
Brown creeper	+	0%	0.997	-	3%	0.403	+	2%	0.495
Winter wren	-	8%	0.139	-	6%	0.206	-	15%	0.040
Varied thrush	-	1%	0.720	-	7%	0.171	-	1%	0.612
Evening grosbeak	+	1%	0.625	+	2%	0.424	-	1%	0.549
Hammond's flycatcher	-	2%	0.527	-	0%	0.835	+	7%	0.165
Chestnut-backed chickadee	+	8%	0.150	-	2%	0.480	-	4%	0.309
Conifer large sawtimber									
Pileated woodpecker	+	12%	0.088	+	15%	0.053	-	2%	0.450
Red-breasted nuthatch	+	8%	0.154	+	3%	0.424	-	3%	0.427
Mixed large sawtimber									
Western tanager[f]	+	17%	0.038	+	3%	0.412	+	13%	0.068
Pole									
Hutton's vireo	+	11%	0.116	+	1%	0.739	-	0%	0.903
Black-throated gray warbler	+	3%	0.426	-	28%	0.008	+	5%	0.317

Table 4.10. Continued.

Patch Type[b]	PC1[d]			PC2[d]			PC3[d]		
Species[c]	b_2	pR^2	P	b_2	pR^2	P	b_2	pR^2	P
Grass/forb									
Western bluebird	-	5%	0.497	-	12%	0.274			
Violet-green swallow[e]	-	17%	0.210	-	0%	0.953			

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[a] Linear model: $\log_{10}(\text{abundance}) = b_0 + b_1(\%\text{area}) + b_2(\text{principal component})$.

[b] See Appendix E for definition of each patch type. Large sawtimber, $n = 29$ subbasins; conifer large sawtimber, $n = 27$ subbasins; mixed large sawtimber, $n = 27$ subbasins; pole, $n = 25$ subbasins; grass/forb, $n = 13$ subbasins.

[c] Scientific names in Appendix D.

[d] See Table 4.5 for the definition of each principal component.

[e] Nonlinear model: $\log_{10}(\text{abundance}) = b_0 + b_1(\%\text{area}) + b_2(\%\text{area}^2) + b_3(\text{principal component})$.

[f] PC4: coefficient, +; $pR_2 = 1\%$; $P = 0.729$.

patches of smaller size than the average landscape. Simple linear regression results supported this finding for 4 of these species (western woodpewee, red-tailed hawk, brown creeper, and Hammond's flycatcher), although the percent of variation accounted for by the patch size gradient was low (R^2, 11-17%; $P < 0.086$; Table 4.9). Moreover, the latter 2 species did not have significant partial correlations ($P > 0.165$, Table 4.10), indicating that mean patch size was not important after habitat area was considered. The other 3 species (gray jay, olive-sided flycatcher, and red-breasted sapsucker) did not have simple linear relationships either with ($P = 0.600$, Table 4.10) or without ($P > 0.160$, Table 4.9) first taking habitat area into account. Two other species (winter wren, and western tanager) had significant partial correlations ($P < 0.068$, Table 4.10) even though their weighted average landscape condition did not differ from the average ($P > 0.159$, Figs. 4.6 and 4.7). Fifteen percent of the variation in winter wren abundance among subbasins was explained by the patch size gradient after taking habitat area into account. Winter wrens were associated with less fragmented landscapes (i.e., those with larger patch sizes than average). Thirteen percent of the variation in western tanager abundance among subbasins was explained by a gradient in patch density and patch size variability after taking into account mixed large sawtimber area. Western tanagers were associated with more heterogeneous landscapes. Thus, like the first principal component, most species were associated with more heterogeneous or fragmented habitat distributions along this gradient, but the relationships between abundance and pattern along this gradient were not strongly supported by the regression analyses.

Both species associated with pole habitat (Hutton's vireo and black-throated gray warbler) occupied landscape structural conditions that were more heterogeneous or fragmented than the average landscape condition as defined by the first principal component gradient ($\underline{P} < 0.061$, Fig. 4.8), but variation in abundance among subbasins was not related to variation along this pattern gradient either with ($\underline{P} > 0.116$, Table 4.10) or without ($\underline{P} > 0.262$, Table 4.9) first taking habitat area into account. Black-throated gray warbler abundance was negatively associated with the second principal component ($\underline{P} < 0.001$, Fig. 4.8). Abundance was inversely related to the degree of edge contrast ($\underline{P} = 0.051$, Table 4.9); 28% of the variation in this species' abundance was explained by a gradient in edge contrast after taking into account the relationship with habitat area ($\underline{P} = 0.008$, Table 4.10). Black-throated gray warblers also were associated with landscapes characterized by more complex patch shapes and less core area (i.e., principal component 3, $\underline{P} < 0.001$, Fig. 4.8), although abundance was not related to this gradient after taking habitat area into account ($\underline{P} = 0.317$, Table 4.10). Thus, this species seems to be weakly associated with more heterogeneous arrangements of pole habitat, but in a low edge-contrast context. Both species associated with grass/forb habitat (western bluebird and violet-green swallow) occupied landscape structural conditions that were more homogeneous or less fragmented than average conditions along both principal component gradients ($\underline{P} < 0.039$, Fig. 4.8). However, variation in abundance among subbasins was not related to these pattern gradients either with ($\underline{P} > 0.210$, Table 4.10) or without ($\underline{P} > 0.184$, Table 4.9) first taking habitat area into account. Thus, there exists weak evidence that fewer, larger grass/forb patches are more beneficial to these species than many small patches.

In a separate analytical approach, I considered the residual pattern indices individually and derived a "best" (see methods) general linear model for each species (Table 4.11). The best combination of explanatory variables for each species explained between 26% and 68% of the variation in abundance among subbasins. Three species did not exhibit any habitat pattern relationships after habitat area was taken into account. Conversely, 4 species exhibited significant relationships with habitat pattern only. Both habitat area and habitat pattern contributed to the other 11 species, although habitat area was the most significant explanatory variable in all cases. Individual residual pattern indices contributed an additional 11-38% explanatory power to the models after accounting for habitat area. Fourteen residual pattern indices were selected in 1 or more of the final models.

DISCUSSION

Public land management agencies and private landowners in the central Oregon Coast Range manage their lands for different objectives. As a result, a wide variety of landscape structural conditions are represented in this area, particularly with respect to the areal extent and spatial distribution patterns of late-seral forest. I quantified these landscape structural gradients using a variety of landscape metrics that measure different aspects of landscape pattern. Specifically, I identified 10 indices of pattern that represented somewhat nonredundant aspects of large sawtimber distribution within 300-ha subbasins. These metrics could be combined into no fewer than 3 principal components to account for roughly 80% of the variation in landscape pattern among 30 subbasins. Each principal component gradient accounted for only 20-30% of the total variation in landscape pattern among subbasins. Results were similar

Table 4.11. Relationships between the abundance of breeding bird species and a "best" and parsimonious combination of habitat area and residual habitat pattern indices (see text) for species associated with several patch types in 30 300-ha subbasins in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92. Data represent birds detected at any distance during 4 visits to 32-38 sampling points within each subbasin, including only detections of new individuals from separate sampling points within a subbasin during a visit. Only species strongly associated with each patch type are included. Note, the statistics for LSIM will not match those in Table 4.8 because of slightly different sample sizes.

Patch Type[a]					Full Model	
Species[b]	Variable[c]	b_1	pR^2	P	R^2	P
Large sawtimber						
Gray jay	LSIM	+	0%	0.882	68%	<0.001
	LSIM^2	+	8%	0.165		
	LCAS	-	17%	0.030		
Brown creeper	LSIM	+	55%	<0.001	55%	<0.001
Winter wren	LSIM	+	55%	<0.001	62%	<0.001
	MCA	+	23%	0.009		
Varied thrush	LSIM	+	47%	<0.001	47%	<0.001
Evening grosbeak	LSIM	+	30%	0.002	30%	0.002
Hammond's flycatcher	LSIM	+	26%	0.007	38%	0.007
	MPFD	-	18%	0.027		
	TECI	+	11%	0.088		
Chestnut-backed chickadee	LSIM	+	38%	<0.001	40%	0.004
	MPS	+	23%	0.011		
	MCAI	-	19%	0.022		
Red crossbill	LSIM	+	22%	0.017	33%	0.042
	MPFD	+	21%	0.019		
	PSCV	+	19%	0.026		
	MPS	+	18%	0.029		
Western wood-pewee	MECI	+	38%	<0.001	51%	<0.001
	CACV	+	28%	0.004		
Olive-sided flycatcher	MECI	+	39%	<0.001	39%	<0.001

Table 4.11. Continued.

Patch Type[a]					Full Model	
Species[b]	Variable[c]	b_1	pR^2	P	R^2	P
Red-tailed hawk	TCAI	-	36%	<0.001	50%	<0.001
	CACV	+	20%	0.017		
Red-breasted sapsucker	TECI	+	26%	0.004	26%	0.004
Conifer large sawtimber						
Pileated woodpecker	LSIM	+	41%	<0.001	52%	<0.001
	ED	+	28%	0.005		
Red-breasted nuthatch	LSIM	+	24%	0.012	33%	0.008
	ED	+	16%	0.045		
Mixed large sawtimber						
Western tanager	LSIM	+	26%	0.009	43%	0.004
	CWED	+	23%	0.015		
	PSCV	+	16%	0.049		
Pole						
Hutton's vireo	LSIM	+	38%	0.001	51%	<0.001
	LPI	-	15%	0.063		
Black-throated gray warbler	LSIM	+	50%	<0.001	62%	<0.001
	TECI	-	31%	0.006		
	CASD	+	19%	0.038		
Grass/forb						
Western bluebird	LSIM	+	60%	<0.001	64%	0.006
	CASD	-	31%	0.058		
Violet-green swallow	LSIM	+	0%	0.884	65%	0.018
	$LSIM^2$	+	6%	0.451		
	CASD	-	38%	0.042		

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[a] See Appendix E for definition of each patch type. Large sawtimber, n = 29 subbasins; conifer large sawtimber, n = 27 subbasins; mixed large sawtimber, n = 27 subbasins; pole, n = 25 subbasins; grass/forb, n = 13 subbasins.

[b] Scientific names in Appendix D.

[c] See Table 4.1 for a description of each index.

for large sawtimber, pole, and grass/forb patch types. Hence, landscape patterns for a variety of patch types could not be defined by a simple, unidimensional gradient. Rather, landscape patterns were complex and consisted of several equally important gradients representing different aspects of pattern. These results suggest that investigators and managers may need to consider a wide variety of aspects of landscape structure when studying or managing bird populations at the landscape scale. Interestingly, edge contrast was separated out as a dominant and independent gradient for all patch types, indicating that edge contrast (as I defined it) was an important means of discriminating among landscape structural conditions in the central Oregon Coast Range.

Fifteen bird species demonstrated strong and exclusive selection for large sawtimber habitats or the juxtaposition of large sawtimber and early-seral, open-canopied habitats in the central Oregon Coast Range. The quantitative relationship between large sawtimber area and bird abundance varied dramatically among species; 0-63% of the variation in bird abundance among subbasins was accounted for by habitat area (Table 4.8). Four species (gray jay, brown creeper, winter wren, and varied thrush) were strongly affected by the proportional abundance of large sawtimber in a subbasin (Table 4.7); 52-63% of the variation in abundance among subbasins was explained by habitat area alone (Table 4.8). Conversely, the abundances of 5 species (red crossbill, western woodpewee, olive-sided flycatcher, red-breasted sapsucker, and red-tailed hawk) were largely unaffected by large sawtimber area ($R^2 < 3\%$, Tables 4.7 and 4.8), even though these species were generally always found in association with this patch type. The strength of relationship between habitat area and bird abundance was similar for the 2 species exhibiting the strongest association with pole and grass/forb habitats (Table 4.8). Thus, even species exhibiting a definitive association with a particular habitat type at the patch level had a great deal of variation in abundance among subbasins not explainable by habitat area alone. Much of the explanatory power was apparently lost when translating patch-level habitat associations to population abundance at the subbasin level. These results suggest that caution should be exercised when attempting to extrapolate bird-habitat relationships derived at 1 scale to other scales; factors affecting the selection of habitats by an individual at the patch scale may affect population abundance at the landscape scale differently (Wiens 1989a,b, Wiens et al. 1993).

Like habitat area relationships, the quantitative relationship between large sawtimber pattern and bird abundance varied dramatically among species. In contrast, however, relationships between landscape pattern and bird abundance were complex and difficult to assess because of the variety of ways in which landscape pattern can be expressed and because of the variety of analytical approaches available to me. My analyses demonstrate that the choice of methods can exert a strong influence on the results. For example, only 2 of 15 species associated with large sawtimber were affected by the distribution or pattern of large sawtimber within levels of large sawtimber abundance, based on an analysis of variance (Table 4.7). However, 10 of 15 species associated with large sawtimber habitats and all 4 species associated with young forest habitats, on the average, occupied landscape structural conditions that differed from the average landscape condition with respect to 1 or more gradients in habitat pattern, based on their weighted average location along the principal component gradients (Figs. 4.5-4.7). Yet, of the 30 significant associations identified using this approach, including all species, patch types, and principal components, only 12 were significant based on simple linear regression analysis of the relationship between bird abundance and each pattern gradient (Table 4.9); R^2's ranged from 11-27%. Moreover, of the 20 significant associations based on weighted average locations along principal components for species with significant area relationships, only 5 were significant when the relationship between habitat area and abundance was first taken into account using partial regression analysis (Table 4.10). Finally, 12 of 15 species associated with large sawtimber habitats and all 4 species associated with the young forest habitats had significant partial correlations with 1 or more of the original residual pattern indices either with or without first taking into account habitat area (Table 4.11). Hence, the choice of analytical approaches can strongly influence conclusions regarding the effects of habitat pattern on bird abundance in this study. I suggest that investigators use several analytical approaches when evaluating landscape structural relationships and use the consistency in results among approaches to gauge confidence in the conclusions.

In my study, conclusions based on the analysis of variance are probably the most conservative (i.e., the least likely to detect significant relationships). Based on this approach, only 2 species (western woodpewee and olive-sided flycatcher) were affected by the distribution of large sawtimber (Table 4.7). Both species were associated with high-contrast edges involving large sawtimber; abundances were greater in subbasins containing highly fragmented patterns of large sawtimber. This conclusion was consistently supported by the other analyses. In particular, the total edge contrast index was the strongest explanatory variable in the component models for both species, and explained between 32-34% of their variation in abundance among subbasins (Table 4.11). In addition to these 2 species, there was consistent evidence from 3 correlational procedures that 5 of the 13 remaining species associated with large sawtimber habitats were responsive to habitat pattern. All 5 species (red-tailed hawk, red-breasted sapsucker, western tanager, pileated woodpecker, and gray jay) were associated with more heterogeneous or fragmented habitat distributions. Based on field observations, western tanagers and red-breasted sapsuckers seemed to be associated with high-contrast edges involving hardwoods in mixed or hardwood-dominated large sawtimber stands. Red-tailed hawks, pileated woodpeckers, and gray jays seemed to be responsive to several aspects of pattern, including patch shapes, core area, edge density, and edge contrast. Finally, there was consistent evidence from 2 correlational procedures that 2 of the 8 remaining species (red-breasted nuthatch and winter wren) associated with large sawtimber habitats were responsive to habitat pattern. Red-breasted nuthatch had a weak and positive correlation with conifer large sawtimber edge density. Winter wren was the only species that demonstrated a weak association with less fragmented landscapes. After accounting for habitat area, mean patch size and mean core area size explained an additional 15-20% of the variation in winter wren abundance among subbasins. Rosenberg and Raphael (1986) and Lehmkuhl et al. (1991) also found winter wren to be one of the few species associated with less fragmented landscapes in the Pacific Northwest. Of the remaining species associated with large sawtimber habitats, 2 species (brown creeper and Hammond's flycatcher) had weak and inconsistent relationships, 3 species (varied thrush, chestnut-backed chickadee, and red crossbill) did not have support from more than 1 analytical approach, and 1 species (evening grosbeak) had no evidence at all of any relationship with habitat pattern. Similarly, only 1 of 4 species (black-throated gray warbler) associated with the young forest patch types had strong and consistent evidence that habitat pattern was important.

Contrary to the dogmatic idea that habitat fragmentation is universally detrimental to species that specialize on a particular habitat, most species that exhibited significant relationships with habitat pattern in my study were positively correlated with gradients in increasing heterogeneity or fragmentation of their selected habitats; that is, they were associated with the more fragmented distribution of habitat. Similarly, it is increasingly assumed by researchers and managers that landscape structure plays a dominant role in the regulation of wildlife populations (e.g., Dunning et al. 1992, Saunders et al. 1991, Kareiva 1990, Turner 1989). My results suggest that, given the current regional landscape context (see below), this assumption may not be true at the scale of my investigation for diurnal breeding bird species in the central Oregon Coast Range, particularly for those species associated with late-seral forest. Of the 19 resident breeding bird species that I analyzed, habitat area (i.e., landscape composition) typically explained less than half of the variation in abundance among subbasins. Similarly, abundance was only weakly, or not at all, related to habitat patterns for most species. Not surprisingly, the strongest relationships were for species associated with edge habitats. But even for these few species, the percent of variation in abundance among subbasins attributable to habitat pattern was only 30-40%. Hence, although landscape structure (both composition and pattern) was demonstratably related to several species' abundances, I cannot claim that it was a dominant factor given the large amount of unexplained variation.

The relative weakness of the relationships between landscape pattern and bird abundance undoubtedly reflects, in part, the limitations of my study discussed below, but also may reflect, among other things, the spatio-temporal vegetation dynamics and regional landscape context of the central Oregon Coast Range. Most of the expectations about bird population response to habitat subdivision stem from studies on forest fragmentation caused by urbanization and agricultural development. In this form of fragmentation, forest tracts are progressively reduced to smaller and more isolated patches embedded within a relatively permanent (barring reforestation) matrix of nonforest. The landscape structure becomes relatively static. Forest patches adjoin nonforest habitat and remain isolated from similar forest patches for long periods of time. From a forest-dwelling animal's perspective, forest fragments become embedded in a matrix of completely unsuitable habitat that reduces or even prohibits the dispersal and movement of animals among isolated forest patches, depending on the species habitat selectivity and vagility. However, as indicated earlier, commercial timber management is the major cause of forest fragmentation in the Pacific Northwest (Lehmkuhl and Ruggiero 1991). Commercial timber management alters landscape patterns by changing the areal abundance and spatial distribution of plant communities and seral stages across the landscape, and this occurs on a backdrop of a natural patch mosaic created by changing landforms and natural disturbances. The natural landscape is a spatially and temporally dynamic mosaic of forest patches (i.e., shifting mosaic) and the scale of this mosaic is dramatically altered by timber management activities. Vertebrate abundance and distribution patterns in forests being fragmented by timber management activities are likely to differ from those in forests being fragmented by urbanization and agricultural development. Sharp forest/nonforest edges are transient in managed forest landscapes because of forest regrowth, and regenerating plantations may not function as nonhabitat for many species, but rather as habitat of variable quality and permeability to animal movements. Late-seral forest patches may never be truly isolated or may be isolated for only a brief period of years. Thus, it is unclear whether the empirical findings on forest fragmentation from urban or agricultural landscapes extend to the dynamic forest landscapes of the Pacific Northwest. Indeed, it seems likely that vertebrate response to habitat subdivision would be less pronounced.

In addition, most of the field studies on fragmentation, primarily from the eastern deciduous forest, have been conducted in landscapes in which the fragmentation process has progressed steadily for a long period of time (100-200 years in many areas) and has reach a point in which forest patches represent truly isolated fragments. In contrast, in the central Oregon Coast Range and elsewhere in the PNW, most of the habitat fragmentation caused by timber management has taken place over the past 30-40 years and late-seral forest still represents the matrix throughout much of the area. Thus, habitat fragmentation is relatively new and has not proceeded very far relative to the fragmentation of eastern deciduous forests. Again, it seems likely that vertebrate response to habitat subdivision would be less pronounced.

Given that the landscapes I studied were "open" systems, another plausible explanation for the weak relationships between bird abundances and landscape structure is that local bird abundance patterns may be produced not only by local processes or events but also by the dynamics of regional populations or events elsewhere in the species' range (Wiens 1981, 1989b, Vaisanen et al. 1986, Haila et al. 1987, Ricklefs 1987). That broad-scale processes act to constrain or influence finer-scale phenomena is one of the key principles of hierarchy theory (Allen and Star 1982) and 'supply-side' ecology (Roughgarden et al. 1987). Large regional source populations of species associated with the matrix habitat type (late-seral forest) may be able to "buffer" any local pattern-related effects. Densities of forest-dwelling, long-distance migratory birds in forest patches in Connecticut were significantly and positively correlated with regional forest abundance (Askins and Philbrick 1987, Askins et. al. 1987). The authors suggested that local bird abundance was influenced by the proximity and size of potential source populations from the regional landscape. If mechanisms are operating on species associated with late-seral forest to reduce population abundance in fragmented landscapes, immigration from large regional source populations may be sufficient to offset any tendency for population declines. This would be particularly likely for vagile species such as birds that can disperse large distances easily.

Given the weak coupling between patch-level habitat associations and landscape-level patterns in abundance, it seems unjustified to compare the results of my study with the many bird studies on fragmentation conducted at the patch scale, with the exception of those conducted in the PNW that may provide additional insight on the regional context and generality of my results. Rosenberg and Raphael (1986) and Lehmkuhl et al. (1991) investigated the relationship between breeding bird communities in late-seral (mean dbh > 26 cm) and old-growth (mean dbh > 81 cm and multistory canopy) forest patches and various measures of fragmentation and structure of the surrounding landscape in northwestern California and western Washington, respectively. They sampled forest patches from landscapes similar in structure to those I sampled. Although they did not sample whole landscapes and their study designs were subject to other limitations, they also failed to detect or detected only weak relationships between species' abundance and landscape structure, and found most species with significant relationships to be positively correlated with gradients of increasing habitat heterogeneity or fragmentation. Welsh and Healy (1993) found that the abundances of most breeding bird species associated with late-seral forests in New Hampshire were not different between small (64 ha), unmanaged landscapes (100% sawtimber forest; mean dbh > 25.4 cm, > 80 years) and similar landscapes that had 40% of their area in young forest stands (mean dbh < 25.4 cm, < 70 years). In a similar study in Missouri Ozark forests, Thompson et al. (1992) sampled breeding bird populations in small (200 ha), unmanaged landscapes (100% pole-sawtimber forest, > 20 years) and similar landscapes that had 20% of their area in young forest stands (< 20 years). Of 9 forest-interior, neotropical migrants, 3 were more abundant in the managed landscapes, 3 were equally abundant in both landscapes, and 3 were more abundant in the unmanaged landscapes. Hence, the limited evidence gathered so far for these spatially and temporally dynamic forest landscapes suggests that we should not blindly accept the dogmatic conceptual framework described in the introduction. Habitat patterning and subdivision may play a role in regulating population abundance, distribution, and dynamics, but the magnitude and nature of this role may vary geographically and over time in relation to changes in regional habitat conditions and other factors, and probably varies among species in relation to habitat selectivity, vagility, and scale.

SCOPE AND LIMITATIONS

The scope of this study was restricted in several ways. These limitations identify additional research needs and should be understood carefully before these results are interpreted or applied in a management context. First, the scale of my investigation placed upper and lower limits of resolution on my ability to detect habitat patterns and assess bird-habitat relationships (Wiens 1989a). The extent of my landscapes was roughly 300 ha; this defined the upper limit of resolution. Undoubtedly, populations of most or all of the species I investigated extend over much larger areas and are subject to demographic influences operating over correspondingly larger areas. The maximum potential number of individuals present in a 300-ha area varies among species, but probably ranges from less than 1 (e.g., spotted owl) to several hundred (e.g., Swainson's thrush) under ideal habitat conditions. Each subbasin is nested within a larger regional landscape context. Because these forested landscapes are "open" systems, the regional context will influence the internal landscape dynamics to some degree, and the magnitude of this influence will likely be greater for smaller and more open landscapes (Wiens 1989a,b). Thus, the bird species I analyzed may be responsive to variations in habitat area and pattern at a coarser scale than I investigated. The relatively weak relationships I detected do not preclude much stronger landscape structural relationships at coarser scales.

I defined minimum patch size as 0.785 ha and ≥ 50 m in the narrowest dimension; this defined the lower limit of resolution. Landscape patterns at finer resolutions were not quantified in this study; therefore, my results do not preclude stronger landscape structural relationships at finer resolutions. Patchiness occurs at many scales and patches can be defined in hierarchical fashion at progressively finer and finer scales (Kotliar and Wiens 1990). Because pattern indices are not invariant to scale (Turner et al. 1989), changing the minimum patch size would have significant effects on measures of landscape structure for specific patch types. A mixed large sawtimber patch, for example, could be broken into progressively smaller and more numerous conifer and hardwood patches, and various indices of pattern could change dramatically and unpredictably. However, reducing minimum patch size would probably not effect metrics for the large sawtimber seral condition class; except for scattered individual tress or very narrow riparian leave strips, sawtimber patches < 0.785 ha rarely occurred within the study area. Similarly, increasing minimum patch size to 2 ha would have had no effect on the large sawtimber metrics because the smallest large sawtimber patch I sampled was 2.06 ha (Table 4.4).

Second, the analysis presented in this paper was limited to a single scale. I quantified the relationship between bird abundances and habitat patterns at the subbasin (among-patch) scale only. As the studies by Wiens and Rotenberry on shrubsteppe birds (Wiens and Rotenberry 1981, Wiens 1985, 1986, Rotenberry 1986, Wiens et al. 1987) and other studies (e.g., Gutzwiller and Anderson 1987, Morris 1987, Hengeveld 1987) demonstrate, habitat selection occurs at multiple scales and habitat associations often vary among scales of investigation or analysis. I am unable to infer about habitat associations at finer or coarser scales from this analysis alone. However, habitat associations at finer and coarser spatial scales and the relative importance of associations among hierarchical scales are the subjects of current analyses.

Third, I classified habitat from a bird community-centered perspective. That is, I defined 27 patch types on the basis of factors (e.g., seral condition, plant community, canopy closure) believed to be important to a wide variety of wildlife in western Oregon and Washington. These factors may or may not be important from an organism-centered perspective. Other habitat features (e.g., snags, vertical foliage diversity, available water) not captured in this classification scheme might be more important in governing the spatial distribution and abundance patterns of any particular species. Indeed, most species probably select habitat on the basis of environmental conditions not completely accounted for by this simple classification scheme. I could redefine patches by combining patch types that are functionally equivalent from an organism-centered perspective, but I would still be constrained by the original patch type map unless I remapped each landscape for each species using a species-specific habitat classification scheme. I avoided this problem by focusing my analysis on those species strongly associated with a single patch type as I had defined them originally. Moreover, vegetation patches were somewhat arbitrarily and subjectively discretized during the cover mapping and digitization process. Plant community differences were in many cases more ecotonal than discrete. Thus, the final patch mosaics represented over-simplified representations of the actual spatial heterogeneity present in these landscapes. By focussing my analysis on large sawtimber, I minimized this problem because most sawtimber patch edges were induced by timber managment activities and therefore were relatively discrete and objectively delineated.

These 3 limitations are inherent to all landscape ecological investigations and deal with the issue of "measured heterogeneity" versus "functional heterogeneity" (Kolasa and Rollo 1991). The scheme used to classify landscapes coupled with the scale of investigation and analysis determines measured heterogeneity because the quantifiable patterns are constrained by these decisions. Measured heterogeneity may or may not correspond to something functionally meaningful to a particular species (Wiens 1989a,b, Kolasa and Rollo 1991). Thus, unless the measured heterogeneity corresponds to patterns that are functionally meaningful to the species under consideration, results may lead to erroneous conclusions. Unfortunately, I did not know a priori what the functionally relevant scales and habitat types were for each species in my study area. Thus, I selected a scale and classification scheme that stood the "best" chance of allowing me to detect functionally meaningful patterns for some species and yet also were meaningful from a land management perspective. Although these limitations are important to consider when interpreting these results, I am not aware of other published attempts to investigate empirical relationships in the field between vertebrate populations and landscape structure at equal or greater extents using a replicated experimental design. Thus, my study both serves as a lesson on the limitations of avian field studies at the landscape scale and provides an empirical basis, in part, for generating a more process-oriented understanding of landscape ecological relationships for bird populations.

Fourth, my analysis was limited to diurnal birds during the breeding season. Nocturnal birds were not considered in this analysis, nor did I assess temporal patterns (e.g., seasonal or yearly changes) in the relationship between bird abundance and landscape structure. I sampled birds in each landscape during a single year only because of constraints on available investigatory resources. Bird populations and habitat associations are known to fluctuate both seasonally and annually to some degree in some cases (Wiens 1989b, Marcot 1985, Rice et al. 1980). Although my resurvey results indicated that annual variation was not significant for most species, the confounding of year and basin in my study design undoubtedly added unexplained variation to the data set, making landscape structural relationships more difficult to detect.

Fifth, I assessed bird abundance patterns only. I did not assess measures of fitness because of the difficultly in doing so at the scale of my investigation. It seems likely that, in response to changes in habitat quality at the landscape level, functional responses would precede numerical responses. Abundance, as determined by counts of singing or calling birds, may not be a good indicator of habitat quality (Van Horne 1983, Wiens 1989b). Thus, individual fitness could have varied in relation to landscape structure without changing overall abundance and I would not have detected it.

Finally, for statistical reasons, my analysis was limited to relatively common and widespread species. Rare and uncommon species (e.g., spotted owl, Vaux's swift) or those with patchy distributions in the study area (e.g., downy woodpecker, marbled murrelet) could not be analyzed using parametric statistical procedures because of violations of assumptions associated with these procedures. Yet these species could very well be the ones most sensitive to landscape structure (Terborgh and Winter 1980, Pimm et al. 1988).

Given these several limitations, the many potential sources of error in measuring bird abundance, and the natural stochastic variation in wildlife populations, it is not too surprising that the relationships I detected were weak; indeed, it is surprising that I detected any significant relationships at all. My study provides empirical evidence that landscape structure is probably important to some degree for many bird species in the central Oregon Coast Range. In addition, my study demonstrates that landscape ecological relationships can and should be studied in the field to support or refute theoretical findings. Given the increasing role of landscape ecology in conservation biology and land management, we must build a stronger empirical basis for understanding landscape ecological relationships. Moreover, my study illustrates some of the difficulties in extrapolating relationships developed at the patch level to the landscape level. Even though several species had strong patch-level habitat associations, this did not translate into strong explanatory relationships between abundance and the total area and pattern of that habitat type at the subbasin level. Thus, modelling population abundances within landscapes based on simple patch type associations could produce erroneous results, and inferences drawn about landscape-level relationships from patch-centered studies should be avoided, if possible, or done with great caution.

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APPENDICES

Appendix A. Example of the FRAGSTATS output file that is formatted for display purposes (i.e., basename.full). Each run of FRAGSTATS on a landscape produces an output file like this one. This output file was shortened arbitrarily for display purposes. These results were obtained using the vector version of FRAGSTATS; thus, CONTAG2 is not reported.

```
Coverage: ncveg
Landscape ID: N

PATCH CHARACTERISTICS

Patch ID: 700                Patch Type: W
Area (ha): 1.118             Perimeter (m):  437.399
Shape Index: 1.167            Fractal Dimension: 1.305
Core Area (ha): 0             Num Core Areas: 0
Core Area Index (%): 0          Landscape Similarity (%): 0.378
Near Neigh Dist (m): NONE         Edge Contrast Index (%): 6.695

Patch ID: 200                Patch Type: MGF
Area (ha): 18.586             Perimeter (m):  1907.330
Shape Index: 1.248            Fractal Dimension: 1.245
Core Area (ha): 4.622          Num Core Areas: 1
Core Area Index (%): 24.868      Landscape Similarity (%): 8.413
Near Neigh Dist (m): 219.300    Edge Contrast Index (%): 80.049

        .
        .
        .
       etc.


CLASS INDICES

Landscape ID: N
Class ID: W
Total Area (ha): 296.073
Class Area (ha): 1.118
Number patches (#): 1
Patch Density (#/100 ha): 0.338
Mean Patch Size (ha): 1.118
Patch Size St Dev (ha): 0
Patch Size Coeff of Variation (%): 0
Landscape Similarity (%): 0.378
Total Core Area (ha): 0
Number of Core Areas: 0
Core Area Density (#/100 ha): 0
Mean Core Area (ha): 0
Core Area St Dev (ha): 0
Core Area Coeff of Variation (%): 0
Landscape Core Area Similarity(%): 0
```

Total Core Area Index (%): 0
Mean Core Area Index (%): 0
Mean Shape Index: 1.167
Area-Weighted Mean Shape Index: 1.167
Landscape Shape Index: 1.243
Mean Patch Fractal Index: 1.305
Double-log Fractal Index: NA
Mean Nearest Neighbor (m): NONE
Nearest Neighbor Standard Dev: NA
Nearest Neighbor Coeff of Variation (%): NA
Contagion1 (%): 13.711
Largest Patch Index (%): 0.378
Total Edge (m): 437.399
Edge Density (m/ha): 1.477
Contrast-Weighted Edge Den (m/ha): 0.099
Mean Edge Contrast Index (%): 6.695
Area-Weighted Mean Edge Contrast Index (%): 6.695
Total Edge Contrast Index (%): 6.695

Landscape ID: N
Class ID: MGF
Total Area (ha): 296.073
Class Area (ha): 24.908
Number patches (#): 2
Patch Density (#/100 ha): 0.676
Mean Patch Size (ha): 12.454
Patch Size St Dev (ha): 8.671
Patch Size Coeff of Variation (%): 69.624
Landscape Similarity (%): 8.413
Total Core Area (ha): 4.638
Number of Core Areas: 2
Core Area Density (#/100 ha): 0.676
Mean Core Area (ha): 2.319
Core Area St Dev (ha): 3.257
Core Area Coeff of Variation (%): 140.465
Landscape Core Area Similarity(%): 1.566
Total Core Area Index (%): 18.619
Mean Core Area Index (%): 12.558
Mean Shape Index: 1.211
Area-Weighted Mean Shape Index: 1.229
Landscape Shape Index: 1.655
Mean Patch Fractal Index: 1.252
Double-log Fractal Index: 1.113
Mean Nearest Neighbor (m): 219.300
Nearest Neighbor Standard Dev: 0
Nearest Neighbor Coeff of Variation (%): 0
Contagion1 (%): 62.578
Largest Patch Index (%): 6.277
Total Edge (m): 2954.218
Edge Density (m/ha): 9.978
Contrast-Weighted Edge Den (m/ha): 8.375
Mean Edge Contrast Index (%): 85.525

Area-Weighted Mean Edge Contrast Index (%): 82.829
Total Edge Contrast Index (%): 83.930

.
.
.
etc.

LANDSCAPE INDICES

Landscape ID: N
Total Area (ha): 296.073
Number Patches: 17
Patch Density (#/100 ha): 5.742
Mean Patch Size (ha): 17.416
Patch Size Standard Deviation (ha): 15.511
Patch Size Coeff of Variation (%): 89.064
Total Core Area (m): 42.862
Number of Core Areas: 14
Core Area Density (#/100 ha): 4.729
Mean Core Area (ha): 2.521
Core Area Standard Deviation (ha): 7.144
Core Area Coeff of Variation (%): 283.355
Total Core Area Index (%): 14.477
Mean Core Area Index (%): 8.468
Mean Shape Index: 1.635
Area-Weighted Mean Shape Index: 1.859
Landscape Shape Index: 3.878
Mean Patch Fractal Index: 1.294
Double-log Fractal Index: 1.489
Patch Richness: 7
Patch Richness Density (#/100 ha): 2.364
Relative Patch Richness (%): 25.926
Shannons Diversity: 1.503
Simpsons Diversity: 0.704
Modified Simpsons Diversity Index: 1.218
Shannons Evenness: 0.772
Simpsons Evenness: 0.821
Modified Simpsons Evenness Index: 0.626
Mean Nearest Neighbor (m): 160.120
Nearest Neighbor Standard Dev (m): 91.896
Nearest Neighbor Coeff of Variation (%): 57.392
Contagion1 (%): 64.713
Largest Patch Index (%): 17.338
Total Edge (m): 19821.831
Edge Density (m/ha): 66.949
Contrast-Weighted Edge Density (m/ha): 21.170
Mean Edge Contrast Index (%): 31.872
Area-Weighted Mean Edge Contrast Index (%): 30.281
Total Edge Contrast Index (%): 26.497

Appendix B. FRAGSTATS user guidelines.

The following instructions provide the information necessary to install and run the vector and raster versions of FRAGSTATS. The command line options are described only briefly here; the OVERVIEW OF FRAGSTATS section should be read to fully understand these guidelines. These instructions assume that users have working knowledge of the UNIX operating environment.

Vector Version

The vector version of the program is an Arc/Info AML. It was developed on a SUN workstation in a UNIX operating environment using Arc/Info version 6.1; it will not run with earlier versions of Arc/Info. The AML calls up 26 C programs that either are not available in AML or are difficult to implement in AML (e.g., calculating logarithms, regression computations associated with the double log fractal dimension index, operations involving reading the optional weight file, and for formatting records in the output files). These C programs were compiled with the SUNOS cc compiler and may not compile with other C compilers. Nearest-neighbor determination must be done in the raster world because Arc/Info does not allow for polygon edge-to-edge distance calculations. Often the rasterization process (polygrid, gridsvf) creates more or less classes than the original polygon coverage. When this occurs, the 1-to-1 correspondence between patches in the raster image and polygons in the vector world is lost and nearest-neighbor distance cannot be calculated for the vector patches (nearest-neighbor distance is reported as 'N/A' when this occurs). Many loops in the FRAGSTATS AML go from 0 to max_classes. Therefore, it is most efficient if the minimum patch type code (see below) is close to zero. A coverage with patch type codes ranging from 1000 to 1200 for example, will take an extremely long time to run. In this case it would be best to subtract 1000 from each patch type code before running the AML. The following instructions assume that users have working knowledge of Arc/Info.

To install FRAGSTATS from DOS compatible diskettes containing the FRAGSTATS program files:

(1) Move all FRAGSTATS program files into the UNIX environment.

(2) In UNIX, rename the file fragstat.aml to fragstats.aml (mv fragstat.aml fragstats.aml).

(3) In UNIX, run the script makeall to build the C programs (makeall).

To run FRAGSTATS in Arc/Info there is a single command line, consisting of several arguments (each described below), issued from the arc prompt as follows:

```
&run fragstats coverage basename patch-att edge-dist max-classes cellsize [classonly]
[landscape-id] [weight-file] [patch-id] [descriptor] [use-bound]
```

NOTE: If fragstats is run without the command line arguments, the user will be prompted for all the necessary inputs.

NOTE: The first 6 parameters are required; use a # in place of skipped OPTIONAL parameters.

Coverage: The name of the input arc/info coverage {char}. The coverage must be built for polygons and lines. The coverage must contain a numeric attribute that defines patch types (classes)[e.g., an attribute called class defined as 4,4,b that contains patch type codes ranging from 1 to 100]. Polygons with patch types greater than or equal to zero are considered to be the landscape of interest. Polygons outside the landscape can be included so that indices requiring adjacency information can be calculated for polygons bordering the landscape boundary. These landscape border polygons should be set to a negative class value.

Basename: The basename for the output ASCII files {char}. The extensions .patch, .class, .land, and .full will be added to the basename. The output files contain the following information:

basename.patch: each record contains all the patch indices for a given patch separated by spaces.

basename.class: each record contains all the class indices for a given class separated by spaces

basename.land: each record contains all the landscape indices for a given landscape separated by spaces

basename.full: a formatted file containing patch, class, and landscape indices for the input coverage

Patch-att: The name of the numeric attribute that defines patch types (classes) {char}. Patch type codes must be within the range 0 to max_classes.

Edge-dist: The distance from patch edge in meters used to determine core area (i.e., buffer size) {integer}.

Max-classes: The maximum number of patch types (classes) that could be present in the landscape {integer}. This is needed for calculating relative patch richness and as an upper bound for terminating loops in the AML.

Cellsize: The cell size in meters used to rasterize the input coverage {integer} for nearest neighbor calculations.

Classonly: Optional {y/n}; if 'y' then class level indices only will be reported. The default is 'no'.

Landscape-id: Optional {char}; a 10 character or less string that describes the input coverage. This string will be written to the output files. If landscape_id is not input, it will be set to the name of the coverage. Note that strings containing spaces should be quoted.

Weight-file: Optional {char}; the name of an ASCII file containing contrast weights for each combination of patch types (classes). Each record should contain the numeric representation of the 2 patch types and a weight, separated by commas or spaces. The weight represents the magnitude of the edge contrast between adjacent patch types and must range between 0 and 1. For example:

1,2,.25
1,3,.32
1,4,.60
2,3,.45 etc.

Patch-id: Optional {char}; the name of an attribute that contains unique ID's for each polygon.

Descriptor: Optional {char}; the name of an attribute that contains character descriptors for each patch type code (class). This attribute must be defined as 10 characters or less.

Use-bound: Optional {y/n}; should the landscape boundary be treated as an edge? This is only required if the input image does not have a landscape border. This effects all edge indices. The default is 'no'.

Raster Version

The raster version of the program also was developed on a SUN workstation in a UNIX operating environment. It is written in C and compiled with the SUNOS cc compiler and consists of 31 separate programs. It may not compile with other C compilers. This raster version of FRAGSTATS has a limit of 200 patch types; patch type codes must range between 0 and 200. The number of patch types can be changed by modifying the parameter MAX_CLASSES in the file stats.h. For example, if the image has patch type codes between 1000-1200, FRAGSTATS will not work unless MAX_CLASSES is changed to 1201. A better solution might be to subtract 1000 from each cell in the input image. This raster version of FRAGSTATS has a limit of 100 patches per class. This can be changed by modifying the parameter MAX_PATCHES in the file stats.h. This raster version of FRAGSTATS has a limit of 100,000 cells per patch. This can be changed by modifying the parameter MAX_PATCH_SIZE in the file stats.h.

To install FRAGSTATS from DOS compatible diskettes containing the FRAGSTATS program files:

(1) Move all FRAGSTATS program files into the UNIX environment.

(2) In UNIX, rename the file fragstat.c to fragstats.c (mv fragstat.c fragstats.c).

(3) In UNIX, rename the file fragstat.mak to fragstats.make (mv fragstat.mak fragstats.make)

(4) In UNIX, build fragstats by issuing the command: make -f fragstats.make

To run FRAGSTATS there is a single command line, consisting of several arguments (each described below), issued from the prompt as follows:

fragstats in-image out-file cellsize edge-dist max-classes data-type [rows] [cols] [background] [weight-file] [id-image] [desc-file] [use-bound]

NOTE: If fragstats is run without the command line arguments, the user will be prompted for all the necessary inputs.

NOTE: The first 9 parameters are required regardless of image format and the last parameter is required if a landscape border is absent; use a # in place of skipped OPTIONAL parameters.

<u>In-image</u>: The name of the input landscape file {char}. File formats are discussed under data_type below. Each cell should contain a patch type (class) value in the range 0 to 200. Patches outside the landscape can be included so that indices requiring adjacency information can be calculated for patches bordering the landscape boundary; these landscape border patches should be set to a negative class value.

<u>Out-file</u>: Basename for output ASCII files {char}. The extensions .patch, .class, .land, and .full will be added to the basename. The output files contain the following information:

basename.patch: each record contains all the patch level indices for a given patch separated by spaces.

basename.class: each record contains all the class level indices for a given class separated by spaces.

basename.land: each record contains all the landscape level indices for a given landscape separated by spaces.

basename.full: a formatted file containing patch, class, and landscape level indices for a given landscape.

Note that if the files already exist, the information for a given landscape will be appended to the existing files.

<u>Cellsize</u>: The size of cells in meters in the input image {float}. Cells must be square. The length of 1 side of a cell should be input.

<u>Edge-dist</u>: The distance from patch edge in meters used to determine core area (i.e, buffer size) {integer}.

<u>Max-classes</u>: The maximum number of patch types (classes) that could be present in the landscape {integer}. This is needed for calculating relative patch richness and as an upper bound for terminating loops in the program.

<u>Data-type</u>: The type of input image file {integer}, as follows:

1 - SVF file; this is a file created with the arc/info "gridsvf" command.

2 - ASCII file, no header. Each record should contain 1 image row. Cell values should be separated by a comma or a space(s).

3 - 8 bit binary file, no header.

4 - 16 bit binary file, no header.

<u>Rows</u>: The number of rows in the input image {integer}. This is only required if data_type is greater than 1.

Cols: The number of columns in the input image {integer}. This is only required if data_type is greater than 1.

Background: The value of background cells {integer}. This is only required if there are cells outside the landscape boundary in a landscape border.

Weight-file: Optional {char}; the name of an ASCII file containing weights for each combination of patch types (classes). Each record should contain the numeric representation of the 2 patch types and a weight, separated by commas or spaces. The weight represents the magnitude of the edge contrast between adjacent patch types and must range between 0 and 1. See vector version instructions for an example.

Id-image: Optional {char}; the name of an image containing patch ID's. The data_type must be the same as the input image.

Desc-file: Optional {char}; the name of an ASCII file containing character descriptors for each patch type (class). Character descriptors must be 10 characters or less. Each record in the file should contain a numeric patch type value and the character descriptor for that patch type, separated by a comma or space(s). For example:

```
1 shrubs
2 conifers
3 deciduous    etc.
```

Use-bound: Should the landscape boundary be counted as an edge? {y/n}. This is only required if the input image does not contain a landscape border. This effects all edge indices.

Appendix C. Definition and description of FRAGSTATS metrics.

In this section, I describe each statistic computed in FRAGSTATS. Statistics are grouped into patch, class, and landscape indices. Within each group, statistics are ordered in logical fashion according to the aspect of landscape structure measured. For example, the core area metrics (i.e., those based on core area measurements) are grouped together. Each metric is defined mathematical terms, and the measurement units and theoretical range in values are reported. The acronym for the metric given on the left-hand side of the equation is the field name used in the ASCII output files. Where the vector and raster algorithms differ, I define both. A single notation scheme is used consistently for all metrics (Table. C.1). To facilitate interpretation of the algorithm, I intentionally separate from each equation any constants used to rescale the metric. For example, in many cases the right-hand side of the equation is multiplied by 100 to convert a proportion to a percentage, or multiplied or divided by 10,000 to convert m^2 to hectares. These conversion factors are separated out by parentheses even though they are often factored into the equation differently in the computational form of the algorithm. For each metric, the mathematical formula is described in narrative terms to facilitate interpretation of the formula. To facilitate the ecological interpretation of each metric, I also refer to the FRAGSTATS output in Figures 3.4-3.6.

Table C.1. Notation used in FRAGSTATS algorithms.

Subscripts

$i = 1, \dots, m$ or m' patch types (classes)

$j = 1, \dots, n$ patches

$k = j, \dots, m$ or m' patch types (classes)

Symbols

$A =$	Total landscape area (m^2).
$a_{ij} =$	area (m^2) of patch ij.
$a^c_{ij} =$	core area (m^2) of patch ij based on specified buffer width (m).
$p_{ij} =$	perimeter (m) of patch ij.
$p_{ijk} =$	length (m) of edge of patch ij adjacent to patch type (class) k.
$E =$	total length (m) of edge in landscape, including landscape boundary segments representing true edge.
$E' =$	total length (m) of edge in landscape, including entire landscape boundary regardless of whether it represents true edge or not.

Table C.1. Continued.

e_{ik} =	total length (m) of edge in landscape between patch types (classes) i and k, including landscape boundary segments representing true edge involving patch type i.
e'_{ik} =	total length (m) of edge in landscape between patch types (classes) i and k, including all landscape boundary segments involving patch type i, including those not representing true edge.
e''_{ik} =	total length (m) of edge in landscape between patch types (classes) i and k, including the entire landscape boundary regardless of whether it represents true edge or not.
d_{ik} =	dissimilarity (edge contrast weight) between patch types i and k.
N =	total number of patches in the landscape.
N' =	total number of patches in the landscape that have nearest neighbors.
$n = n_i$ =	number of patches in the landscape of patch type (class) i.
$n' = n'_i$ =	number of patches in the landscape of patch type (class) i that have nearest neighbors.
n^c_{ij} =	number of disjunct core areas in patch ij based on specified buffer width (m).
m =	number of patch types (classes) present in the landscape, excluding the landscape border if present.
m' =	number of patch types (classes) present in the landscape, including the landscape border if present.
m_{max} =	maximum number of patch types (classes) present in a landscape.
h_{ij} =	nearest (m) neighboring patch to patch ij of the same type (class).
G_{ik} =	number of adjacencies (joins) between pixels of patch types (classes) i and k.
P_i =	proportion of the landscape occupied by patch type (class) i.

Patch Indices

(P1) Landscape ID

The first field in the patch output file is landscape ID (LID). The vector version of FRAGSTATS contains a command line option (landscape_id) to name the landscape. If landscape_id is not specified, LID is set to the name of the input coverage (coverage). In the raster version of FRAGSTATS, LID is set to the name of the input image (in_image).

(P2) Patch ID

The second field in the patch output file is patch ID (PID). The vector version of FRAGSTATS contains a command line option (patch_id) to name an attribute that contains unique ID's for each patch. Likewise, the raster version of FRAGSTATS contains a command line option (id_image) to name an image that contains unique ID's for each patch. In both versions, if the patch ID options are not used, FRAGSTATS will create unique ID's for each patch and produce an image that contains patch ID's that correspond to the FRAGSTATS output.

(P3) Patch Type

The third field in the patch output file is patch type (TYPE). The vector version of FRAGSTATS contains a command line option (descriptor) to name an attribute that contains character descriptors for each patch type. Likewise, the raster version of FRAGSTATS contains a command line option (desc_file) to name an ASCII file that contains character descriptors for each patch type. In both versions, if the patch type options are not used, FRAGSTATS will write the numeric patch type codes to TYPE.

(P4) Area

Vector/Raster

$$\boxed{\text{AREA} = a_{ij}\left(\frac{1}{10{,}000}\right)}$$

Units: Hectares

Range: AREA > 0, without limit.

Ultimately, AREA is limited by the grain and extent of the image and, in a particular application, AREA may be further limited by the specification of a minimum patch size that is larger than the grain.

Description: AREA equals the area (m^2) of the patch, divided by 10,000 (to convert to hectares).

(P5) Perimeter

Vector/Raster

$$\boxed{\text{PERIM} = p_{ij}}$$

Units: Meters

Range: PERIM > 0, without limit.

Description: PERIM equals the perimeter (m) of the patch.

(P6) Shape Index

Vector

$$\boxed{\text{SHAPE} = \frac{p_{ij}}{2\sqrt{\pi \cdot a_{ij}}}}$$

Raster

$$\boxed{\text{SHAPE} = \frac{.25\ p_{ij}}{\sqrt{a_{ij}}}}$$

Units: None

Range: SHAPE ≥ 1, without limit.

SHAPE = 1 when patch is circular (vector) or square (raster) and increases without limit as patch shape becomes more irregular.

Description: SHAPE equals patch perimeter (m)[PERIM] divided by the square root of patch area (m^2)[AREA], adjusted by a constant to adjust for a circular standard (vector) or square standard (raster).

Example: Figure 3.4 depicts 3 patches extracted from a sample landscape that vary in shape. In particular, patch A has a much more complex shape than either patch B or C. Accordingly, the SHAPE index for the former patch is almost twice as large as that for the latter 2 patches. In addition, the subtle difference in shape complexity between patch B and C is reflected in a rather small difference in their SHAPE indices. Overall, SHAPE does a good job of quantifying differences in shape complexity among these patches.

(P7) Fractal Dimension

Vector

$$\boxed{FRACT = \frac{2 \ln p_{ij}}{\ln a_{ij}}}$$

Raster

$$\boxed{FRACT = \frac{2 \ln (.25\ p_{ij})}{\ln a_{ij}}}$$

Units: None

Range: $1 \leq FRACT \leq 2$

A fractal dimension grater than 1 for a 2-dimensional patch indicates a departure from a euclidean geometry (i.e., an increase in shape complexity). FRACT approaches 1 for shapes with very simple perimeters such as circles or squares, and approaches 2 for shapes with highly convoluted, plane-filling perimeters.

Description: FRACT equals 2 times the logarithm of patch perimeter (m)[PERIM] divided by the logarithm of patch area (m^2)[AREA]; the raster formula is adjusted to correct for the bias in perimeter (Li 1989).

Example: Figure 3.4 depicts 3 patches extracted from a sample landscape that vary in shape. In particular, patch A has a much more complex shape than either patch B or C. Accordingly, the FRACT index for the former patch is somewhat larger than that for the latter 2 patches. However, the magnitude of difference between FRACT values is notably less than SHAPE values. In addition, the subtle difference in shape complexity between patch B and C is barely reflected in their FRACT indices. Overall, FRACT does reflect differences in shape complexity, but appears to be less sensitive to differences than SHAPE.

(P8) Core Area

Vector/Raster

$$\boxed{\text{CORE} = a_{ij}^{c}\left(\frac{1}{10{,}000}\right)}$$

Units: Hectares

Range: CORE ≥ 0, without limit.

CORE = 0 when every location within the patch is within the specified edge distance from the patch perimeter (i.e., edge width). CORE approaches AREA as the specified edge distances decrease and as patch shape is simplified.

Description: CORE equals the area (m^2) within the patch that is greater than the specified edge distance from the patch perimeter, divided by 10,000 (to convert to hectares).

Example: Figure 3.4 depicts 3 patches extracted from a sample landscape that vary in core area based on a 100 m edge width for all edge types. Although patch A is almost 3 times larger than patch C, it has less than twice the core area of C. This is because patch A has a more complex shape than patch C and therefore a greater edge-to-interior ratio. Note also that although patch B and C are almost equal in size, patch B has half the core area of patch C. This is a result of the interaction among patch size, patch shape, and edge width. With a 100 m edge width, the subtle difference in shape between patch B and C results in a large difference in core area. A much larger edge width (e.g., 200 m) would result in both patches having zero core area because of their small size, and a much smaller edge width (e.g., 10 m) would result in both patches having similar core areas. Thus, the effect of patch shape on core area is dependent on both patch size and edge width.

(P9) Number of Core Areas

Vector/Raster

$$\boxed{\text{NCORE} = n_{ij}^{c}}$$

Units: None

Range: NCORE ≥ 0, without limit.

NCORE = 0 when CORE = 0 [i.e., every location within the patch is within the specified edge distance from the patch perimeter (i.e., edge width)]. NCORE > 1 when, because of shape, the patch contains disjunct core areas.

Description: NCORE equals the number of disjunct core areas contained within the patch boundary.

Example: Figure 3.4 depicts 3 patches extracted from a sample landscape that vary in number of core areas based on a 100 m edge width for all edge types. Patches B and C both contain 1 core area because of their simple shapes. Patch A, however, contains 2 core areas because it is narrower than 200 m in 1 section and wider on both sides. Thus, under certain conditions it may be more meaningful to treat patch A as 2 separate patches. For example, if an organism avoided edge habitat up to a distance of 100 m, then from the organism's perspective, patch A may actually contain 2 separate suitable habitat patches. However, like CORE, NCORE is affected by the interaction of patch size, patch shape, and edge width. With a much larger edge width (e.g., 200 m) or much smaller edge width (e.g., 10 m), patch A would contain only 1 core area.

(P10) Core Area Index

Vector/Raster

$$\boxed{CAI = \frac{a_{ij}^{c}}{a_{ij}} (100)}$$

Units: Percent

Range: $0 \leq CAI < 100$

CAI = 0 when CORE = 0 (i.e., every location within the patch is within the specified edge distance from the patch perimeter (i.e., edge width); that is, when the patch contains no core area. CAI approaches 100 when the patch, because of size, shape, and edge width, contains mostly core area.

Description: CAI equals the patch core area (m^2)[CORE] divided by total patch area (m^2)[AREA], multiplied by 100 (to convert to a percentage); in other words, CAI equals the percentage of a patch that is core area.

Example: Figure 3.4 depicts 3 patches extracted from a sample landscape that vary in core area index based on a 100 m edge width for all edge types. Although patch A is almost 3 times larger than patch B and has a more complex shape, it has roughly the same CAI as patch B. Thus, these 2 patches have about the same proportion of core area, even though they differ markedly in absolute size and shape. In contrast, patch B has about half the CAI as patch C, even though they are similar in size and shape. Because of the interaction of patch size, patch shape, and edge width, the slightly more complex shape of patch B results in disproportionately less core area and therefore a much smaller CAI than patch C. Again, note the effect of the interaction among patch size, patch shape, and edge width on this index.

(P11) Landscape Similarity

Vector/Raster

$$\boxed{\mathrm{LSIM} = P_i = \frac{\sum_{j=1}^{n} a_{ij}}{A}(100)}$$

Units: Percent

Range: $0 < \mathrm{LSIM} \leq 100$

LSIM approaches 0 when the corresponding patch type (class) becomes increasingly rare in the landscape. LSIM = 100 when the entire landscape consists of a single patch type; that is, when the entire image is comprised of a single patch.

Description: LSIM equals total class area (m^2)[CA] divided by total landscape area (m^2)[TA], multiplied by 100 (to convert to a percentage); in other words, LSIM equals the percentage the landscape comprised of the corresponding patch type.

Example: Figure 3.4 depicts 3 patches extracted from a sample landscape that vary in landscape similarity. According to LSIM, roughly 50% of the sample landscape is MLS (mixed, large sawtimber). Thus, patch A is not very insular because half of surrounding landscape is of the same type. In contrast, patches B and C represent relatively rare patch types because only 8% of the sample landscape is similar to the respective patch types. The dynamics of some ecological processes are likely to be quite different between patch A and patches B and C. For example, an organism inhabiting patch A and dependent on the MLS patch type is likely to experience a different population dynamic than a similar organism occupying either patch B or C because of the larger regional population size and probable increased interaction among individuals inhabiting the landscape. On the other hand, because of their rarity, patch B and C probably contribute more to landscape diversity and, e.g., vertebrate diversity, than patch A.

(P12) Nearest Neighbor

Vector/Raster

$$\boxed{\mathrm{NEAR} = h_{ij}}$$

Units: Meters

Range: NEAR > 0, without limit.

NEAR is reported as "None" in the formatted output file and "N/A" in the ASCII output file if no other patch of the same type exists in the landscape. Likewise, in the vector version, if the rasterization process creates more or less patches than are present in the vector image (see below), then NEAR is reported as "N/A".

Description: NEAR equals the distance (m) to the nearest neighboring patch of the same type, based on nearest edge-to-edge distance.

Example: Figure 3.4 depicts 3 patches extracted from a sample landscape that vary in nearest neighbor distance. Patch A has the closest nearest neighbor, followed by patch B and C. This index supports the conclusion drawn from LSIM that patch A is the least insular of the 3 patches. However, because of the relatively small landscape extent relative to patch size, nearest neighbor distances are probably not meaningful in this sample landscape.

(P13) Edge Contrast Index

Vector/Raster

$$\boxed{EDGECON = \frac{\sum_{k=1}^{m'} (p_{ijk} \cdot d_{ik})}{p_{ij}} (100)}$$

Units: Percent

Range: $0 \le EDGECON \le 100$

EDGECON = 0 if the landscape consists of only 1 patch and the boundary contains no edge (when a border is present) or the boundary is not to be treated as edge (when a border is absent). EDGECON = 100 when the patch perimeter is entirely maximum-contrast edge ($d = 1$). EDGECON < 100 when a portion of the patch perimeter is less than maximum-contrast edge ($d < 1$).

Description: EDGECON equals the sum of the patch perimeter segment lengths (m) multiplied by their corresponding contrast weights, divided by total patch perimeter (m)[PERIM], multiplied by 100 (to convert to a percentage).

Example: Figure 3.4 depicts 3 patches extracted from a sample landscape that vary in edge contrast. Patch A has the least contrast with its neighborhood, where contrast represents the degree of floristic and structural differences in the vegetation. This is because patch A is a mixed, large sawtimber patch surrounded largely by conifer and hardwood, large sawtimber patches. Thus, the differences in plant composition and stand structure along the patch edges are relatively subtle. Moreover, the transitions between patch A and these other large sawtimber patches are probably somewhat gradual. Consequently, although there are important differences between these adjacent patches that warrant their discrimination, the contrast between them is very low. An animal dispersing from patch A, for example, might not be impeded at all by the low-contrast boundary of patch A. In contrast to patch A, patch C is a mixed, grass/forb (MGF) patch surrounded mostly by large sawtimber patches. Hence, the degree of structural contrast between patch C and its neighborhood is very high. The EDGECON values indicate that the perimeter of patch C has the equivalent of 80% of its perimeter in maximum-contrast edge, whereas the perimeter of patch A has the equivalent of only 17% of its perimeter in maximum-contrast edge. EDGECON appears to do a good job of quantifying differences in insularity among these patches.

Class Indices

(C1) Landscape ID (LID)

The first field in the class output file is landscape ID (LID); it is defined as in the patch output file (see previous discussion).

(C2) Patch Type (TYPE)

The second field in the class output file is patch type (TYPE); it is defined as in the patch output file (see previous discussion).

(C3) Total Area

Vector/Raster

$$\boxed{TA = A\left(\frac{1}{10{,}000}\right)}$$

Units: Hectares

Range: $TA > 0$, without limit.

Description: TA equals the area (m^2) of the landscape, divided by 10,000 (to convert to hectares).

(C4) Class Area

Vector/Raster

$$\boxed{CA = \sum_{j=1}^{n} a_{ij}\left(\frac{1}{10,000}\right)}$$

Units: Hectares

Range: CA > 0, without limit.

CA approaches 0 as the patch type becomes increasing rare in the landscape. CA = TA when the entire landscape consists of a single patch type; that is, when the entire image is comprised of a single patch.

Description: CA equals the sum of the areas (m^2) of all patches of the corresponding patch type, divided by 10,000 (to convert to hectares); that is, total class area.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. Landscapes B and C have similar amounts of MLS, whereas landscape A has considerably less. Thus, the dynamics of some ecological processes are likely to be quite different in landscape A compared to either B or C. For example, populations of organisms associated with MLS are likely to be much smaller in landscape A and perhaps subject to a higher probability of local extinction than in either B or C. On the other hand, MLS probably contributes proportionately more to landscape diversity and, e.g., species diversity, in landscape A than in either B or C.

(C5) Number of Patches

Vector/Raster

$$\boxed{NP = n_i}$$

Units: None

Range: NP ≥ 1, without limit.

NP = 1 when the landscape contains only 1 patch of the corresponding patch type; that is, when the class consists of a single patch.

Description: NP equals the number of patches of the corresponding patch type (class).

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. Although the 3 landscapes vary considerably in both amount and distribution of MLS, NP alone does not capture these landscape structural differences very well. For example, landscapes A and B differ dramatically in amounts of MLS (see CA), yet have about the same number of patches of MLS. NP does indicate, however, that the MLS is more subdivided in landscape B than landscape C, and because class area is roughly the same, landscape B may be considered more fragmented than landscape C. Thus, in the example landscapes, NP is best considered only in conjunction with other indices such as class area.

(C6) Patch Density

Vector/Raster

$$\boxed{PD = \frac{n_i}{A}(10{,}000)(100)}$$

Units: Number per 100 hectares

Range: PD > 0, without limit.

Description: PD equals the number of patches of the corresponding patch type (NP) divided by total landscape area, multiplied by 10,000 and 100 (to convert to 100 hectares).

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. Although the 3 landscapes vary considerably in both amount and distribution of MLS, PD alone does not capture these landscape structural differences very well. Because total landscape area is similar among the landscapes, PD and NP convey the same information (see NP discussion). In the example landscapes, PD is best considered in conjunction with other indices such as class area.

(C7) Mean Patch Size

Vector/Raster

$$\boxed{MPS = \frac{\sum_{j=1}^{n} a_{ij}}{n_i}\left(\frac{1}{10{,}000}\right)}$$

Units: Hectares

Range: MPS > 0, without limit.

Ultimately, the range in MPS is limited by the grain and extent of the image and the minimum patch size in the same manner as patch area (AREA).

Description: MPS equals the sum of the areas (m^2) of all patches of the corresponding patch type, divided by the number of patches of the same type (NP), divided by 10,000 (to convert to hectares).

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. MPS alone does a good job of ranking the 3 landscapes with respect to MLS fragmentation (A being most fragmented, C being least). However, MPS is most informative when interpreted in conjunction with class area (CA), patch density (PD) and patch size variability (PSSD or PSCV). Based on these metrics, landscape A contains several very small, but similar sized, patches of MLS; whereas, landscape B also contains several similar sized patches of MLS, but the patches are much larger. Thus, the MLS in landscape A and B is fragmented to a similar a degree, but landscape A has undergone much more loss of MLS forest than landscape B. Overall, landscape A is much farther along in the fragmentation process than landscape B. Similarly, landscape B and C contain the same amount of MLS, but the MLS is fragmented into several smaller fragments in landscape B, whereas in landscape C, the MLS is broken into fewer fragments of greatly varying size. Thus, the MLS in landscape B is more fragmented than in landscape C, although they have both undergone the same degree of loss in MLS area.

(C8) Patch Size Standard Deviation

Vector/Raster

$$\boxed{\mathrm{PSSD} = \sqrt{\frac{\sum_{j=1}^{n}\left[a_{ij} - \left(\frac{\sum_{j=1}^{n} a_{ij}}{n_i}\right)\right]^2}{n_i}}\left(\frac{1}{10{,}000}\right)}$$

Units: Hectares

Range: PSSD ≥ 0, without limit.

PSSD = 0 when all patches in the class are the same size or when there is only 1 patch (i.e., when there is no variability in patch size).

Description: PSSD equals the square root of the sum of the squared deviations of each patch area (m^2) from the mean patch size of the corresponding patch type, divided by the number of patches of the same type (NP), divided by 10,000 (to convert to hectares); that is, the root mean squared error (deviation from the mean) in patch size. Note, this is the population standard deviation, not the sample standard deviation.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. PSSD alone does not tell us much about relative differences in patch size variability among the landscapes. For example, PSSD for landscape A is several times smaller than for landscape B, yet relative to their respective mean patch sizes, these 2 landscapes have similar variability in patch sizes (i.e., standard deviation roughly equivalent to the mean in both landscapes).

(C9) Patch Size Coefficient of Variation

Vector/Raster

$$\boxed{PSCV = \frac{PSSD}{MPS}(100)}$$

Units: Percent

Range: PSCV ≥ 0, without limit.

PSCV = 0 when all patches in the class are the same size or when there is only 1 patch (i.e., when there is no variability in patch size).

Description: PSCV equals the standard deviation in patch size (PSSD) divided by the mean patch size of the corresponding patch type (MPS), multiplied by 100 (to convert to percent); that is, the variability in patch size relative to the mean patch size. Note, this is the population coefficient of variation, not the sample coefficient of variation.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. PSCV indicates that patch size variability in landscape A is roughly the same as in landscape B, even though mean patch size (MPS) is considerably smaller in landscape A. In other words, variation about the means are similar. The greater PSCV in landscape C indicates a much larger variation in patch sizes. Landscapes A and B have been subject to greater human disturbance in the form of timber management activities than landscape C. Differences in PSCV suggest that the human-altered landscapes contain less heterogeneity in terms of patch sizes than the unaltered landscape.

(C10) Landscape Similarity

Vector/Raster

$$\boxed{LSIM = P_i = \frac{\sum_{j=1}^{n} a_{ij}}{A}(100)}$$

Units: Percent

Range: $0 < \text{LSIM} \leq 100$

LSIM approaches 0 when the corresponding patch type (class) becomes increasingly rare in the landscape. LSIM = 100 when the entire landscape consists of a single patch type; that is, when the entire image is comprised of a single patch.

Description: LSIM equals the sum of the areas (m^2) of all patches of the corresponding patch type, divided by total landscape area (m^2), multiplied by 100 (to convert to a percentage); in other words, LSIM equals the percentage the landscape comprised of the corresponding patch type.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. According to LSIM, roughly 50% of landscapes B and C are MLS, whereas only 5% of landscape A is MLS. Consequently, the dynamics of some ecological processes are likely to be quite different between landscape A and landscapes B and C. For example, an organism dependent on the MLS patch type is likely to experience a different population dynamic in landscape A than in either landscape B or C because of smaller populations and greater isolation. In addition, LSIM indicates that landscapes B and C are very similar in composition with respect to MLS, although other indices suggest that they vary greatly in pattern.

(C11) Total Core Area

Vector/Raster

$$\boxed{\text{TCA} = \sum_{j=1}^{n} a_{ij}^{c} \left(\frac{1}{10{,}000} \right)}$$

Units: Hectares

Range: $\text{TCA} \geq 0$, without limit.

TCA = 0 when every location within each patch of the corresponding patch type is within the specified edge distances from the patch perimeters. TCA approaches CA as the specified edge distances decrease and as patch shapes are simplified.

Description: TCA equals the sum of the core areas of each patch (m^2) of the corresponding patch type, divided by 10,000 (to convert to hectares).

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. TCA indicates that although landscape A contains 4 MLS patches encompassing a total of 13 ha, there is no MLS core area; that is, no point in an MLS patch greater than 100 m from the patch perimeter. Although landscapes B and C have similar amounts of MLS, TCA indicates that landscape B has much less core area than landscape C, suggesting a much more fragmented (greater edge-to-interior ratio) arrangement of MLS in landscape B than C. Note also that TCA, like CORE, is a result of the interaction among patch size, patch shape, and edge width (see example for CORE under patch indices).

(C12) Number of Core Areas

Vector/Raster

$$\boxed{NCA = \sum_{j=1}^{n} n_{ij}^{c}}$$

Units: None

Range: NCA ≥ 0, without limit.

NCA = 0 when TCA = 0 (i.e., every location within patches of the corresponding patch type are within the specified edge distances from the patch perimeters).

Description: NCA equals the sum of the number of disjunct core areas contained within each patch (NCORE) of the corresponding patch type; that is, the number of disjunct core areas contained within the landscape.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. NCA and TCA differ among landscapes similarly. Relative to NP, the differences between landscape B and C are even more pronounced with NCA, indicating that the MLS in landscape B is indeed more fragmented than in landscape C. Note also that NCA, like TCA, is affected by the interaction of patch size, patch shape, and edge width. For example, with a much larger edge width (e.g., 200 m) or much smaller edge width (e.g., 10 m), NCA would change dramatically, especially in landscapes A and B because of the size and shapes of the MLS patches in those landscapes..

(C13) Core Area Density

Vector/Raster

$$\boxed{CAD = \frac{\sum_{j=1}^{n} n_{ij}^{c}}{A}(10{,}000)(100)}$$

Units: Number per 100 hectares

Range: CAD ≥ 0, without limit.

CAD = 0 when TCA = 0 (i.e., every location within patches of the corresponding patch type are within the specified edge distances from the patch perimeters); in other words, when there are no core areas.

Description: CAD equals the sum of number of disjunct core areas contained within each patch (NCORE) of the corresponding patch type (NCA), divided by total landscape area, multiplied by 10,000 and 100 (to convert to 100 hectares).

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. Compared to PD, CAD does a much better job of characterizing differences in landscape structure. For example, although landscapes A and B have similar patch densities, CAD differs dramatically between them. Landscape A has no core areas, indicating that the MLS is highly fragmented into very small patches; whereas, landscape B has a comparatively high core area density. Similarly, although landscapes B and C have similar amounts of MLS (CA), the core area in landscape B is fragmented into several disjunct areas, whereas in landscape C it is more contiguous. Although the 3 landscapes vary considerably in both amount and distribution of MLS, it is difficult to interpret these landscape structural differences by CAD alone; CAD is best interpreted in conjunction with other indices such as total class area. Also, because total landscape area is similar among the landscapes, CAD and NCA convey the same information.

(C14) Mean Core Area

Vector/Raster

$$\boxed{MCA = \frac{\sum_{j=1}^{n} a_{ij}^{c}}{n_i}\left(\frac{1}{10{,}000}\right)}$$

Units: Hectares

Range: MCA ≥ 0, without limit.

Ultimately, the range in MCA is limited by the grain and extent of the image and the minimum patch size in the same manner as mean patch size (MPS), but MCA is also effected by the specified edge widths. MCA = 0 when TCA = 0 (i.e., every location within patches of the corresponding patch type are within the specified edge distances from the patch perimeters); in other words, when there are no core areas. MCA approaches MPS as the specified edge widths decrease and as patch shapes are simplified.

Description: MCA equals the sum of the core areas of each patch (m^2) of the corresponding patch type, divided by the number of patches of the same type (NP), divided by 10,000 (to convert to hectares).

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. Although MPS does a good job of ranking the 3 landscapes with respect to MLS fragmentation (A being most fragmented, C being least), MCA distinguishes the different stages of fragmentation even more distinctly. Like MPS, MCA is most informative when interpreted in conjunction other indices such as total class area (CA), patch density (PD) and patch size variability (PSSD or PSCV). For example, it is difficult to tell from MCA alone if the differences between landscapes B and C are because of differences in MLS area or MLS pattern. However, by interpreting both CA and MCA, it becomes clear that the differences are due solely to pattern.

(C15) Core Area Standard Deviation

Vector/Raster

$$\boxed{\mathrm{CASD} = \sqrt{\frac{\sum_{j=1}^{n}\left[a_{ij}^{c} - \left(\frac{\sum_{j=1}^{n} a_{ij}^{c}}{n_i}\right)\right]^2}{n_i}}\left(\frac{1}{10{,}000}\right)}$$

Units: Hectares

Range: CASD ≥ 0, without limit.

CASD = 0 when all patches in the class have the same core area or when there is only 1 patch (i.e., when there is no variability in core area).

Description: CASD equals the square root of the sum of the squared deviations of each patch core area (m^2) from the mean core area of the corresponding patch type, divided by the number of patches of the same type (NP), divided by 10,000 (to convert to hectares); that is, the root mean squared error (deviation from the mean) in patch core area. Note, this is the population standard deviation, not the sample standard deviation.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. CASD alone does not tell us much about differences in structure among the 3 landscapes. For example, it is difficult to interpret the difference in CASD between landscapes B and C without simultaneously considering MCA.

(C16) Core Area Coefficient of Variation

Vector/Raster

$$\boxed{\mathrm{CACV} = \frac{\mathrm{CASD}}{\mathrm{MCA}}(100)}$$

Units: Percent

Range: CACV ≥ 0, without limit.

CACV = 0 when all patches in the class have the same core area or when there is only 1 patch (i.e., when there is no variability in core area).

Description: CACV equals the standard deviation in core area (CASD) divided by the mean core area of the corresponding patch type (MCA), multiplied by 100 (to convert to percent); that is, the variability in core area relative to the mean core area. Note, this is the population coefficient of variation, not the sample coefficient of variation.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. CACV indicates that core area variability decreases progressively from the least (C) to the most (A) fragmented landscape. As discussed previously for PSCV, this suggests that timber management activities have tended to reduce heterogeneity in terms of patch sizes.

(C17) Landscape Core Area Similarity

Vector/Raster

$$\boxed{\mathrm{LCAS} = \frac{\sum_{j=1}^{n} a_{ij}^{c}}{A}(100)}$$

Units: Percent

Range: 0 < LCAS < 100

LCAS approaches 0 when core area of the corresponding patch type (class) becomes increasingly rare in the landscape, because of increasing smaller patches and/or more convoluted patch shapes. LCAS approaches 100 when the entire landscape consists of a single patch type (i.e., when the entire image is comprised of a single patch) and the specified edge widths approach zero.

Description: LCAS equals the sum of the core areas of each patch (m^2) of the corresponding patch type, divided by total landscape area (m^2), multiplied by 100 (to convert to a percentage); in other words, LCAS equals the percentage

100 (to convert to a percentage); in other words, LCAS equals the percentage the landscape comprised of core area of the corresponding patch type.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. According to LSIM, roughly 50% of landscapes B and C are MLS. However, according to LCAS, only 10% of landscape B is MLS core area, whereas 23% of landscape C is MLS core area. Thus, LCAS clearly indicates that landscape B is fragmented to a much greater degree than landscape C. Inspection of LCAS alone does not indicate whether differences in the amount of core area are because of differences in total MLS area, the pattern of MLS, or both. Nevertheless, for an MLS-interior specialist, LCAS suggests that landscape C contains twice the suitable habitat as landscape B.

(C18) Total Core Area Index

Vector/Raster

$$\boxed{TCAI = \frac{\sum_{j=1}^{n} a_{ij}^{c}}{\sum_{j=1}^{n} a_{ij}} (100)}$$

Units: Percent

Range: $0 \leq TCAI < 100$

TCAI = 0 when none of the patches of the corresponding patch type contain any core area (i.e., CORE = 0 for every patch); that is, when the landscape contains no core area for the corresponding patch type. TCAI approaches 100 when the patches of the corresponding patch type, because of size, shape, and edge width, contain mostly core area.

Description: TCAI equals the sum of the core areas of each patch (m^2) of the corresponding patch type, divided by the sum of the areas of each patch (m^2) of the same type, multiplied by 100 (to convert to a percentage); that is, TCAI equals the percentage of a patch type in the landscape that is core area.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. Alone, TCAI accurately represents the 3 landscapes along a continuum from most to least fragmented. Only 20% of the MLS in landscape B is interior, the remaining 80% is edge habitat. Thus, without any other information on landscape B, it could be deduced that the MLS is highly fragmented. However, interpreted in conjunction with LSIM and compared to Landscape C, it becomes even more clear that landscapes B and C differ exclusively in pattern and not area and that landscape B is indeed more fragmented than landscape C.

(C19) Mean Core Area Index

Vector/Raster

$$\boxed{\mathrm{MCAI} = \frac{\sum_{j=1}^{n}\left(\frac{a_{ij}^{c}}{a_{ij}}\right)}{n_i}(100)}$$

Units: Percent

Range: $0 \leq \mathrm{MCAI} < 100$

MCAI = 0 when none of the patches of the corresponding patch type contain any core area (i.e., CORE = 0 for every patch); that is, when the landscape contains no core area for the corresponding patch type. MCAI approaches 100 when the patches of the corresponding patch type, because of size, shape, and edge width, contain mostly core area.

Description: MCAI equals the sum of the proportion of each patch that is core area {i.e., core area of each patch (m^2) divided by the area of each patch (m^2), or CAI} of the corresponding patch type, divided by the number of patches of the same type (NP), multiplied by 100 (to convert to a percentage); In other words, MCAI equals the average percentage of a patch of the corresponding patch type in the landscape that is core area.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. Alone, MCAI indicates that all 3 landscapes are highly fragmented and, in particular, that landscapes B and C are roughly equally fragmented. I know from TCAI and other indices that landscape B is in fact more fragmented than landscape C. MCAI for landscape C is much lower than TCAI because of the high variability in core area among the 3 patches (CACV). The large core area of the one patch is offset by the zero core area of the smallest patch and the very small core area of the middle-sized patch. This bias is characteristic of first-order statistics such the mean, and is particularly pronounced because of the small sample size (n=3 patches) in landscape C. As a result, MCAI does not do a good job of representing the obvious differences among the 3 landscapes.

(C20) Landscape Shape Index

Vector

$$LSI = \frac{\sum_{k=1}^{m} e'_{ik}}{2\sqrt{\pi \cdot A}}$$

Raster

$$LSI = \frac{.25\sum_{k=1}^{m} e'_{ik}}{\sqrt{A}}$$

Units: None

Range: LSI ≥ 1, without limit.

LSI = 1 when the landscape consists of a single patch of the corresponding type and is circular (vector) or square (raster); LSI increases without limit as landscape shape becomes more irregular and/or as the length of edge within the landscape of the corresponding patch type increases.

Description: LSI equals the sum of the landscape boundary (regardless of whether it represents true edge or not) and all edge segments (m) within the landscape boundary involving the corresponding patch type, divided by the square root of the total landscape area (m^2), adjusted by a constant for a circular standard (vector) or square standard (raster).

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. In this case, the landscape boundary does not all represent MLS edge and therefore LSI is not particularly meaningful.

(C21) Mean Shape Index

Vector

$$MSI = \frac{\sum_{j=1}^{n}\left(\frac{p_{ij}}{2\sqrt{\pi \cdot a_{ij}}}\right)}{n_i}$$

Raster

$$MSI = \frac{\sum_{j=1}^{n}\left(\frac{.25p_{ij}}{\sqrt{a_{ij}}}\right)}{n_i}$$

Units: None

Range: MSI ≥ 1, without limit.

MSI = 1 when all patches of the corresponding patch type are circular (vector) or square (raster); MSI increases without limit as the patch shapes become more irregular.

Description: MSI equals the sum of the patch perimeter (m)[PERIM] divided by the square root of patch area (m^2) for each patch of the corresponding patch type, adjusted by a constant to adjust for a circular standard (vector) or square standard (raster), divided by the number of patches of the same type (NP); in other words, MSI equals the average shape index (SHAPE) of patches of the corresponding patch type.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. MSI values for all 3 landscapes are greater than one, indicating that the average patch shape in all 3 landscapes is noncircular. The MLS patches in landscape A area least irregular while the MLS patches in landscape C are most irregular. This agrees with previous conclusions that the more fragmented, human-altered landscapes are more homogeneous in pattern and that the undisturbed landscape contains greater heterogeneity in patch size and shape.

(C22) Area-Weighted Mean Shape Index

Vector

$$\boxed{\mathrm{AWMSI} = \sum_{j=1}^{n} \left[\left(\frac{p_{ij}}{2\sqrt{\pi \circ a_{ij}}} \right) \left(\frac{a_{ij}}{\sum\limits_{j=1}^{n} a_{ij}} \right) \right]}$$

Raster

$$\boxed{\mathrm{AWMSI} = \sum_{j=1}^{n} \left[\left(\frac{.25p_{ij}}{\sqrt{a_{ij}}} \right) \left(\frac{a_{ij}}{\sum\limits_{j=1}^{n} a_{ij}} \right) \right]}$$

Units: None

Range: AWMSI ≥ 1, without limit.

AWMSI = 1 when all patches of the corresponding patch type are circular (vector) or square (raster); AWMSI increases without limit as the patch shapes become more irregular.

Description: AWMSI equals the sum, across all patches of the corresponding patch type, of each patch perimeter (m)[PERIM] divided by the square root of patch area (m^2), adjusted by a constant to adjust for a circular standard (vector) or square standard (raster), multiplied by the patch area (m^2) divided by total class area (sum of patch area for each patch of the corresponding patch type). In other words, AWMSI equals the average shape index (SHAPE) of patches of the corresponding patch type, weighted by patch area so that larger patches weigh more than smaller patches.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. AWMSI supports the conclusions drawn from MSI (see MSI discussion). However, AWMSI values for all 3 landscapes are greater than MSI values, indicating the larger patches in each landscape that contribute more to the weighted average are more irregular in shape than the average.

(C23) Double Log Fractal Dimension

Vector/Raster

$$DLFD = \frac{2}{\dfrac{\left[n_i \sum_{j=1}^{n} (\ln p_{ij} \cdot \ln a_{ij})\right] - \left[\left(\sum_{j=1}^{n} \ln p_{ij}\right)\left(\sum_{j=1}^{n} \ln a_{ij}\right)\right]}{\left(n_i \sum_{j=1}^{n} \ln p_{ij}^2\right) - \left(\sum_{j=1}^{n} \ln p_{ij}\right)^2}}$$

Units: None

Range: $1 \leq DLFD \leq 2$

A fractal dimension greater than 1 for a 2-dimensional landscape mosaic indicates a departure from a euclidean geometry (i.e., an increase in patch shape complexity). DLFD approaches 1 for shapes with very simple perimeters such as circles or squares, and approaches 2 for shapes with highly convoluted, plane-filling perimeters.

Description: DLFD equals 2 divided by the slope of regression line obtained by regressing the logarithm of patch area (m^2) against the logarithm of patch perimeter (m)[PERIM].

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. Because of the small sample sizes, DLFD is probably not a reliable index for these 3 landscapes.

(C24) Mean Patch Fractal Dimension

Vector

$$MPFD = \frac{\sum_{j=1}^{n} \left(\frac{2 \ln p_{ij}}{\ln a_{ij}}\right)}{n_i}$$

Raster

$$MPFD = \frac{\sum_{j=1}^{n} \left(\frac{2 \ln (.25 p_{ij})}{\ln a_{ij}}\right)}{n_i}$$

Units: None

Range: $1 \leq MPFD \leq 2$

A fractal dimension greater than 1 for a 2-dimensional landscape mosaic indicates a departure from a euclidean geometry (i.e., an increase in patch shape complexity). MPFD approaches 1 for shapes with very simple perimeters such as circles or squares, and approaches 2 for shapes with highly convoluted, plane-filling perimeters.

Description: MPFD equals the sum of 2 times the logarithm of patch perimeter (m)[PERIM] divided by the logarithm of patch area (m^2) for each patch of the corresponding patch type, divided by the number of patches of the same type (NP); the raster formula is adjusted to correct for the bias in perimeter (Li 1989).

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. MPFD values are similar for all 3 landscapes, however, the rank order of values does not agree with mean shape index (MSI) values. According to MSI, landscape A contains the simplest average MLS patches, but according to MPFD, the opposite is true. The reason for the discrepancy between these indices is not clear; however, MSI agrees more closely with the results of other indices and is therefore considered more reliable in this case.

(C25) Largest Patch Index

Vector/Raster

$$\boxed{LPI = \frac{\max a_{ij}}{A}(100)}$$

Units: Percent

Range: $0 < LPI \leq 100$

LPI approaches 0 when the largest patch of the corresponding patch type is increasing small. LPI = 100 when the entire landscape consists of a single patch of the corresponding patch type; that is, when the largest patch comprises 100% of the landscape.

Description: LPI equals the area (m^2) of the largest patch of the corresponding patch type divided by total landscape area, multiplied by 100 (to convert to a percentage); in other words, LPI equals the percent of the landscape that the largest patch comprises.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. Alone, LPI accurately represents the 3 landscapes along a continuum from most to least fragmented. The largest patch in landscape A comprises only 2.5% of the landscape, whereas in landscape C it comprises 47% of the landscape. Interpreted in conjunction with CA or LSIM, LPI discriminates clearly between the fragmentation levels of landscapes B and C. Although MLS is equally abundant in both landscapes, LPI indicates that the MLS is more fragmented into smaller patches in landscape B than landscape C.

(C26) Total Edge

Vector/Raster

$$\boxed{TCE = \sum_{k=1}^{m'} e_{ik}}$$

Units: Meters

Range: TE ≥ 0, without limit.

TE = 0 when there is no class edge in the landscape; that is, when the entire landscape and landscape border, if present, consists of the corresponding patch type and the landscape boundary is not treated as edge if a landscape border is absent.

Description: TE equals the sum of the lengths (m) of all edge segments involving the corresponding patch type. If a landscape border is present, TE includes landscape boundary segments representing true edge only (i.e., contrast weight > 0). If a landscape border is absent and the user specifies that the boundary be treated as true edge, TE includes landscape boundary segments involving the corresponding patch type; otherwise, all boundary segments are ignored.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. Total edge is lowest for landscape A and highest for landscape B. Depending on the application, TE can be interpreted differently. For example, the process of habitat fragmentation involves both habitat loss and changes in habitat pattern. Over the course of fragmentation, the percent of the landscape composed of the particular habitat type (LSIM) would go from 100% to 0%. Total class edge would be expected to peak at LSIM = 50%, depending on the pattern of habitat loss (Franklin and Forman (1987). Thus, from a fragmentation perspective, TE is best interpreted in conjunction with LSIM. In this case, although landscapes B and C have undergone the same amount of MLS loss (i.e., similar LSIM values), TE indicates that the MLS in landscape B is more highly fragmented than in landscape C. Alternatively, consider a species that requires MLS edge habitat. Total edge might be used to model habitat suitability. In this case, landscape A would be least suitable, landscape B most suitable, and landscape C in between.

(C27) Edge Density

Vector/Raster

$$CED = \frac{\sum_{k=1}^{m'} e_{ik}}{A}(10{,}000)$$

Units: Meters per hectare.

Range: ED ≥ 0, without limit.

ED = 0 when there is no class edge in the landscape; that is, when the entire landscape and landscape border, if present, consists of the corresponding patch type and the landscape boundary is not treated as edge if a landscape border is absent.

Description: ED equals the sum of the lengths (m) of all edge segments involving the corresponding patch type (TCE), divided by the total landscape area (m^2), multiplied by 10,000 (to convert to hectares). If a landscape border is present, ED includes landscape boundary segments representing true edge only (i.e., contrast weight > 0). If a landscape border is absent and the user specifies that the boundary be treated as true edge, ED includes landscape boundary segments involving the corresponding patch type; otherwise, all boundary segments are ignored.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. Because these landscapes are similar in size, ED and TE are largely redundant; therefore, the conclusions drawn from ED and TE are the same (see TE example).

(C28) Contrast-Weighted Edge Density

Vector/Raster

$$CWCED = \frac{\sum_{k=1}^{m'} (e_{ik} \cdot d_{ik})}{A}(10{,}000)$$

Units: Meters per hectare.

Range: CWED ≥ 0, without limit.

CWED = 0 when there is no class edge in the landscape; that is, when the entire landscape and landscape border, if present, consists of the corresponding patch type and the landscape boundary is not treated as edge if a landscape border is absent. CWED increases as the amount of class edge in the landscape increases and/or as the contrast in edges involving the corresponding patch type increase (i.e., contrast weight approaches 1).

Description: CWED equals the sum of the lengths (m) of each edge segment involving the corresponding patch type multiplied by the corresponding contrast weight, divided by the total landscape area (m^2), multiplied by 10,000 (to convert to hectares). If a landscape border is present, CWED includes landscape boundary segments representing true edge only (i.e., contrast weight > 0). If a landscape border is absent and the user specifies that the boundary be treated as true edge, CWED includes landscape boundary segments involving the corresponding patch type as maximum contrast edge (i.e., contrast weight = 1); otherwise, all boundary segments are ignored.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. CWED indicates that although landscape C has roughly 33 meters of MLS edge per hectare, it has the equivalent of roughly only 2 meters of MLS edge per hectare. Thus, the MLS in Landscape C is not very insular; that is, it is surrounded by patches very similar in structure, and any edge effects on MLS (or organisms inhabiting MLS) are likely to be relatively weak. CWED indicates that landscape C has the least equivalent maximum-contrast edge density. This differs from the results of TE and ED, which both suggest that landscape A has the least edge. If the contrast weighting scheme used here is particularly meaningful, then CWED may be a more meaningful index to edge effects than either TE or ED.

(C29) Total Edge Contrast Index

Vector/Raster

$$\boxed{TCECI = \frac{\sum_{k=1}^{m'} (e_{ik} \cdot d_{ik})}{\sum_{k=1}^{m'} e'_{ik}} (100)}$$

Units: Percent.

Range: $0 \leq TECI \leq 100$

TECI = 0 when there is no class edge in the landscape; that is, when the entire landscape and landscape border, if present, consists of the corresponding patch type and the landscape boundary is not treated as edge if a landscape border is absent. TCECI approaches 0 as the contrast in edges involving the corresponding patch type lesson (i.e., contrast weight approaches 0). TECI = 100 when all class edge is maximum contrast (i.e., contrast weight = 1).

Description: TECI equals the sum of the lengths (m) of each edge segment involving the corresponding patch type multiplied by the corresponding contrast weight, divided by the sum of the lengths (m) of all edge segments involving the same type, multiplied by 100 (to convert to a percentage). If a landscape border is present, TECI includes all landscape boundary segments involving the corresponding patch type, regardless of whether they represent true edge (i.e., contrast weight > 0) or not. If a landscape border is absent and the user specifies that the boundary be treated as true edge, TECI includes landscape boundary segments involving the corresponding patch type as maximum contrast edge (i.e., contrast weight = 1); otherwise, all boundary segments involving the corresponding patch type are treated as zero-contrast edges (i.e., contrast weight = 0).

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. TECI indicates that the MLS edge present in landscape C is of very low contrast; specifically, every 100 meters of edge has a maximum-contrast equivalent of only 4 meters. In contrast, the MLS edge in landscape A is of much higher contrast; every 100 meters of edge has a maximum-contrast equivalent of 40 meters. TECI indicates that although landscape A has the lowest total class edge (TE) and class edge density (ED), the edge contrast is greatest. Similarly, although landscape B has the greatest amount of MLS edge, the contrast is moderate relative to landscapes A and C. In combination, TECI and TE (or ED) provide a good indication of the potential edge effects in these 3 landscapes.

(C30) Mean Edge Contrast Index

Vector/Raster

$$\boxed{\mathrm{MCECI} = \frac{\displaystyle\sum_{j=1}^{n} \left[\frac{\displaystyle\sum_{k=1}^{m'} (p_{ijk} \cdot d_{ik})}{p_{ij}} \right]}{n_i} (100)}$$

Units: Percent.

Range: $0 \leq \mathrm{MECI} \leq 100$

MECI = 0 when there is no class edge in the landscape; that is, when the entire landscape and landscape border, if present, consists of the corresponding patch type and the landscape boundary is not treated as edge if a landscape border is absent. MECI approaches 0 as the contrast in edges involving the corresponding patch type lesson (i.e., contrast weight approaches 0). MECI = 100 when all class edge is maximum contrast (i.e., contrast weight = 1).

Description: MECI equals the sum of the segment lengths (m) of each patches' perimeter multiplied by their corresponding contrast weights, divided by total patch perimeter (m)[PERIM], summed across all patches of the corresponding patch type, divided by the number of patches of the same type (NP), multiplied by 100 (to convert to a percentage). If a landscape border is present, MECI treats patch perimeter segments along the landscape boundary according to their contrast weights as designated in the contrast weight file. If a landscape border is absent and the user specifies that the boundary be treated as true edge, MECI treats patch perimeter segments along the landscape boundary as maximum contrast edge (i.e., contrast weight = 1); otherwise, all patch perimeter segments along the landscape boundary are treated as zero-contrast edges (i.e., contrast weight = 0).

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. MECI and TECI are largely redundant for these indicates; therefore the conclusions drawn from these indices are the same (see TECI example).

(C31) Area-Weighted Mean Edge Contrast Index

Vector/Raster

$$\boxed{AWMCECI = \sum_{j=1}^{n} \left(\left[\frac{\sum_{k=1}^{m'} (p_{ijk} \circ d_{ik})}{p_{ij}} \right] \left[\frac{a_{ij}}{\sum_{j=1}^{n} a_{ij}} \right] \right) (100)}$$

Units: Percent.

Range: $0 \leq AWMECI \leq 100$

AWMECI = 0 when there is no class edge in the landscape; that is, when the entire landscape and landscape border, if present, consists of the corresponding patch type and the landscape boundary is not treated as edge if a landscape border is absent. AWMECI approaches 0 as the contrast in edges involving the corresponding patch type lesson (i.e., contrast weight approaches 0). AWMECI = 100 when all class edge is maximum contrast (i.e., contrast weight = 1).

Description: AWMECI equals the sum of the segment lengths (m) of each patches' perimeter multiplied by their corresponding contrast weights, divided by total patch perimeter (m)[PERIM], multiplied by patch area (m^2) divided by the sum of patch areas, summed across all patches of the corresponding patch type, multiplied by 100 (to convert to a percentage). If a landscape border is present, AWMECI treats patch perimeter segments along the landscape boundary according to their contrast weights as designated in the contrast weight file. If a landscape border is absent and the user specifies that the boundary be treated as true edge, AWMECI treats patch perimeter segments along the landscape boundary as maximum contrast edge (i.e., contrast weight

= 1); otherwise, all patch perimeter segments along the landscape boundary are treated as zero-contrast edges (i.e., contrast weight = 0).

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. AWMECI, MECI and TECI are largely redundant for these indicates; therefore the conclusions drawn from these indices are the same (see TECI example).

(C32) Contagion 1

Vector/Raster

$$\boxed{\mathrm{CONTAG1} = \frac{-\sum_{k=1}^{m'}\left[\left(\frac{e_{ik}}{\sum_{k=1}^{m'} e_{ik}}\right)\ln\left(\frac{e_{ik}}{\sum_{k=1}^{m'} e_{ik}}\right)\right]}{\ln(m'-1)}(100)}$$

Units: Percent.

Range: $0 < \mathrm{CONTAG1} \leq 100$

CONTAG1 approaches 0 when the corresponding patch type is adjacent to only 1 other patch type and the number of patch types increases. CONTAG1 = 100 when the corresponding patch type is equally adjacent to all other patch types (i.e., maximally interspersed and juxtaposed to other patch types). CONTAG1 is undefined, and reported as "N/A", if the number of patch types is less than 3.

Description: CONTAG1 equals minus the sum of the length (m) of each unique edge type involving the corresponding patch type divided by the total length (m) of edge (m) involving the same type, multiplied by the logarithm of the same quantity, summed over each unique edge type; divided by the logarithm of 1 minus the number of patch types; multiplied by 100 (to convert to a percentage). In other words, the observed contagion over the maximum possible contagion for the given number of patch types. Note, CONTAG1 considers all patch types present on an image, including any present in the landscape border, if present.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. CONTAG1 indicates the MLS edge present in landscape B is more equitably distributed among patch types than in either landscape A or C. Note also, that although landscapes A and C contain very different numbers of patch types (10 vs. 3), CONTAG1 is roughly the same, indicating that the MLS edge is distributed among the available patch types at about 50% of the maximum possible equitable distribution in both landscapes, even though the absolutes amounts of edge and proportions associated with each edge type are undoubtedly quite different.

(C33) Mean Nearest Neighbor

Vector/Raster

$$\boxed{MNN = \frac{\sum_{j=1}^{n'} h_{ij}}{n'_i}}$$

Units: Meters

Range: $MNN > 0$, without limit.

MNN is reported as "None" in the formatted output file and "N/A" in the ASCII output file if there is only 1 patch of the corresponding patch type. Likewise, in the vector version, if the rasterization process creates more or less patches than are present in the vector image (see below), then MNN is reported as "N/A".

Description: MNN equals the sum of the distance (m) to the nearest neighboring patch of the same type, based on nearest edge-to-edge distance, for each patch of the corresponding patch type, divided by the number of patches of the same type (NP).

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. Because of the relatively small extent of these landscapes, MNN is not particularly meaningful. The "N/A" in landscape A resulted from loss of direct correspondence during the rasterization process.

(C34) Nearest Neighbor Standard Deviation

Vector/Raster

$$\boxed{NNSD = \sqrt{\frac{\sum_{j=1}^{n'} \left[h_{ij} - \left(\frac{\sum_{j=1}^{n'} h_{ij}}{n'_i} \right) \right]^2}{n'_i}}}$$

Units: Meters

Range: $NNSD \geq 0$, without limit.

NNSD = 0 when there are only 2 patches in the class or all patches have the same nearest neighbor distance (i.e., when there is no variability in nearest neighbor distance). NNSD is reported as "N/A" if there is only 1 patch of the corresponding patch type. Likewise, in the vector version, if the rasterization process creates more or less patches than are present in the vector image (see below), then NNSD is reported as "N/A".

Description: NNSD equals the square root of the sum of the squared deviations of each patches' nearest neighbor distance (m)[NEAR] from the mean nearest neighbor distance of the corresponding patch type (MNN), divided by the number of patches of the same type (NP); that is, the root mean squared error (deviation from the mean) in patch nearest neighbor distance. Note, this is the population standard deviation, not the sample standard deviation.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. Because of the relatively small extent of these landscapes, NNSD is not particularly meaningful. The "N/A" in landscape A resulted from loss of direct correspondence during the rasterization process.

(C35) Nearest Neighbor Coefficient of Variation

Vector/Raster

$$\boxed{NNCV = \frac{NNSD}{MNN}(100)}$$

Units: Percent

Range: NNCV ≥ 0, without limit.

NNCV = 0 when there are only 2 patches in the class or all patches have the same nearest neighbor distance (i.e., when there is no variability in nearest neighbor distance; NNSD = 0). NNCV is reported as "N/A" if there is only 1 patch of the corresponding patch type. Likewise, in the vector version, if the rasterization process creates more or less patches than are present in the vector image (see below), then NNCV is reported as "N/A".

Description: NNCV equals the standard deviation in nearest neighbor distances (NNSD) divided by the mean nearest neighbor distance of the corresponding patch type (MNN), multiplied by 100 (to convert to percent); that is, the variability in nearest neighbor distance relative to the mean nearest neighbor distance. Note, this is the population coefficient of variation, not the sample coefficient of variation.

Example: Figure 3.5 depicts 3 sample landscapes that vary in the amount and pattern of the MLS patch type. Because of the relatively small extent of these landscapes, NNSD is not particularly meaningful. The "N/A" in landscape A resulted from loss of direct correspondence during the rasterization process.

Landscape Indices

(L1) Landscape ID (LID)

The first field in the landscape output file is landscape ID (LID); it is defined as in the patch output file (see previous discussion).

(L2) Total Area

Vector/Raster

$$\boxed{TA = A\left(\frac{1}{10{,}000}\right)}$$

Units: Hectares

Range: $TA > 0$, without limit.

Description: TA equals the total area (m^2) of the landscape, divided by 10,000 (to convert to hectares).

(L3) Number of Patches

Vector/Raster

$$\boxed{NP = N}$$

Units: None

Range: $NP \geq 1$, without limit.

$NP = 1$ when the landscape contains only 1 patch.

Description: NP equals the number of patches in the landscape.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. Because these landscapes are very similar in size, NP does a good job of describing or indexing the strong landscape diversity or heterogeneity gradient represented by these 3 landscapes. Although, NP indicates that the habitat patterns in landscape A are much finer grained than those in B and C, it does not indicate anything about the number of different habitats or patch types present or their relative abundance and spatial distribution. Thus, in the example landscapes, NP is best considered only in conjunction with other indices.

(L4) Patch Density

Vector/Raster

$$\boxed{PD = \frac{N}{A}(10{,}000)(100)}$$

Units: Number per 100 hectares

Range: PD > 0, without limit.

Description: PD equals the number of patches in the landscape (NP) divided by total landscape area, multiplied by 10,000 and 100 (to convert to 100 hectares).

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. Because total landscape area is similar among the landscapes, PD and NP convey the same information (see NP example above).

(L5) Mean patch Size

Vector/Raster

$$\boxed{MPS = \frac{A}{N}\left(\frac{1}{10{,}000}\right)}$$

Units: Hectares

Range: MPS > 0, without limit.

Ultimately, the range in MPS is limited by the grain and extent of the image and the minimum patch size in the same manner as patch area (AREA).

Description: MPS equals the total landscape area (m^2), divided by the total number of patches, divided by 10,000 (to convert to hectares).

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. Because total landscape area is similar among the landscapes, MPS, PD and NP all convey the same information (see NP example above).

(L6) Patch Size Standard Deviation

Vector/Raster

$$\boxed{PSSD = \sqrt{\frac{\sum_{i=1}^{m}\sum_{j=1}^{n}\left[a_{ij}-\left(\frac{A}{N}\right)\right]^2}{N}}\left(\frac{1}{10{,}000}\right)}$$

Units: Hectares

Range: PSSD ≥ 0, without limit.

PSSD = 0 when all patches in the landscape are the same size or when there is only 1 patch (i.e., when there is no variability in patch size).

Description: PSSD equals the square root of the sum of the squared deviations of each patch area (m^2) from the mean patch size, divided by the total number of patches (NP), divided by 10,000 (to convert to hectares); that is, the root mean squared error (deviation from the mean) in patch size. Note, this is the population standard deviation, not the sample standard deviation.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. PSSD measures absolute variation. In absolute terms, patches in landscape A vary much less than patches in landscape C. Sixty-five percent of the patches in landscape A are within 20 ha difference in size (± 1 standard deviation); whereas 65% of the patches in landscape C are within 100 ha difference in size. Therefore, based on PSSD, the variation in patch size is much greater in Landscape C than landscape A. However, relative to the mean patch size, the patches in landscape A are actually much more variable in size than in landscape C (PSCV). Depending on whether you view variation in absolute (PSSD) or relative (PSCV) terms, you can reach very different conclusions regarding these sample landscapes. The choice between measures will depend on the application, but in most cases PSCV is preferable.

(L7) Patch Size Coefficient of Variation

Vector/Raster

$$\boxed{PSCV = \frac{PSSD}{MPS}(100)}$$

Units: Percent

Range: PSCV ≥ 0, without limit.

PSCV = 0 when all patches in the landscape are the same size or when there is only 1 patch (i.e., when there is no variability in patch size).

<u>Description</u>: PSCV equals the standard deviation in patch size (PSSD) divided by the mean patch size (MPS), multiplied by 100 (to convert to percent); that is, the variability in patch size relative to the mean patch size. Note, this is the population coefficient of variation, not the sample coefficient of variation.

<u>Example</u>: See PSSD example above.

(L8) Total Core Area

Vector/Raster

$$\boxed{\mathrm{TCA} = \sum_{i=1}^{m}\sum_{j=1}^{n} a_{ij}^{c}\left(\frac{1}{10{,}000}\right)}$$

<u>Units</u>: Hectares

<u>Range</u>: TCA ≥ 0, without limit.

TCA = 0 when every location within every patch is within the specified edge distances from the patch perimeters. TCA approaches total landscape area as the specified edge distances decrease and as patch shapes are simplified.

<u>Description</u>: TCA equals the sum of the core areas of each patch (m^2), divided by 10,000 (to convert to hectares).

<u>Example</u>: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. TCA indicates that landscapes A, B, C contain much progressively more core area. Because total landscape area is similar among these landscapes, TCA indicates that landscapes A, B, and C are progressively less fragmented. Note also that TCA is a result of the interaction among patch size, patch shape, and edge width (see example for CORE under patch indices).

(L9) Number of Core Areas

Vector/Raster

$$\boxed{\mathrm{NCA} = \sum_{i=j}^{m}\sum_{j=1}^{n} n_{ij}^{c}}$$

<u>Units</u>: None

<u>Range</u>: NCA ≥ 0, without limit.

NCA = 0 when TCA = 0 (i.e., every location within every patch is within the specified edge distances from the patch perimeters).

Description: NCA equals the sum of the number of disjunct core areas contained within each patch (NCORE) in the landscape; that is, the number of disjunct core areas contained within the landscape.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. Relative to NP, the differences among landscapes are less pronounced with NCA, because many of the patches in landscape A do not have any core area. Note that although landscapes A and B have fewer core areas than patches, landscape C has more core areas than patches. Note also that NCA, like TCA, is affected by the interaction of patch size, patch shape, and edge width. The rank order of landscapes based on NCA is different than that based on TCA; landscape A has the least TCA, yet is intermediate in NCA. This reversal occurs because of the relationship between patch sizes and shapes in these landscapes and the designated edge width of 100 m. With a much larger edge width (e.g., 200 m) or much smaller edge width (e.g., 10 m), NCA would change dramatically, especially in landscapes A and B because of the size and shapes of the patches in those landscapes. For this reason, particular attention should be given to the interpretation of NCA and TCA since they can lead to a different rank ordering of landscapes along a gradient in landscape heterogeneity.

(L10) Core Area Density

Vector/Raster

$$\boxed{CAD = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n} n_{ij}^{c}}{A}(10{,}000)(100)}$$

Units: Number per 100 hectares

Range: CAD ≥ 0, without limit.

CAD = 0 when TCA = 0 (i.e., every location within every patch is within the specified edge distances from the patch perimeters); in other words, when there are no core areas.

Description: CAD equals the sum of number of disjunct core areas contained within each patch (NCORE), divided by total landscape area, multiplied by 10,000 and 100 (to convert to 100 hectares).

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. Because total landscape area is similar among landscapes, CAD and NCA express the same information (see NCA example above).

(L11) Mean Core Area

Vector/Raster

$$\boxed{\mathrm{MCA} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n} a_{ij}^{c}}{N}\left(\frac{1}{10{,}000}\right)}$$

Units: Hectares

Range: MCA ≥ 0, without limit.

Ultimately, the range in MCA is limited by the grain and extent of the image and the minimum patch size in the same manner as mean patch size (MPS), but MCA is also affected by the specified edge widths. MCA = 0 when TCA = 0 (i.e., every location within every patch is within the specified edge distances from the patch perimeters); in other words, when there are no core areas. MCA approaches MPS as the specified edge widths decrease and as patch shapes are simplified.

Description: MCA equals the sum of the core areas of each patch (m^2), divided by the number of patches of the same type (NP), divided by 10,000 (to convert to hectares).

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. Although MPS does a good job of ranking the 3 landscapes with respect to their spatial heterogeneity, MCA distinguishes among these landscape even more distinctly. Because MCA is effected by patch shape, it captures an aspect of spatial pattern not captured by MPS. Like MPS, MCA is most informative when interpreted in conjunction other indices such as total landscape area (TA), patch density (PD) and patch size variability (PSSD or PSCV).

(L12) Core Area Standard Deviation

Vector/Raster

$$\boxed{\mathrm{CASD} = \sqrt{\frac{\sum_{i=1}^{m}\sum_{j=1}^{n}\left[a_{ij}^{c}-\left(\frac{\sum_{i=1}^{m}\sum_{j=1}^{n}a_{ij}^{c}}{N}\right)\right]^{2}}{N}}\left(\frac{1}{10{,}000}\right)}$$

Units: Hectares

Range: CASD ≥ 0, without limit.

CASD = 0 when all patches in the landscape have the same core area or when there is only 1 patch (i.e., when there is no variability in core area).

Description: CASD equals the square root of the sum of the squared deviations of each patch core area (m^2) from the mean core area, divided by the number of patches (NP), divided by 10,000 (to convert to hectares); that is, the root mean squared error (deviation from the mean) in patch core area. Note, this is the population standard deviation, not the sample standard deviation.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. In this case, CASD and PSSD rank the landscapes in the same manner and have the same interpretation and limitations (see PSSD example).

(L13) Core Area Coefficient of Variation

Vector/Raster

$$\boxed{\mathrm{CACV} = \frac{\mathrm{CASD}}{\mathrm{MCA}}(100)}$$

Units: Percent

Range: CACV ≥ 0, without limit.

CACV = 0 when all patches in the landscape have the same core area or when there is only 1 patch (i.e., when there is no variability in core area).

Description: CACV equals the standard deviation in core area (CASD) divided by the mean core area (MCA), multiplied by 100 (to convert to percent); that is, the variability in core area relative to the mean core area. Note, this is the population coefficient of variation, not the sample coefficient of variation.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. CACV indicates that core area variability increases progressively from the least (C) to the most (A) heterogeneous landscape. Note that PSCV and CACV rank landscapes B and C differently.

(L14) Total Core Area Index

Vector/Raster

$$\boxed{TCAI = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n} a_{ij}^{c}}{A}\,(100)}$$

Units: Percent

Range: $0 \leq TCAI < 100$

TCAI = 0 when none of the patches in the landscape contain any core area (i.e., CORE = 0 for every patch); that is, when the landscape contains no core area. TCAI approaches 100 when the patches, because of size, shape, and edge width, contain mostly core area.

Description: TCAI equals the sum of the core areas of each patch (m^2), divided by the total landscape area (m^2), multiplied by 100 (to convert to a percentage); that is, TCAI equals the percentage of the landscape that is core area.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. Alone, TCAI accurately represents the 3 landscapes along a continuum from most to least fragmented. Only 10% of landscape A is core area, the remaining 90% is edge habitat. Thus, without any other information on landscape A, it could be deduced that landscape A contains a great deal of spatial heterogeneity. However, TCAI does not indicate how much total core area exists or how many patches the core area is distributed among.

(L15) Mean Core Area Index

Vector/Raster

$$\boxed{MCAI = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n}\left(\frac{a_{ij}^{c}}{a_{ij}}\right)}{N}\,(100)}$$

Units: Percent

Range: $0 \leq \text{MCAI} < 100$

MCAI = 0 when none of the patches in the landscape contain any core area (i.e., CORE = 0 for every patch); that is, when the landscape contains no core area. MCAI approaches 100 when the patches, because of size, shape, and edge width, contain mostly core area.

Description: MCAI equals the sum of the proportion of each patch that is core area {i.e., core area of each patch (m^2) divided by the area of each patch (m^2), or CAI}, divided by the number of patches (NP), multiplied by 100 (to convert to a percentage); In other words, MCAI equals the average percentage of a patch in the landscape that is core area.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. MCAI and TCAI portray the same differences among these landscapes (see TCAI example above).

(L16) Landscape Shape Index

Vector

$$\boxed{\text{LSI} = \frac{E'}{2\sqrt{\pi \cdot A}}}$$

Raster

$$\boxed{\text{LSI} = \frac{.25\,E'}{\sqrt{A}}}$$

Units: None

Range: $\text{LSI} \geq 1$, without limit.

LSI = 1 when the landscape consists of a single circular (vector) or square (raster) patch; LSI increases without limit as landscape shape becomes more irregular and/or as the length of edge within the landscape increases.

Description: LSI equals the sum of the landscape boundary (regardless of whether it represents true edge or not) and all edge segments (m) within the landscape boundary, divided by the square root of the total landscape area (m^2), adjusted by a constant for a circular standard (vector) or square standard (raster).

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. In this case, even though the landscape boundary does not all represent true edge, LSI still ranks the landscapes along an intuitive gradient from least to most heterogeneous.

(L17) Mean Shape Index

Vector

$$\boxed{MSI = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n}\left(\frac{p_{ij}}{2\sqrt{\pi \circ a_{ij}}}\right)}{N}}$$

Raster

$$\boxed{MSI = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n}\left(\frac{.25p_{ij}}{\sqrt{a_{ij}}}\right)}{N}}$$

Units: None

Range: MSI ≥ 1, without limit.

MSI = 1 when all patches in the landscape are circular (vector) or square (raster); MSI increases without limit as the patch shapes become more irregular.

Description: MSI equals the sum of the patch perimeter (m)[PERIM] divided by the square root of patch area (m^2) for each patch in the landscape, adjusted by a constant to adjust for a circular standard (vector) or square standard (raster), divided by the number of patches (NP); in other words, MSI equals the average shape index (SHAPE) of patches in the landscape.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. MSI values for all 3 landscapes are greater than one, indicating that the average patch shape in all 3 landscapes is noncircular. The patches in landscape A area least irregular while the patches in landscape C are most irregular. This reflects the simple shapes of management units in landscape A compared to the natural shapes of patches in the undisturbed landscape C.

(L18) Area-Weighted Mean Shape Index

Vector

$$\boxed{AWMSI = \sum_{i=1}^{m}\sum_{j=1}^{n}\left[\left(\frac{p_{ij}}{2\sqrt{\pi \circ a_{ij}}}\right)\left(\frac{a_{ij}}{A}\right)\right]}$$

Raster

$$\boxed{AWMSI = \sum_{i=1}^{m}\sum_{j=1}^{n}\left[\left(\frac{.25p_{ij}}{\sqrt{a_{ij}}}\right)\left(\frac{a_{ij}}{A}\right)\right]}$$

Units: None

Range: AWMSI ≥ 1, without limit.

AWMSI = 1 when all patches in the landscape are circular (vector) or square (raster); AWMSI increases without limit as the patch shapes become more irregular.

Description: AWMSI equals the sum, across all patches, of each patch perimeter (m)[PERIM] divided by the square root of patch area (m^2), adjusted by a constant to adjust for a circular standard (vector) or square standard (raster), multiplied by the patch area (m^2) divided by total landscape area. In other words, AWMSI equals the average shape index (SHAPE) of patches, weighted by patch area so that larger patches weigh more than smaller patches.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. AWMSI and MSI portray the same differences among these landscapes (see MSI example above).

(L19) Double Log Fractal Dimension

Vector/Raster

$$DLFD = \frac{2}{\dfrac{\left[N \sum_{i=1}^{m} \sum_{j=1}^{n} (\ln p_{ij} \cdot \ln a_{ij})\right] - \left[\left(\sum_{i=1}^{m} \sum_{j=1}^{n} \ln p_{ij}\right)\left(\sum_{i=1}^{m} \sum_{j=1}^{n} \ln a_{ij}\right)\right]}{\left(N \sum_{i=1}^{m} \sum_{j=1}^{n} \ln p_{ij}^{2}\right) - \left(\sum_{i=1}^{m} \sum_{j=1}^{n} \ln p_{ij}\right)^{2}}}$$

Units: None

Range: $1 \leq DLFD \leq 2$

A fractal dimension greater than 1 for a 2-dimensional landscape mosaic indicates a departure from a euclidean geometry (i.e., an increase in patch shape complexity). DLFD approaches 1 for shapes with very simple perimeters such as circles or squares, and approaches 2 for shapes with highly convoluted, plane-filling perimeters.

Description: DLFD equals 2 divided by the slope of regression line obtained by regressing the logarithm of patch area (m^2) against the logarithm of patch perimeter (m)[PERIM].

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. Because of the small sample size in landscape C, DLFD is probably not a reliable index for this landscape. However, DLFD in landscapes A and B compares nicely with MSI and AWMSI.

(L20) Mean Patch Fractal Dimension

Vector

$$\boxed{MPFD = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n}\left(\frac{2\ln p_{ij}}{\ln a_{ij}}\right)}{N}}$$

Raster

$$\boxed{MPFD = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n}\left(\frac{2\ln(.25p_{ij})}{\ln a_{ij}}\right)}{N}}$$

Units: None

Range: $1 \leq MPFD \leq 2$

A fractal dimension greater than 1 for a 2-dimensional landscape mosaic indicates a departure from a euclidean geometry (i.e., an increase in patch shape complexity). MPFD approaches 1 for shapes with very simple perimeters such as circles or squares, and approaches 2 for shapes with highly convoluted, plane-filling perimeters.

Description: MPFD equals the sum of 2 times the logarithm of patch perimeter (m)[PERIM] divided by the logarithm of patch area (m^2) for each patch in the landscape, divided by the number of patches (NP); the raster formula is adjusted to correct for the bias in perimeter (Li 1989).

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. The rank order of MPFD values do not agree with MSI or AWMSI values, or with DLFD values for landscape A and B. The reason for the discrepancy between these indices is not clear; however, since MSI, AWMSI, and DLFD all agree, then MPFD is probably less reliable in this case.

(L21) Patch Richness

Vector/Raster

$$\boxed{PR = m}$$

Units: None

Range: $PR \geq 1$, without limit

Description: PR equals the number of different patch types present within the landscape boundary.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. The number of different patch types varies from 3 in landscape C to 10 in landscape A.

(L22) Patch Richness Density

Vector/Raster

$$\boxed{PRD = \frac{m}{A}(10{,}000)(100)}$$

Units: Number per 100 hectares

Range: PRD > 0, without limit

Description: PR equals the number of different patch types present within the landscape boundary (PR) divided by total landscape area (m^2), multiplied by 10,000 and 100 (to convert to 100 hectares).

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. Because these landscapes are similar in area, PRD and PR convey the same information.

(L23) Relative Patch Richness

Vector/Raster

$$\boxed{RPR = \frac{m}{m_{max}}(100)}$$

Units: Percent

Range: $0 < RPR \leq 100$

RPR approaches 0 when the landscape contains a single patch type, yet the number of potential patch types is very large. RPR = 100 when all possible patch types are represented in the landscape.

Description: RPR equals the number of different patch types present within the landscape boundary (PR) divided by the maximum potential number of patch types based on the patch type classification scheme, multiplied by 100 (to convert to percent).

Example: See PR example above.

(L24) Shannon's Diversity Index

Vector/Raster

$$\boxed{\mathrm{SHDI} = -\sum_{i=1}^{m} (P_i \cdot \ln P_i)}$$

Units: None

Range: SHDI ≥ 0, without limit

SHDI = 0 when the landscape contains only 1 patch (i.e., no diversity). SHDI increases as the number of different patch types (i.e., patch richness, PR) increases and/or the proportional distribution of area among patch types becomes more equitable.

Description: SHDI equals minus the sum, across all patch types, of the proportional abundance of each patch type multiplied by that proportion.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. In this case, SHDI largely reflects differences in patch richness. Thus, the conclusions based on SHDI are the same as those based on PR, PRD, and RPR.

(L25) Simpson's Diversity Index

Vector/Raster

$$\boxed{\mathrm{SIDI} = 1 - \sum_{i=1}^{m} P_i^2}$$

Units: None

Range: 0 ≤ SIDI < 1

SIDI = 0 when the landscape contains only 1 patch (i.e., no diversity). SIDI approaches 1 as the number of different patch types (i.e., patch richness, PR) increases and the proportional distribution of area among patch types becomes more equitable.

Description: SIDI equals 1 minus the sum, across all patch types, of the proportional abundance of each patch type squared.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. In this case, SIDI and SHDI largely reflect differences in patch richness. Thus, the conclusions based on either diversity index are the same as those based on PR, PRD, and RPR.

(L26) Modified Simpson's Diversity Index

Vector/Raster

$$\boxed{\mathrm{MSIDI} = -\ln \sum_{i=1}^{m} P_i^2}$$

Units: None

Range: MSIDI ≥ 0

MSIDI = 0 when the landscape contains only 1 patch (i.e., no diversity). MSIDI increases as the number of different patch types (i.e., patch richness, PR) increases and the proportional distribution of area among patch types becomes more equitable.

Description: MSIDI equals minus the logarithm of the sum, across all patch types, of the proportional abundance of each patch type squared.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. In this case, MSIDI and SHDI largely reflect differences in patch richness. Thus, the conclusions based on either diversity index are the same as those based on PR, PRD, and RPR.

(L27) Shannon's Evenness Index

Vector/Raster

$$\boxed{\mathrm{SHEI} = \frac{-\sum_{i=1}^{m} (P_i \circ \ln P_i)}{\ln m}}$$

Units: None

Range: 0 ≤ SHEI ≤ 1

SHDI = 0 when the landscape contains only 1 patch (i.e., no diversity) and approaches 0 as the distribution of area among the different patch types becomes increasingly uneven (i.e., dominated by 1 type). SHDI = 1 when distribution of area among patch types is perfectly even (i.e., proportional abundances are the same).

Description: SHEI equals minus the sum, across all patch types, of the proportional abundance of each patch type multiplied by that proportion (SHDI), divided by the logarithm of the number of patch types (PR). In other words, the observed Shannon's Diversity Index divided by the maximum Shannon's Diversity Index for that number of patch types.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. Although landscape C is least diverse based on the 3 diversity indices, it has the most even distribution among patch types. This illustrates the potential importance of interpreting richness and evenness independently and the importance of interpreting evenness separate from diversity which is influenced strongly by richness.

(L28) Simpson's Evenness Index

Vector/Raster

$$\boxed{SIEI = \frac{1-\sum_{i=1}^{m} P_i^2}{1-\left(\frac{1}{m}\right)}}$$

Units: None

Range: $0 \le SIEI \le 1$

SIDI = 0 when the landscape contains only 1 patch (i.e., no diversity) and approaches 0 as the distribution of area among the different patch types becomes increasingly uneven (i.e., dominated by 1 type). SIDI = 1 when distribution of area among patch types is perfectly even (i.e., proportional abundances are the same).

Description: SIEI equals 1 minus the sum, across all patch types, of the proportional abundance of each patch type squared (SIDI), divided by 1 minus 1 divided by the number of patch types (PR). In other words, the observed Simpson's Diversity Index divided by the maximum Simpson's Diversity Index for that number of patch types.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. SIEI and SHEI portray the same differences among landscapes, although differences based on SIEI are less pronounced, perhaps because Simpson's diversity measure is less influenced by rare patch types.

(L29) Modified Simpson's Evenness Index

Vector/Raster

$$\boxed{\mathrm{MSIEI} = \frac{-\ln \sum_{i=1}^{m} P_i^2}{\ln m}}$$

Units: None

Range: $0 \leq \mathrm{MSIEI} \leq 1$

MSIDI = 0 when the landscape contains only 1 patch (i.e., no diversity) and approaches 0 as the distribution of area among the different patch types becomes increasingly uneven (i.e., dominated by 1 type). MSIDI = 1 when distribution of area among patch types is perfectly even (i.e., proportional abundances are the same).

Description: MSIEI equals minus the logarithm of the sum, across all patch types, of the proportional abundance of each patch type squared (MSIDI), divided by the logarithm of the number of patch types (PR). In other words, the observed modified Simpson's diversity index divided by the maximum modified Simpson's diversity index for that number of patch types.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. MSIEI, SIEI and SHEI portray the same differences among landscapes.

(L30) Largest Patch Index

Vector/Raster

$$\boxed{\mathrm{LPI} = \frac{\max a_{ij}}{A}(100)}$$

Units: Percent

Range: $0 < \mathrm{LPI} \leq 100$

LPI approaches 0 when the largest patch in the landscape is increasing small. LPI = 100 when the entire landscape consists of a single patch; that is, when the largest patch comprises 100% of the landscape.

Description: LPI equals the area (m^2) of the largest patch in the landscape divided by total landscape area (m^2), multiplied by 100 (to convert to a percentage); in other words, LPI equals the percent of the landscape that the largest patch comprises.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. LPI indicates that almost half of landscape C, the least heterogeneous landscape, is comprised of a single patch. However, the largest patch in landscape A comprises much more of the landscape than the largest patch in landscape B, even though landscape A is considerably more heterogeneous than B. If a single large patch comprising > 25% is important for the presence of a particular species then landscape A could be suitable but not B. This illustrates both the potential usefulness of this index in particular applications and the limitations of this index as a measure of overall heterogeneity.

(L31) Total Edge (m)

Vector/Raster

$$\boxed{TE = E}$$

Units: Meters

Range: TE ≥ 0, without limit.

TE = 0 when there is no edge in the landscape; that is, when the entire landscape consists of a single patch and the landscape border, if present also consists of that same patch type or, if absent, the boundary is not treated as edge.

Description: TE equals the sum of the lengths (m) of all edge segments in the landscape. If a landscape border is present, TCE includes landscape boundary segments representing true edge only (i.e., contrast weight > 0). If a landscape border is absent and the user specifies that the boundary be treated as true edge, TCE includes landscape boundary segments involving the corresponding patch type; otherwise, all boundary segments are ignored.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. TE is lowest for landscape C and highest for landscape A, corresponding nicely to the overall magnitude of spatial heterogeneity in these landscapes. Because these landscapes are similar in size, TE is useful for comparing among landscapes.

(L32) Edge Density

Vector/Raster

$$\boxed{ED = \frac{E}{A}(10{,}000)}$$

Units: Meters per hectare.

Range: ED ≥ 0, without limit.

ED = 0 when there is no edge in the landscape; that is, when the entire landscape and landscape border, if present, consists of a single patch type and the landscape boundary is not treated as edge if a landscape border is absent.

Description: ED equals the sum of the lengths (m) of all edge segments in the landscape (TE), divided by the total landscape area (m^2), multiplied by 10,000 (to convert to hectares). If a landscape border is present, ED includes landscape boundary segments representing true edge only (i.e., contrast weight > 0). If a landscape border is absent and the user specifies that the boundary be treated as true edge, ED includes the entire landscape boundary; otherwise, the landscape boundary is ignored.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. Because these landscapes are similar in size, ED and TE are largely redundant; therefore, the conclusions drawn from ED and TE are the same (see TE example).

(L33) Contrast Weighted Edge Density

Vector/Raster

$$\boxed{\mathrm{CWED} = \frac{\sum_{i=1}^{m'} \sum_{k=i+1}^{m'} (e_{ik} \cdot d_{ik})}{A} (10{,}000)}$$

Units: Meters per hectare.

Range: CWED ≥ 0, without limit.

CWED = 0 when there is no edge in the landscape; that is, when the entire landscape and landscape border, if present, consists of a single patch type and the landscape boundary is not treated as edge if a landscape border is absent. CWED increases as the amount of edge in the landscape increases and/or as the contrast in edges increase (i.e., contrast weight approaches 1).

Description: CWED equals the sum of the lengths (m) of each edge segment in the landscape multiplied by the corresponding contrast weight, divided by the total landscape area (m^2), multiplied by 10,000 (to convert to hectares). If a landscape border is present, CWED includes landscape boundary segments representing true edge only (i.e., contrast weight > 0). If a landscape border is absent and the user specifies that the boundary be treated as true edge, CWED includes the entire landscape boundary as maximum contrast edge (i.e., contrast weight = 1); otherwise, the landscape boundary is ignored.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. The conclusions based on CWED, ED, and TE are similar (see TE example), although it is apparent from CWED that landscape C contains very low contrast edges amounting to an equivalent of only 3.5 m/ha of maximum contrast edge. Landscape B has roughly twice as much total edge as landscape C, but roughly 6 times more equivalent maximum contrast edge.

(L34) Total Edge Contrast Index

Vector/Raster

$$\mathrm{TECI} = \frac{\sum_{i=1}^{m'} \sum_{k=i+1}^{m'} (e_{ik} \circ d_{ik})}{E'} (100)$$

Units: Percent.

Range: $0 \leq \mathrm{TECI} \leq 100$

TECI = 0 when there is no edge in the landscape; that is, when the entire landscape and landscape border, if present, consists of a single patch type and the landscape boundary is not treated as edge if a landscape border is absent. TECI approaches 0 as the contrast in edges lesson (i.e., contrast weight approaches 0). TECI = 100 when all edge is maximum contrast (i.e., contrast weight = 1).

Description: TECI equals the sum of the lengths (m) of each edge segment in the landscape multiplied by the corresponding contrast weight, divided by the total length (m) of edge in the landscape, multiplied by 100 (to convert to a percentage). If a landscape border is present, TECI includes all landscape boundary segments, regardless of whether they represent true edge (i.e., contrast weight > 0) or not. If a landscape border is absent and the user specifies that the boundary be treated as true edge, TECI includes the entire landscape boundary as maximum contrast edge (i.e., contrast weight = 1); otherwise, the landscape boundary is ignored.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. The conclusions based on TECI and CWED are similar (see CWED example).

(L35) Mean Edge Contrast Index

Vector/Raster

$$\mathrm{MECI} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n}\left[\frac{\sum_{k=1}^{m'}(p_{ijk} \circ d_{ik})}{p_{ij}}\right]}{N}(100)$$

Units: Percent.

Range: $0 \leq \mathrm{MECI} \leq 100$

MECI = 0 when there is no edge in the landscape; that is, when the entire landscape and landscape border, if present, consists of a single patch type and the landscape boundary is not treated as edge if a landscape border is absent. MECI approaches 0 as the contrast in edges lesson (i.e., contrast weight approaches 0). MECI = 100 when all edge is maximum contrast (i.e., contrast weight = 1).

Description: MECI equals the sum of the segment lengths (m) of each patches' perimeter multiplied by their corresponding contrast weights, divided by total patch perimeter (m)[PERIM], divided by the total number of patches (NP), multiplied by 100 (to convert to a percentage). If a landscape border is present, MECI treats patch perimeter segments along the landscape boundary according to their contrast weights as designated in the contrast weight file. If a landscape border is absent and the user specifies that the boundary be treated as true edge, MECI treats patch perimeter segments along the landscape boundary as maximum contrast edge (i.e., contrast weight = 1); otherwise, all patch perimeter segments along the landscape boundary are treated as zero-contrast edges (i.e., contrast weight = 0).

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. The conclusions based on MECI, TECI, and CWED are similar (see CWED example).

(L36) Area-Weighted Mean Edge Contrast Index

Vector/Raster

$$\mathrm{AWMECI} = \sum_{i=1}^{m}\sum_{j=1}^{n}\left(\left[\frac{\sum_{k=1}^{m'}(p_{ijk} \circ d_{ik})}{p_{ij}}\right]\left[\frac{a_{ij}}{A}\right]\right)(100)$$

Units: Percent.

Range: 0 ≤ AWMECI ≤ 100

AWMECI = 0 when there is no edge in the landscape; that is, when the entire landscape and landscape border, if present, consists of a single patch type and the landscape boundary is not treated as edge if a landscape border is absent. AWMECI approaches 0 as the contrast in edges lesson (i.e., contrast weight approaches 0). AWMECI = 100 when all edge is maximum contrast (i.e., contrast weight = 1).

Description: AWMECI equals the sum of the segment lengths (m) of each patches' perimeter multiplied by their corresponding contrast weights, divided by total patch perimeter (m)[PERIM], multiplied by patch area (m^2) divided by total landscape areas (m^2), summed across all patches in the landscape, multiplied by 100 (to convert to a percentage). If a landscape border is present, AWMECI treats patch perimeter segments along the landscape boundary according to their contrast weights as designated in the contrast weight file. If a landscape border is absent and the user specifies that the boundary be treated as true edge, AWMECI treats patch perimeter segments along the landscape boundary as maximum contrast edge (i.e., contrast weight = 1); otherwise, all patch perimeter segments along the landscape boundary are treated as zero-contrast edges (i.e., contrast weight = 0).

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. The conclusions based on AWMECI, MECI, TECI, and CWED are similar (see CWED example).

(L37) Contagion 1

Vector/Raster

$$\boxed{\mathrm{CONTAG1} = \frac{-\sum_{i=1}^{m'}\sum_{k=i+1}^{m'}\left[\left(\frac{e_{ik}}{E}\right)\circ\ln\left(\frac{e_{ik}}{E}\right)\right]}{\ln(1/2[m'(m'-1)])}(100)}$$

Units: Percent.

Range: 0 < CONTAG1 ≤ 100

CONTAG1 approaches 0 when the distribution of adjacencies among unique patch types becomes increasingly uneven. CONTAG1 = 100 when all patch types are equally adjacent to all other patch types (i.e., maximum interspersion and juxtaposition. CONTAG1 is undefined, and reported as "N/A", if the number of patch types is less than 3.

Description: CONTAG1 equals minus the sum of the length (m) of each unique edge type divided by the total landscape edge (m), multiplied by the logarithm of the same quantity, summed over each unique edge type; divided by the logarithm of the number of patch types times the number of patch types minus 1 divided by 2; multiplied by 100 (to convert to a percentage). In other words, the observed contagion over the maximum possible contagion for the given number of patch types. Note, CONTAG1 considers all patch types present on an image, including any present in the landscape border, if present.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. CONTAG1 indicates the juxtaposition of available patch types is greatest in landscape A and least in landscape C. This occurs because landscape C contains 2 patch types that are present only in the landscape border the amount of edge involving these 2 types is very small. Thus, the distribution of edge lengths among unique types is very uneven.

(L38) Contagion 2

Raster

$$\text{CONTAG2} = \frac{-\sum_{i=1}^{m}\sum_{k=1}^{m}\left[(P_i)\left(\frac{G_{ik}}{\sum_{k=1}^{m} G_{ik}}\right)\right] \circ \left[\ln(P_i)\left(\frac{G_{ik}}{\sum_{k=1}^{m} G_{ik}}\right)\right]}{2\ln(m)}(100)$$

Units: Percent.

Range: $0 < \text{CONTAG2} \leq 100$

CONTAG2 approaches 0 when the distribution of adjacencies (at the level of individual pixels) among unique patch types becomes increasingly uneven. CONTAG2 = 100 when all patch types are equally adjacent to all other patch types (i.e., maximum interspersion and juxtaposition. CONTAG1 is undefined, and reported as "N/A", if the number of patch types is less than 2.

Description: CONTAG2 equals minus the sum of the proportional abundance of each patch type multiplied by number of adjacencies between pixels of that patch type and all other patch types, multiplied by the logarithm of the same quantity, summed over each patch type; divided by 2 times the logarithm of the number of patch types; multiplied by 100 (to convert to a percentage). In other words, the observed contagion over the maximum possible contagion for the given number of patch types. Note, CONTAG2 considers all patch types present on an image, including any present in the landscape border, if present, and considers like adjacencies (i.e., pixels of a patch type adjacent to pixels of the same type).

Example: I used the vector version of FRAGSTATS to compute the landscape indices in Figure 3.6. Therefore, CONTAG2 was not computed.

(L39) Mean Nearest Neighbor

Vector/Raster

$$\boxed{MNN = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n'} h_{ij}}{N'}}$$

Units: Meters

Range: MNN > 0, without limit.

MNN is reported as "None" in the formatted output file and "N/A" in the ASCII output file if none of the patches have a nearest neighbor (i.e., every patch type consists of only 1 patch). Likewise, in the vector version, if the rasterization process creates more or less patches than are present in the vector image (see below), then MNN is reported as "N/A".

Description: MNN equals the sum of the distance (m) to the nearest neighboring patch of the same type, based on nearest edge-to-edge distance, for each patch in the landscape with a neighbor, divided by the number of patches with a neighbor.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. Because of the relatively small extent of these landscapes, nearest neighbor indices are not particularly meaningful. The "N/A" in landscape A resulted from loss of direct correspondence during the rasterization process.

(L40) Nearest Neighbor Standard Deviation

Vector/Raster

$$\boxed{NNSD = \sqrt{\frac{\sum_{i=1}^{m}\sum_{j=1}^{n'}\left[h_{ij} - \left(\frac{\sum_{i=1}^{m}\sum_{j=1}^{n'} h_{ij}}{N'}\right)\right]^2}{N'}}}$$

Units: Meters

Range: NNSD ≥ 0, without limit.

NNSD = 0 when all patches have the same nearest neighbor distance (i.e., when there is no variability in nearest neighbor distance). NNSD is reported as "N/A" if none of the patches has a nearest neighbor. Likewise, in the vector version, if the rasterization process creates more or less patches than are present in the vector image (see below), then NNSD is reported as "N/A".

Description: NNSD equals the square root of the sum of the squared deviations of each patches' nearest neighbor distance (m)[NEAR] from the mean nearest neighbor distance of the corresponding patch type (MNN), divided by the number of patches; that is, the root mean squared error (deviation from the mean) in patch nearest neighbor distance. Note, this is the population standard deviation, not the sample standard deviation.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. Because of the relatively small extent of these landscapes, nearest neighbor indices are not particularly meaningful. The "N/A" in landscape A resulted from loss of direct correspondence during the rasterization process.

(L41) Nearest Neighbor Coefficient of Variation

Vector/Raster

$$\boxed{NNCV = \frac{NNSD}{MNN}(100)}$$

Units: Percent

Range: NNCV ≥ 0, without limit.

NNCV = 0 when all patches have the same nearest neighbor distance (i.e., when there is no variability in nearest neighbor distance; NNSD = 0). NNCV is reported as "N/A" if none of the patches have a nearest neighbor. Likewise, in the vector version, if the rasterization process creates more or less patches than are present in the vector image (see below), then NNCV is reported as "N/A".

Description: NNCV equals the standard deviation in nearest neighbor distances (NNSD) divided by the mean nearest neighbor distance (MNN), multiplied by 100 (to convert to percent); that is, the variability in nearest neighbor distance relative to the mean nearest neighbor distance. Note, this is the population coefficient of variation, not the sample coefficient of variation.

Example: Figure 3.6 depicts 3 sample landscapes that vary in composition and pattern. Because of the relatively small extent of these landscapes, nearest neighbor indices are not particularly meaningful. The "N/A" in landscape A resulted from loss of direct correspondence during the rasterization process.

Appendix D. Number of detections and effective detection distance for bird species detected in 30 300-ha subbasins in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92. Species are ordered from most to least common based on total number of detections.

Acronym	Species (scientific name)	N_t^a	N_{new}^b	N_{50}^c	%Edge[d]	Edd[e]
SWTH	Swainson's thrush (Catharus ustulatus)	8758	8457	4281	4.04	80
WIWA	Wilson's warbler (Wilsonia pusilla)	8588	8149	3638	4.89	90
WIWR	Winter wren (Troglodytes)	8291	7757	3245	2.37	95
PSFL	Pacific slope flycatcher (Empidonax difficilis)	6031	5769	2877	2.92	80
VATH	Varied thrush (Ixoreus naevius)	5133	3960	505	1.39	100
HEWA	Hermit warbler (Dendroica occidentalis)	4096	3604	1170	2.31	100
EVGR	Evening grosbeak (Coccothraustes vespertinus)	3470	3164	449	1.78	95
STJA	Steller's jay (Cyanocitta stelleri)	3256	2416	507	8.09	130
RECR	Red crossbill (Loxia curvirostra)	2779	2547	457	9.85	95
CBCH	Chestnut-backed chickadee (Parus rufescens)	2626	2596	2142	5.65	50
BHGR	Black-headed grosbeak (Pheucticus melanocephalus)	2043	1631	549	6.56	100
SOSP	Song sparrow (Melospiza melodia)	1981	1844	765	4.05	90
OCWA	Orange-crowned warbler (Vermivora celata)	1653	1466	413	5.33	100
GCKI	Golden-crowned kinglet (Regulus satrapa)	1601	1593	1440	2.64	40
AMRO	American robin (Turdus migratorius)	1573	1387	385	8.57	100
BTPI	Band-tailed pigeon (Columba fasciata)	1349	1131	177	10.17	105
WAVI	Warbling vireo (Vireo gilvus)	1311	1080	304	4.61	110
BRCR	Brown creeper (Certhia americana)	1164	1145	801	0.75	55
MGWA	Macgillivray's warbler (Oporornis tolmiei)	1057	930	279	2.51	100
HAFL	Hammond's flycatcher (Empidonax hammondii)	984	897	341	0.88	90
WCSP	White-crowned sparrow (Zonotrichia leucophrys)	954	803	192	1.56	115

Appendix D. Continued.

Acronym	Species (scientific name)	N_t[a]	N_{new}[b]	N_{50}[c]	%Edge[d]	Edd[e]
DEJU	Dark-eyed junco (Junco hyemalis)	907	842	337	6.23	95
HAWO	Hairy woodpecker (Picoides villosus)	898	788	286	11.19	100
RSTO	Rufous-sided towhee (Pipilo erythrophthalmus)	828	743	221	2.26	100
WETA	Western tanager (Piranga ludoviciana)	741	587	88	6.82	115
RUHU	Rufous hummingbird (Selasphorus rufus)	642	640	611	5.89	20
WREN	Wrentit (Chamaea fasciata)	636	547	86	2.33	100
PIWO	Pileated woodpecker (Dryocopus pileatus)	611	439	23	13.04	160
PUFI	Purple finch (Carpodacus purpureus)	600	525	122	9.02	100
OSFL	Olive-sided flycatcher (Contopus borealis)	540	306	33	42.42	175
HUVI	Hutton's vireo (Vireo huttoni)	537	496	139	4.32	95
AMGO	American goldfinch (Carduelis tristis)	533	504	150	4.67	85
RBNU	Red-breasted nuthatch (Sitta canadensis)	481	430	88	2.27	100
NOFL	Northern flicker (Colaptes auratus)	455	338	34	20.59	150
GRJA	Gray jay (Perisoreus canadensis)	418	385	191	3.66	85
CORA	Common Raven (Corvus corax)	402	288	15	6.67	170
HOWR	House wren (Troglodytes aedon)	366	294	77	0.00	100
WIFL	Willow flycatcher (Empidonax traillii)	356	311	70	2.86	100
BGWA	Black-throated gray warbler (Dendroica nigrescens)	316	281	98	2.04	100
CEWA	Cedar waxwing (Bombycilla cedrorum)	253	249	131	11.45	50
MOQU	Mountain quail (Oreortyx pictus)	209	146	2	0.00	195
MAMU	Marbled murrelet (Brachyramphus marmoratum)	190	184	4	25.00	---
BEWR	Bewick's wren (Thryomanes bewickii)	190	175	56	5.36	100
WWPE	Western wood-pewee (Contopus sordidulus)	154	107	16	56.25	150

Appendix D. Continued.

Acronym	Species (scientific name)	N_t[a]	N_{new}[b]	N_{50}[c]	%Edge[d]	Edd[e]
PYOW	Northern pygmy owl (Glaucidium gnoma)	141	94	7	14.29	180
RTHA	Red-tailed hawk (Buteo jamaicensis)	131	103	14	7.14	200
RBSA	Red-breasted sapsucker (Saphyrapicus ruber)	129	118	22	9.09	130
VGSW	Violet-green swallow (Tachycineta thalassina)	105	86	35	0.00	85
HETH	Hermit thrush (Hylocichla guttata)	101	89	15	0.00	95
BUSH	Bushtit (Psaltriparus minimus)	91	91	68	10.29	40
PISI	Pine siskin (Carduelis pinus)	66	64	12	8.33	80
TOSO	Townsend's solitaire (Myadestes townsendi)	66	49	16	6.25	115
RUGR	Ruffed grouse (Bonasa umbellus)	64	52	5	0.00	90
AMCR	American Crow (Corvus brachyrhynchos)	64	48	2	0.00	---
CONI	Common nighthawk (Chordeiles minor)	57	54	0	0.00	---
YRWA	Yellow-rumped warbler (Dendroica coronata)	56	50	29	41.38	70
WEBL	Western bluebird (Sialia mexicana)	52	48	23	4.35	95
TRSW	Tree swallow (Tachycineta bicolor)	49	42	7	0.00	90
BCCH	Black-capped chickadee (Parus atricapillus)	42	35	17	0.00	75
TUVU	Turkey vulture (Cathartes aura)	35	35	0	0.00	---
BUGR	Blue Grouse (Dendragapus obscurus)	35	18	0	0.00	---
DOWO	Downy Woodpecker (Dendrocopos pubescens)	30	29	13	38.46	85
TOWA	Townsend's warbler (Dendroica townsendi)[f]	29	28	14	7.14	90
RCKI	Ruby-crowned kinglet (Regulus calendula)[f]	19	18	9	0.00	---
GHOW	Great-horned owl (Bubo virginianus)	18	18	0	0.00	---
BEKI	Belted kingfisher (Ceryle alcyon)	18	15	0	0.00	---
GCSP	Golden-crowned sparrow (Zonotrichia atricapilla)[f]	17	17	11	0.00	---

Appendix D. Continued.

Acronym	Species (scientific name)	N_t[a]	N_{new}[b]	N_{50}[c]	%Edge[d]	Edd[e]
COYE	Common yellowthroat (Geothlypis trichas)	13	12	3	0.00	---
MALL	Mallard (Anas platyrhynchos)	12	12	2	0.00	---
SCOW	Screech owl (Otus kennicottii)	11	11	1	0.00	---
BHCO	Brown-headed cowbird (Molothrus ater)	10	10	3	0.00	---
GBHE	Great blue heron (Ardea herodias)	9	9	0	0.00	---
SPOW	Spotted owl (Strix occidentalis)	9	5	2	0.00	---
HOME	Hooded merganser (Lophodytes cucullatus)	8	8	5	0.00	---
EUST	European starling (Sturnus vulgaris)	7	7	1	0.00	---
WODU	Wood duck (Aix sponsa)	6	6	3	0.00	---
SSHA	Sharp-shinned hawk (Accipiter striatus)	6	6	1	0.00	---
SOVI	Solitary vireo (Vireo solitarius)	6	4	1	0.00	---
DIPP	American dipper (Cinclus mexicanus)	5	5	3	0.00	---
BASW	Barn swallow (Hirundo rustica)	4	4	0	0.00	---
COME	Common merganser (Mergus merganser)	4	4	0	0.00	---
VASW	Vaux's swift (Chaetura vauxi)	4	4	0	0.00	---
BAEA	Bald eagle (Haliaeetus leucocephalus)	2	2	0	0.00	---
CAGO	Canada goose (Branta canadensis)[g]	2	2	0	0.00	---
COHA	Cooper's Hawk (Accipiter cooperii)	2	2	0	0.00	---
RWBL	Red-winged blackbird (Agelaius phoeniceus)	2	2	0	0.00	---
SWOW	Northern saw-whet owl (Aegolius acadicus)	2	2	0	0.00	---
SCJA	Scrub jay (Aphelocoma coerulescens)	1	1	0	0.00	---

Appendix D. Continued.

Acronym	Species (scientific name)	N_t[a]	N_{new}[b]	N_{50}[c]	%Edge[d]	Edd[e]

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[a] N_t = Total number of detections at all distances, including new and repeat detections of individuals from separate sampling points within a subbasin.

[b] N_{new} = Total number of detections at all distances, including only detections of new individuals within a subbasin.

[c] N_{50} = Total number of detections within 50 m of a sampling point, including new and repeat detections of individuals from separate sampling points within a subbasin.

[d] %Edge = Percent of detections within 50 m of a sampling point (N_{50}) within 10 m of a seral condition patch edge (see Appendix 4.2 for definition of seral conditions).

[e] EDD = 75% cumulative detection distance; 75% of detections with estimated distance were ≤ EDD.

[f] Species not known to breed within the study area.

[g] Large migratory flocks detected flying overhead, number of individuals were not estimated.

Appendix E. Patch type classification system (modified from Brown, 1985:17-31) used to classify vegetation in 30 300-ha subbasins in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990-92.

Patch Type	Definition
PLANT COMMUNITY: All patches have a designated plant community.	
Nonforested	Areas that do or will not over the near future support forest vegetation because of natural or human-induced conditions.
Water	Open water (e.g. ponds, lakes).
Herbaceous Wetlands	Bogs, marshes, and meadows dominated by herbaceous plants and having a site potential and minimal shrub cover (<60% woody cover); generally dominated by rushes, sedges, and grasses.
Hardwood/Shrubby Wetlands	Wetlands dominated by woody vegetation with woody crown cover >60%; commonly dominated by alder, bigleaf maple, willows, or Oregon ash.
Grass-Forb Dry Hillsides	Grasslands with <40% woody cover; mainly caused by humans who control the tree or shrub vegetation to maintain the area in permanent pasture.
Brush Fields	Brush dominated areas that will remain in brush unless some sort of disturbance alters the site and makes tree growth possible.
Forested	Areas that do or will in the near future support forest vegetation.
Hardwood Community	>70% hardwood (red alder) composition.
Conifer Community	>70% conifer composition.
Conifer-Hardwood Community	<70% hardwood or conifer composition.
SERAL CONDITION: All forested plant communities have a designated seral condition.	
Grass-Forb	Shrubs: <40% crown cover; <1.5 m mean height Trees: <20% crown cover; <3 m mean height; <1 in mean dbh[a]
Shrub	Shrubs: >40% crown cover any height Trees: <20% crown cover; <3 m mean height; <1 in mean dbh

Appendix E. Continued.

Patch Type	Definition
SERAL CONDITION--continued.	
Sapling	Tress: >20% crown cover Conifers: >3 m mean height; 1-4 in mean dbh Hardwoods: 3-15 m mean height; 1-4 in mean dbh
Pole Condition	Trees: >20% crown cover Conifers: >3 m mean height; 4-12 in mean dbh Hardwoods: 3-15 m mean height; 4-12 in mean dbh
Small Sawtimber	Trees: >20% cover; 12-21 in mean dbh
Large Sawtimber	Trees: >20% cover; >21 in mean dbh
CANOPY CLOSURE:	All forested plant communities with sapling and pole seral condition have a designated canopy closure condition.
Open Canopy	20-70% tree crown cover
Closed Canopy	70-100% tree crown cover

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[a] dbh = diameter breast height.