Chapter 7

Landscape Dynamics and Considerations

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Introduction

Landscape ecology is the study of spatial heterogeneity and its influence on organisms and ecological processes (Risser et al. 1984). Recent advances in remote sensing technologies, computer software and hardware, and methods for quantifying spatial heterogeneity have contributed to the emergence of landscape ecology as a powerful approach for analyzing spatial patterns and their ecological consequences. The following references provide a good overview of the field of landscape ecology: Forman and Godron (1986), Naveh and Leiberman (1994), Pickett and Cadenasso (1995), Risser et al. (1984), Turner and Gardner (1991), and Urban et al. (1987).

Table 1 defines key terms in landscape ecology used in this chapter. Exact definitions of landscape, patch type, and patch depend on the specific organisms and processes being studied (Dunning et al. 1992; McGarigal and Marks 1995; Wiens 1976; Wiens and Milne 1989). Typically, landscapes occupy a spatial scale intermediate between an organism's home range and its regional distribution (Dunning et al. 1992). Thus, for songbirds in the Southwest, landscapes may be defined ranging in size from a few hectares to thousands of square kilometers. The patch type of primary interest here is ponderosa pine forest, or forest in which ponderosa pine is the sole dominant plant species. Individual patches may range in size from a few trees to hundreds of square kilometers, depending on the phenomena and species under investigation, the scale of the study and the resolution of any remote sensing imagery used.

Landscape ecologists generally divide spatial patterns observed in landscapes into two categories: landscape composition and landscape configuration. Landscape composition refers to the variety and abundance of patch types within a landscape without considering the location of individual patches (Dunning et al. 1992; McGarigal and Marks 1995). An example of a measure of landscape composition is the proportion of a given landscape covered by ponderosa pine forest. Landscape configuration refers to the spatial relationships between patches in a landscape (McGarigal and Marks 1995). For example, one might be interested not only in the total amount of ponderosa pine present in a landscape but also in the degree to which individual ponderosa pine patches are isolated from each other. Both landscape composition and configuration have been shown to have significant influences on the distribution and abundance of songbirds (Freemark et al. 1995).

Many studies in Southwestern ponderosa pine forests have investigated the relationships between songbirds and

Table 1. Definition of several key terms used in landscape ecology.

Term	Definition	Reference[a]
landscape	a mosaic of patches relevant to the phenomenon under consideration (at any scale)	1
patch	distinguished by discontinuities in environmental character states from its surroundings; implicit is the notion that the discontinuities have biological significance	2
patch type	a description of the environmental character states differentiating a patch or group of similar patches from surrounding areas[b]	1
landscape composition	features associated with the presence and amount of each patch type within the landscape but without being spatially explicit	1
landscape configuration	physical distribution or spatial character of patches within the landscape	1
grain	the resolution of the data, that is, the area represented by each data unit[c]	3
extent	the overall size of the study area[c]	3
local population	set of individuals that all interact with each other with a high probability	4
metapopulation	set of local populations that interact via individuals moving among populations	4

[a] References: 1. McGarigal and Marks (1995); 2. Wiens (1976); 3. Turner et al. (1989); 4. Hanski and Gilpin (1991).
[b] Our definition. The term is used, although not explicitly defined, by McGarigal and Marks (1995).
[c] The terms "grain" and "extent" are also used to refer to the smallest and largest scales at which an organism responds to spatial heterogeneity (Kotliar and Wiens 1990). We present the above definitions because we use these terms in describing spatial data sets in the text.

habitat characteristics at the level of individual patches (Hall et al. and Finch et al., this volume). To date, though, no published studies from Southwestern ponderosa pine forests have examined the relationships between songbirds and spatial patterns at the level of entire landscapes. In this chapter, we will discuss the importance of scale in ecological research, highlight several tools available for characterizing landscape patterns in Southwestern ponderosa pine forests, and describe specific research needs at fine, intermediate, and large spatial scales. We will also address research needs relevant to habitats and species of special concern.

The Importance of Scale

Different ecological processes occur at different spatial scales (Kotliar and Wiens 1990; Urban et al. 1987; Wiens 1989). Factors affecting habitat selection by individuals within patches may differ from factors influencing the distribution and abundance of organisms across landscapes (Wiens 1989; Wiens et al. 1987; McGarigal and McComb 1995). To fully understand the ecology of songbirds in Southwestern ponderosa pine forests, additional research is needed at multiple spatial scales, including fine-scale studies at the level of individual patches; intermediate-scale studies at the level of landscapes several hundred hectares in size; and large-scale studies at the level of landscapes hundreds to thousands of square kilometers in size.

At different scales, different spatial patterns emerge for ponderosa pine forests in the Southwest. At a scale of several hundred hectares, ponderosa pine forests generally appear as integral components of larger forests. Ponderosa pine forests often meet and blend with pinyon-juniper along lower elevational boundaries and with Douglas-fir and mixed-conifer along upper elevational boundaries. At a scale of hundreds to thousands of square kilometers, though, Southwestern ponderosa pine forests tend to appear highly fragmented.

How these spatial patterns influence the songbirds that use these forests is unknown. Many studies in forests of eastern and central North America have found that smaller, more isolated patches tend to have fewer songbird species and fewer individuals of those species than larger, less isolated patches (for example, Ambuel and Temple 1983; Askins and Philbrick 1987; Blake 1986; Blake 1991; Blake and Karr 1984; Blake and Karr 1987; Freemark and Collins 1992; Freemark and Merriam 1986; Lynch and Whigham 1984; Robbins et al. 1989; Whitcomb et al. 1981). These studies have generally focused on patches of forest surrounded by non-forested agricultural and suburban areas. In contrast, several studies in western North America have shown little relationship between patch size and songbird species richness or abundance in forest patches surrounded by forests of different species composition or age and size class (Aney 1984; Lehmkuhl et al. 1991; Rosenberg and Raphael 1986). Conceivably, songbirds in ponderosa pine forests may show responses characteristic of birds in Eastern fragmented forests at large spatial scales, while showing responses characteristic of birds in other Western forests at intermediate spatial scales. Until landscape-level research on songbirds in Southwestern ponderosa pine forests is carried out, though, such comparisons will remain speculative.

Characterization of Landscape Patterns

A prerequisite for most research in landscape ecology is the availability of data on the spatial patterns of interest. All spatial data sets have a certain grain and extent. "Grain" refers to the resolution of the data (Turner et al. 1989). For example, on a relatively fine-grain map, it might be possible to distinguish features 1 m in size, while on a relatively coarse-grain map these features might not be visible. Extent refers to the area covered by the data set. A spatial data set is only useful for a given study if it has a grain and extent appropriate for the research being carried out (McGarigal and Marks 1995; Turner et al. 1989). The data must have a fine enough grain that patch types and patches relevant to the organisms and phenomena being investigated can be readily distinguished. In addition, the extent must be large enough that meaningful spatial patterns can be identified.

Table 2 provides information on several spatial data sets currently available or soon to be available that include data on Southwestern ponderosa pine forests. The USDA Forest Service General Ecosystem Survey and Terrestrial Ecosystem Surveys are limited in their applicability for research on songbirds since only Forest Service land is included, and since map units are based on potential natural vegetation rather than current vegetation. The data sets based on advanced very high resolution radiometer (AVHRR) imagery are limited in their applicability, as well. They are very coarse-grain, with a resolution of 1 km. Keitt et al. (1995) suggest that some details of the Earth Resources Observation Systems (EROS) classification are rather suspect from a biogeographic standpoint, and they use the USDA Forest Service classification in their analysis of potential habitat patches for the Mexican spotted owl. However, the Forest Service classification does not distinguish between forest dominated by ponderosa pine and forest dominated by Douglas-fir, rendering it inadequate for studies focusing on ponderosa pine forest.

Table 2. Selected data sets currently available or soon to be available for characterizing landscape patterns Influencing songbirds in Southwestern ponderosa pine forests.

Data set	Source of imagery	Scale or resolution	Availability[a]	References[b]
USDA Forest Service (Southwestern Region) General Ecosystem Survey	aerial photography	1:250,000	currently available	1
USDA Forest Service Terrestrial Ecosystem Surveys	aerial photography	1:24,000	currently available	2
Vegetative cover types from EROS	AVHRR	1 km	currently available	3
USDA Forest Service forest cover types	AVHRR	1 km	currently available	4, 5, 6
AZ Gap Analysis	TM	30 m	fall 1997	7
NM Gap Analysis	TM	30 m	currently available	8, 9

[a] Currently available refers to data sets available as of August 1996.
[b] References: 1. USDA Forest Service (1989); 2. USDA Forest Service (1986); 3. Loveland et al. (1991); 4. Evans and Zhu (1993); 5. Powell et al. (1993); 6. Zhu and Evans (1992); 7. K. Thomas, personal communication; 8. Muldavin (1994); 9. B. Thompson, personal communication.

The Arizona and New Mexico Gap Analysis data sets will provide a valuable addition to the spatial data available for landscape ecological studies of songbirds in ponderosa pine forests. Since they are based on Landsat thematic mapper (TM) imagery with a 30-m resolution, though, they will be somewhat limited in their usefulness for addressing questions requiring very detailed, fine-grain data on forest composition and structure. The development of spatial data sets with a relatively high resolution, on the order of 1 m, would provide an extremely useful resource for studies on the effects of fine-grain forest attributes on songbirds in the Southwest.

McGarigal and Marks (1995) have published a computer program called FRAGSTATS that provides researchers with a powerful tool for quantifying landscape composition and configuration. Versions of FRAGSTATS are available for use with either vector or raster image files. FRAGSTATS computes a comprehensive array of landscape metrics including area metrics, patch size metrics, edge metrics, shape metrics, core area metrics, nearest neighbor metrics, patch diversity metrics, and contagion and interspersion metrics. The accompanying documentation includes a thorough description of each metric, including mathematical definitions and a discussion of each metric's ecological applications and limitations (McGarigal and Marks 1995).

Fine-Scale Studies

Although studies of the relationships between habitat characteristics and songbird species' richness and abundance have been carried out at the individual patch level in Southwestern ponderosa pine forests, more research is needed to clarify these relationships. More research is needed to determine the effects of vegetation species composition, tree size and age class, density of overstory and understory vegetation, and fire and grazing history on songbird diversity and abundance at the patch level (Hall et al. and Finch et al., this volume). Such information will be useful for managing forest patches (for example, forest stands) to maintain local songbird diversity and abundance.

In addition, research is needed to determine the extent to which individual species are obligate users of ponderosa pine forest. Many songbird species are known to occur in ponderosa pine forest. Some species, such as Grace's warbler, appear to be ponderosa pine specialists and may require the presence of ponderosa pine forest to survive and reproduce (Hall et al., this volume). Other species, such as the mountain chickadee, appear to be forest generalists and may be able to thrive in a variety of forest types. Still other species, such as the American robin, appear to be extreme generalists and are frequently found in a wide variety of forest and non-forest habitats. Clearly, individual songbird species can differ greatly in their habitat requirements, and research is needed to elucidate the specific habitat requirements for songbirds found in ponderosa pine forests. Information is needed on the extent to which individual songbird species require ponderosa pine habitat in the breeding season, during migration, and as winter residents.

The degree to which songbird species are ponderosa pine specialists versus broader habitat generalists has potential implications for the scale at which those species respond to spatial heterogeneity. Ponderosa pine specialists are likely to respond to spatial heterogeneity at a finer scale than habitat generalists. For example, Grace's warblers may be more sensitive than American robins to differences in tree size and age class, density of overstory and understory vegetation, and grazing intensity within a ponderosa pine forest. Such hypotheses need to be tested in field studies that compare the responses of habitat specialists and generalists to different fine-scale patterns of spatial heterogeneity. This type of study will likely reveal indicator species (presumably habitat specialists) useful for monitoring ponderosa pine forest habitat quality.

Ponderosa pine specialists also undoubtedly differ from habitat generalists in their responses to broad-scale patterns of spatial heterogeneity. For a Grace's warbler, a series of ponderosa pine forests separated by pinyon-juniper woodland might appear to be a fragmented landscape. For an American robin, however, the same landscape may appear relatively continuous. Understanding the finescale habitat requirements of individual species is an important element in understanding the responses of those species to spatial patterns at broader scales.

Intermediate-Scale Studies

In addition to studies at the patch level in which individual patches represent independent data points, studies at the landscape level in which landscapes represent independent data points are needed to examine the relationships between landscape characteristics and songbird distribution and abundance. Examples of such studies carried out in other regions include a study by McGarigal and McComb (1995) in mixed-conifer forest in the central Oregon Coast Range, and a study by Evans (1995) in mixed-conifer forest in west-central Idaho. In both studies, landscapes were defined at a scale of several hundred hectares and chosen to represent a wide spectrum of spatial patterns reflecting different forest management regimes. McGarigal and McComb (1995) used ground-truthed aerial photographs for baseline data on spatial attributes, while Evans (1995) used a ground-truthed timber strata map generated from a Payette National Forest timber inventory. In both studies, FRAGSTATS (McGarigal and Marks 1995) was used to compute measures of landscape composition and configuration.

McGarigal and McComb (1995) and Evans (1995) both found significant relationships between several measures of landscape composition and configuration and the abundance of one or more songbird species. Interestingly, McGarigal and McComb (1995) found that for species strongly associated with a particular patch type at the patch level, the relationships between abundance and the amount of preferred patch type present at the landscape level varied greatly. McGarigal and McComb's (1995) study supports the idea that different processes occur at different spatial scales, and that relationships seen at the patch level cannot necessarily be extrapolated over landscapes.

Large-Scale Studies

Research is also needed at a relatively large scale of hundreds to thousands of square kilometers to determine patterns of songbird distribution and abundance and shed light on ecological processes at this scale. Ecological interactions between individuals of a given species and biotic and abiotic factors in the environment are likely to vary across the range of that species. To understand the ecology of a species, one must understand ecological processes occurring throughout its range. Thus, to fully understand the ecology of songbirds in Southwestern ponderosa pine forests, one must understand ecological processes occurring across the ranges of these species.

At large spatial scales, ponderosa pine forests in the Southwest tend to occur within "Sky Islands" of mountain forest surrounded by seas of arid grassland and desert (DeBano et al. 1995; Gehlbach 1981). One area of potential interest in studying songbirds in these forests is the area of metapopulation dynamics. Metapopulations are groups of two or more populations connected by infrequently dispersing individuals, and they typically occur when populations occupy areas of suitable habitat separated by areas of unsuitable habitat (Hanski and Gilpin 1991). Some metapopulations may exhibit "source-sink" characteristics (Brawn and Robinson 1996; Howe et al. 1991; Pulliam 1988; Pulliam and Danielson 1991). In these cases, it is believed that individuals from source populations, in which productivity exceeds mortality, disperse to sink populations, which would go locally extinct in the absence of such migration.

Little is known about the extent to which songbird species in Southwestern ponderosa pine forests exhibit metapopulation dynamics. Given the fragmented patterns of ponderosa pine forest found at large spatial scales in the Southwest, it is likely that at least some songbird species found in this habitat exist as metapopulations. However, the degree to which a given species exists as a metapopulation is no doubt influenced by the habitat preferences and requirements of the species and the extent to which it can disperse through unsuitable habitat. Overall, one would predict that ponderosa pine specialists, such as Grace's warbler, would exhibit very different metapopulation dynamics than broader forest generalists, such as the mountain chickadee. Mountain chickadees may in turn exhibit very different metapopulation dynamics than extreme habitat generalists, such as the American robin.

Likewise, the nature of source-sink dynamics within metapopulations undoubtedly varies from species to species. For some species, ponderosa pine forest may represent source habitat in which productivity is relatively high. For other species, ponderosa pine forest may represent sink habitat in which mortality and emigration exceed productivity. Source-sink dynamics are further complicated in migratory species by the fact that some areas may be unimportant for breeding but critical as stopover sites during migration or as wintering habitat.

Attempting to understand metapopulation dynamics is an ideal example of an endeavor that requires research at multiple spatial scales. Studies at fine scales are needed to determine exactly how the species in question uses different habitat types. Studies at intermediate scales are needed to learn more about habitat requirements, including how landscape composition and configuration affect habitat selection. Studies at larger scales are needed to determine overall patterns of habitat availability, how habitat use varies throughout the range, and how patterns of habitat availability and use relate to metapopulation dynamics. For migratory species, information at each spatial scale is needed for breeding areas, for stopover sites used during migration, and for wintering habitat.

One key aspect of understanding the population dynamics of a species is understanding dispersal patterns of individuals through different habitat types. We know that most songbirds are capable of traveling great distances (many migrate to the tropics for the winter). However, vagility, or the physical ability of a species to move, should not be equated with dispersal, or the movement of individuals to new areas to settle there and breed (Villard et al. 1995). Little is known about dispersal in songbirds. Some studies (Drilling and Thompson 1988; Holmes and Sherry 1992; Kendeigh 1941) suggest that typical dispersal distances for adults in some species of songbirds may be less than 350 m. However, these studies provide limited data for a small number of species. Even less is known about dispersal in first-year songbirds, that is, how far first-year birds tend to nest from their birth sites. Greenwood and Harvey (1982) suggest that the median first-year dispersal for both sexes is usually less than 10 territories away from the birth site. However, Villard et al. (1995) argue that this generalization may not be valid since recapture rates of songbirds banded as nestlings are usually lower than 10 percent. In forest patches of central Illinois, Robinson (1992) observes that songbirds have very low reproductive success, and he suggests that populations in the area may be maintained by individuals dispersing from forests over 200 km away.

To date, no studies have been published estimating dispersal distances for songbirds in ponderosa pine forests in the Southwest. Information on dispersal distances could potentially be gathered through extensive banding operations and attempts at recapture across large areas. Another alternative would be to identify isolated patches in which one or more species have been extirpated due to stochastic processes, forest fires, or human activities such as logging, and then survey those patches to determine whether those species reappear over time. If those species do reappear, this would suggest that they were able to disperse from an area at least as far away as the nearest suitable habitat (Villard et al. 1995). Such studies would be especially useful when the areas of nearest suitable habitat are a considerable distance away (for example, in another Sky Island), as they might provide insights into maximum dispersal distances for songbirds over different habitat types.

Spatial data sets from the Arizona and New Mexico Gap Analysis projects should provide information useful for large-scale studies on songbirds in Southwestern ponderosa pine forests (table 2). To adequately study most ecological patterns and processes important for songbirds in ponderosa pine forests, though, analyses of spatial data from imagery will need to be accompanied by field investigations. This will likely present some logistical challenges at scales of hundreds to thousands of square kilometers. Nonetheless, data from imagery are generally of little use unless they are ground-truthed and closely linked with data collected in the field. The collection of field data across large spatial scales may be facilitated by collaboration among researchers and by the careful selection of field sites based on high-quality imagery.

Habitats and Species of Special Concern

Because of the relatively small area of old-growth ponderosa pine forests remaining in the Southwest and economic pressures to harvest these forests, research into songbird responses to landscape characteristics of old-growth ponderosa pine forests at multiple scales should be a top priority. At the patch level, more research is needed to determine exactly how songbirds use old-growth ponderosa pine forests and the extent to which they depend on them. At larger landscape levels, research is needed to determine how the proportion and spatial configuration of old-growth ponderosa pine forest in a landscape influences songbird distribution and abundance.

Research on songbird responses to landscape composition and configuration at multiple scales is needed that considers both overall songbird diversity and the abundance of individual species. Measuring the local diversity of songbird species in an area provides insight into the ability of that area to support a variety of different kinds of songbirds. However, from a regional perspective, the number of species in a given area may not be as important as which species are present. For example, a clearcut patch may be found to have a relatively high diversity of songbird species, but those species may be common throughout the region. Thus, widespread clearcutting in the region might produce areas of high local species diversity while dramatically reducing overall regional diversity.

Studies that focus on individual songbird species are necessary for understanding the relationships between individual species and different types of habitat and for gaining insights into population and metapopulation dynamics. Landscape-level studies focusing on those songbird species most vulnerable to local extirpation or rangewide extinction are especially urgent. No such studies have been carried out, and landscape-level information is needed to inform management decisions affecting regional avian diversity and the long-term viability of those species.

A list of bird species on managed ponderosa pine Breeding Bird Survey routes in Arizona and New Mexico whose populations have been declining is provided in Chapter 4 of this volume (from Miller 1992), as is a list of bird species found in ponderosa pine forests ranked as being of high or moderate concern by the Arizona and New Mexico Partners in Flight programs. These lists offer a starting point for identifying target species for landscape-level studies in Southwestern ponderosa pine forests.

Typically, landscape-level studies of songbirds in other regions have involved sampling all songbird species encountered across different landscapes using standardized techniques. In many studies, rare species were not considered in the analysis of abundance data because they did not lend themselves well to the statistical methods used (for example, Evans 1995; Hagan et al. 1996; Knick and Rotenberry 1995; McGarigal and McComb 1995; Rosenberg and Raphael 1986). To overcome this problem in Southwestern ponderosa pine forests, research must be carried out over broad enough spatial and temporal scales that sufficient data on rare species are gathered for statistical analysis.

Rare species form a critical component of bird communities. In most studies of bird communities, a small number of species are found at all or most sites while many species occur at only a few (for example, Evans 1995; Hansen et al. 1995; Hejl and Woods 1991; Rosenberg and Raphael 1986; Verner and Larson 1989). Landscape-level research that focuses on rare species is needed to gather more information about these species and to provide a scientific basis for managing rare species and their habitats. Maintaining viable populations of rare species is essential for maintaining overall avian diversity in the Southwest, as well as for maintaining healthy, intact communities and ecosystems.

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