15 Landscape Structure and Composition

LANDSCAPES

In art, they are paintings of places, usually from a distance, a mosaic of forms interwoven to portray a recognizable place familiar and pleasing to the eye. That is the function of the painting. Ecological landscapes also can be viewed as a mosaic. They have structure, as portrayed by the pattern of the patches comprising the landscape. They have composition, as portrayed by the types of patches on the landscape. They have function, as defined by the resources of concern—in our case, patches of habitat for a species or collection of species. Forested landscapes, as habitat for vertebrates, are patterns of habitat patches distributed over forest-dominated areas, with each patch representing a set of resources used or needed by the species. The pattern of habitat patches across a landscape differs from one species to another. We, as humans, tend to view forested landscapes as collections of forest stands, a mosaic of units of vegetation that is relatively uniform within stands, but heterogeneous among them. We do that because, to us, those stands represent different resources, such as economic value, places to hike, or different aesthetics. For some other vertebrates, the stands that we see also represent patches of different values, habitat values. But not for all species. Take the shrub-associated Swainson's thrush that is widely distributed across North America (Figure 15.1). What type of mosaic of patches would a Swainson's thrush see? The thrushes' search image (what they seek) for a territory, likely includes patches of shrubs with varying quality for foraging on insects in the leaf litter and foliage, as well as nest sites low in the shrubs. The overstory vegetation seems to have little, if any, influence on what Swainson's thrushes see as habitat patches, except through the effect it has on shrub development. Old-growth, stand establishment, or understory reinitiation conditions are not really as important to this species as the shrub cover present in the stand. If we were to develop a very simple map of habitat with white patches being habitat and black being unusable, then we would map patches of shrubs of a certain cover and height for Swainson's thrushes, and these patches might be quite unrelated to tree species' composition or structure.

Mapping habitat for northern flying squirrels would focus more on snags, tree species, size and canopy cover, and not so much on shrubs. And, to make things even more complicated, consider habitat for cottontail rabbits that feed in grassy areas but use dense shrubs as cover. They live on the edge between these two types of vegetation, and the acceptable habitat (white) on our map would be a linear strip extending perhaps 30 m into the grassy area and 20 m into the shrubs. Everything else would be black. Three species, three landscape patterns, all in the same forest. Managing stands in this forest could influence the patterns of habitat for each of these species, depending on the types of vegetation and other features provided in each stand.

We know that habitat varies in its quality from place to place and over time. At the very least, we might consider sources and sinks for each species, but even these represent a gradient of habitat quality (as expressed through individual fitness). It is more appropriate to think of a mosaic of habitat as represented by shades of gray, or perhaps, more appropriately, a collage of habitat values, with edges that are more or less blurry. A spectrum of resources painted across an area for each species. If we are concerned about providing habitat for 100 species in our forest, then there are 100 landscapes in our forest, each with its own collage of habitat. For each species, management decisions made at places in our forest represent the building blocks of a habitat mosaic for that species that we manipulate through our forest management activities. So the structure, composition, and

FIGURE 15.1 Swainson's thrushes select patches of shrubs as habitat across a landscape mosaic. (Photo from the North Cascades National Park, USDI National Park Service.)

function of a landscape depend entirely on the species or other values that we wish to produce from that landscape.

We can take this one step further. Dr. Sam Cushman and his colleagues questioned the value of patches when defining landscapes as habitat for a particular species (Cushman et al. 2010b). Not only did they find that different people define patches inconsistently, but that the resources of value to a species are not homogenous within a patch. Sam and others suggest that we think of landscapes as gradients of resource availability, and not as a collage of patches, each representing a certain level of habitat quality. Gradient-based analysis of landscapes that represent habitat for individual species is clearly the future of landscape ecology (Cushman et al. 2010a). Indeed, new gradient-based measures of the landscape have been developed (McGarigal et al. 2009). But most work to date has been based on patches, so the remainder of the chapter focuses on patch-based approaches. Just keep in mind that you may need to think of landscapes as a series of gradients of habitat quality, rather than patches.

DEFINING THE LANDSCAPE

There are several attributes of a landscape that must be defined when considering habitat function for a species across a landscape: Grain, extent, and context. The *grain* represents the smallest unit of space that we (or the species of interest) use and identify. Recall the hierarchical selection of habitat discussed in Chapter 3. Each species scales its habitat differently at each of four (or more) levels of habitat selection (Johnson 1980). Depending on the scale of habitat selection we wish to understand, when managing the species, the smallest unit of space (that we would need to consider) varies. For many species, the grain might best be an individual tree or shrub, where resources are available: browse plants for a herbivore; fruit from a yaupon shrub; or blackgum trees where dens are available for squirrels. But considering the spatial pattern of all trees and shrubs in a forest is impractical when developing a management plan. Rather, we typically consider the patches within which these resources occur (however, see the gradient-based approach suggested by Sam Cushman, provided earlier). The way in which we define patches on the ground, or on a map, defines a grain, which is some minimum size that is both meaningful to the species of interest and practical to consider during management. For example, we might define patches of shrubs of various species, 0.5 ha or larger, as resource patches for white-tailed deer. Or we could simply characterize each stand in our forest as having certain levels of food or cover resources within the stand, without explicitly considering where in the stand these resources occur. From a management standpoint, we would just know that some stands have more high-quality browse than other stands.

Now let us assume that the forest landscape that we are managing is 20,000 ha; this would define an *extent*, the area over which we are managing resources. Alternatively, we could define the extent as the population of deer that we are managing and the area over which they occur. If we are managing the 20,000 ha landscape with a grain size of 0.5 ha, then we would need to keep track of up to 40,000 patches of browse across the landscape over time. We can do that with the aid of computers and geographic information systems (GIS); but from a forest management standpoint, such a fine level of information may not be practical to monitor or manage over time. Instead, resource patches such as these are often considered as part of a stand prescription. Prescriptions for stands could (and often should) include the variability and spatial arrangements of habitat elements within a stand, so that fine-scale patterns across landscapes are inherently considered, even if they are not mapped.

If we have a 20,000-ha landscape that we are managing, then it resides in a larger area, an area that we are not managing but which affects the function of our landscape. The *context* for the landscape can have a significant effect on what can be achieved through management of the landscape. This is analogous to management of stands in our forest. Manipulating the habitat elements in a stand *may* be effective in managing habitat for a species, depending on the resources available in the surrounding stands. Managing resources across a landscape *may* be effective, depending on the resources available in the surrounding landscapes. Managing pileated woodpeckers in Central Park, in New York City, is highly constrained by the surrounding urban context. Managing them in a small watershed of similar size in the Catskill Mountains of upstate New York may present far different constraints and opportunities in that context. Manipulating the resources among the patches represented by the grain, over the extent as constrained by the context, is the essence of landscape management for various species.

So how large is a landscape? By now you should know that the answer is, “It depends!” From a functional standpoint, there is no ideal upper or lower bound that describes a landscape. A decaying log on the forest floor represents a landscape with a mosaic of fungal colonies, bryophytes, bacterial colonies, and tree regeneration. The grain is the patch of fungus or the patch of tree seedlings. The extent is the log. The context is the forest in which it resides. Alternatively, the area extending from intermountain rangelands in North America to the pampas of Argentina represents a landscape of appropriate size for Swainson’s hawks. They nest and feed in the northern hemisphere and spend the winter in South America (actually Argentina’s summer is our winter; so they are never in winter!). Patches representing feeding, nesting, and roosting sites in both hemispheres and along the migratory pathway, represent a landscape used as the basis for management of this species.

From a practical standpoint, landscapes are usually considered areas of hundreds to thousands of hectares, areas where consideration of a meaningful grain does not become overwhelming to map and manage over the extent of the landscape. One characteristic of a landscape that is particularly important when managing animals, especially mobile animals, is that the extent applies to all owners within the landscape. Recall that in the United States, wildlife are public resources. And most are somewhat mobile. And they do not respect property lines or political boundaries. So a landscape that you define when managing a set of resources, that includes multiple owners, must not be restricted to just ownership. Habitat among all owners is what the animals will respond to (Spies et al. 2007). Too often, large forest owners restrict consideration of impacts of their management on a species to those impacts occurring on their lands, not the multiownership landscape of habitat to which the population responds.

HABITAT QUALITY AT THE LANDSCAPE SCALE

Recall that habitat quality is a function of individual and population fitness. Habitat elements distributed among patches on a landscape change over time. They change as plants grow, soil erodes, and disturbances occur. The quality of the habitat for a species also changes among patches over time. We can direct those changes, to at least some degree, by management actions. Over landscapes, we may wish to increase, maintain, or reduce (depending on our goals), the fitness of the individuals in the population of concern. This is usually done in concert with forest management activities, as well as natural disturbances and subsequent plant regrowth. Consequently, we manipulate habitat elements within stands, and other management patches on the landscape, to influence the direction of the cumulative changes in these resources, over time.

Depending on how a species scales its environment, we might expect a population response from these actions. Populations do not respond solely to changes in availability of habitat elements. Disease, competitors, predators, parasites, and other density-dependent factors, which may or may not be mediated by habitat elements, can influence population responses. Altering habitat simply provides the potential for populations to respond in certain ways. There is always uncertainty in what responses we will see. Disturbances occur but are usually unpredictable. Climate is changing. Invasive species are competing with native populations. Consequently, tracking the vital rates of the population and understanding the long-term changes in birth rates, death rates, and *lambda* (the population parameter used to define if a population is increasing or declining) allow us to understand the consequences of management actions over large areas. These population parameters are usually used to define habitat quality across a landscape, which reflects the cumulative value of habitat among patches across the landscape. But the location of the patches matters. If a species needs 40% of its home range in high-quality food patches to achieve high levels of fitness, and you manage to provide 40% of a landscape in these patch types, then the food patches must be distributed so that each of multiple potential home ranges are distributed appropriately. Locating all high-quality patches on one side of a landscape would leave the other side of no value to this species.

LIVING ON THE EDGE

A feature of landscapes that has an inordinate effect on habitat quality for many species, is the boundary between patches. Edges between patches, as well as other linear features such as roads, rivers, and ridge-tops, all influence habitat quality for various species. Even though these linear features occupy only a very small part of a landscape, they can have a disproportionate effect on the function of a landscape for a species. Depending on the species and the type of edge, edges can be beneficial, detrimental, or have no effect whatsoever. Certain types of edges *are* habitat for species such as cottontail rabbits, but other species are adversely affected by certain types of edges. Edges are usually characterized as induced or inherent (Figure 15.2). *Induced edges* are those that occur between two patch types of different successional condition, are usually caused by a disturbance, and represent structural differences between the patches. Edges between early and late successional forests, forests and utility right-of-ways, or forests and agricultural lands, are examples of induced edges, though each of these types of edge functions differently, depending on the species. *Inherent edges* are those formed because the composition of the forests differs between the patches. Although this may ultimately be the result of disturbance, it is less a structural interface, and more a floristic interface.

Induced edges between forests and agricultural lands are ideal conditions for brown-headed cowbirds to nest (Figure 15.3). Cowbirds fed among bison herds historically and now feed among cattle; cowbirds eat insects disturbed by the grazing animals. They reproduce by laying their eggs

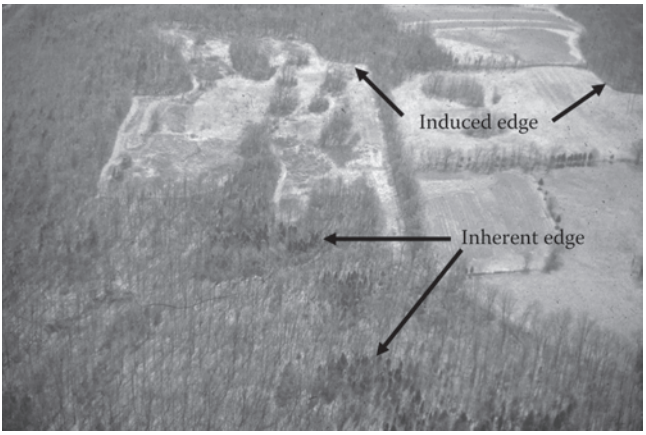

FIGURE 15.2 Induced edges reflect structural differences between two patch types, while inherent edges represent floristic differences between patches.

in the nests of other birds, a reproductive strategy called *brood parasitism*. Once the female is fertilized, she flies into the forests adjacent to the grazing lands and seeks hosts for her eggs. These hosts are often *neotropical migratory birds* that generally produce one *brood* (cohort of young birds) per year. Once the female finds a host nest, she removes the host's eggs and lays her egg in their place. Should the host continue to lay eggs, then the host eggs hatch after the cowbird egg has hatched. The nestling cowbird grows quickly and the host parent raises it as its own. Being larger and more aggressive, it tends to get most of the food provided by the host parents, and the host nestlings often die as a result of competition for food. Consequently, the cowbird has a high probability of fledging (successfully leaving the nest), and the host nestlings are unlikely to fledge. Host species within a

FIGURE 15.3 Brown-headed cowbirds (large nestling in this photo) are brood parasites that can reduce nest success of other bird species, often neotropical migrants, when they nest near edges. (Photo provided by Dr. Jim Rivers. With permission.)

few hundred meters of agricultural or grassland edges often have depressed levels of nest success, due to cowbird parasitism. They can also experience higher levels of predation along edges than in the interior of the forest because raccoons, rat snakes, opossums, and deer mice also forage near edges. So creating these edges between grasslands and forests can be source habitats for brown-headed cowbirds, cottontail rabbits, and rat snakes, but sinks for neotropical migrant birds, that experience high levels of brood parasitism and predation along the edges.

Species can be classified based on their associations with edges. *Edge associates* are those species that find the best quality habitat where there is access to required resources in two or more vegetation patch types. There are also *edge specialists*, those such as cottontail rabbits that are likely to only occur where these edges exist. And there are some species that are found along edges but do not require the edge; rather, their home ranges simply abut the edge. And there are *forest interior species*, those that avoid edges and use the interior or core of a patch. Managing these groups together on one landscape often results in a high diversity of species along edges (specialists, associates, and those that occur in each of the adjoining patch types). You tend to find more species along edges than in the interior of forests or grasslands (Figure 15.4). Since Aldo Leopold's book *Game Management* was first published in 1933, managers have often focused on providing edges as a way of increasing populations of some game species or increasing species' diversity across a landscape. As in all other management choices, some species are winners and others are losers. Increasing edges can be to the detriment of forest-interior species.

In addition to increased levels of predation and parasitism along edges, some species can be either positively or adversely affected by edges, due to changes in the microclimate, probability of natural disturbances, vegetation structure, and a suite of human effects. Microclimatic changes along induced edges are highly influenced by edge contrast, or the degree of difference in forest structure between the two patches. If a forest adjoins an open area, then the edge of that forest receives more sunlight (depending on aspect and slope), is drier, receives more wind, and relative humidity is likely to fluctuate more throughout the day. These conditions can affect habitat quality

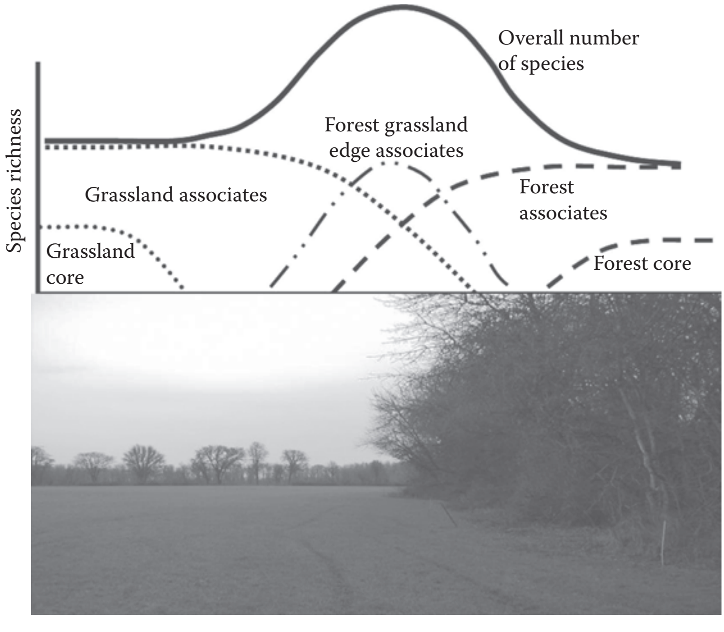

FIGURE 15.4 Species richness is often high along edges due to the contributions of species to edges from both adjoining patches as well as edge specialist species. Note though that patch interior species avoid these edges.

for some species directly, especially reptiles and amphibians (and other ectotherms), and can result in changes in vegetation structure. Time since edge creation is often an important factor influencing the structure of an edge. An edge formed by a clearcut decreases in contrast with the adjacent forest as the trees in the clearcut grow. The edge in the forest that receives more sunlight after the clearcut occurs, will also fill in with shrubs, trees, and forbs, creating a “softer,” less abrupt, edge.

Disturbances also can be influenced by the presence of an edge. Fuels for fires that differ between patches can allow intense fire to affect the edges of patches that otherwise would not be so severely affected. Abrupt edges in wind-prone sites can lead to continuous windthrow of the trees along the edge, resulting in accumulations of dead wood (or timber salvage opportunities). Consequently, disturbance intensity can be unusually high along edges, leading to changes in the structure and function of the recovering forest following the disturbance.

Humans not only create edges, they use them. Hunters often will follow edges to find game animals. Roads and fences often occur in conjunction with edges. Consequently, domesticated animals tend to use the edges as well so grazing pressure can be higher there. Free-ranging dogs and cats can have a significant impact on native animals, and they often hunt near edges. The geographic ranges of nearly all mid-sized marsupials in Australia have been greatly reduced due to predation by feral cats and foxes. The Wildlife Society produced a position paper on this topic in 2006; excerpts follow: “The estimated numbers of pet cats in urban and rural regions of the United States have grown … to nearly 65 million in 2000. …domestic cats are a significant factor in the mortality of small mammals, birds, reptiles, and amphibians. …Effects of cat predation are most pronounced in island settings (both actual islands and islands of habitat), where prey populations are already low or stressed by other factors, or in natural areas where cat colonies are established. Competition with native predators, disease implications for wildlife populations, and pet owners’ attitudes toward wildlife and wildlife management also are important issues.” Houses in forests perforate—if not fragment—the forest, proliferating edges. Many of these houses support nonnative plants and animals so the proliferation of effects of these nonnative species on native species is further exacerbated. Indeed, many landowners have planted exotic plants specifically to attract wildlife, which may have long-lasting adverse effects on native plant species.

EDGE GEOMETRY

The effect of an interface between patches on habitat quality for a species is often dependent on the amount of edge occurring within an animal’s home range. Size matters—both the size of the patches constituting the edge, as well as in the length of the edge between patches. Consider the patches in Figure 15.5. A 10 ha square patch has 1265 m of edge. But two 5-ha patches have 1789 m of edge, and five 2 ha patches have 2828 m of edge. So minimizing edge for forest interior species can be achieved by having fewer large patches, and maximizing edge for edge specialists can be achieved by having many smaller patches.

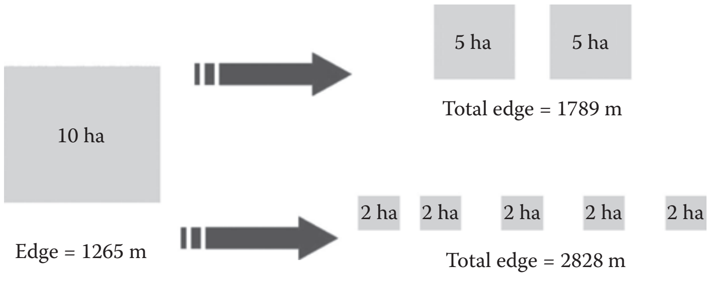

FIGURE 15.5 Decreasing patch size but keeping total area constant increases the total amount of edge. Increasing patch size per habitat area increases core.

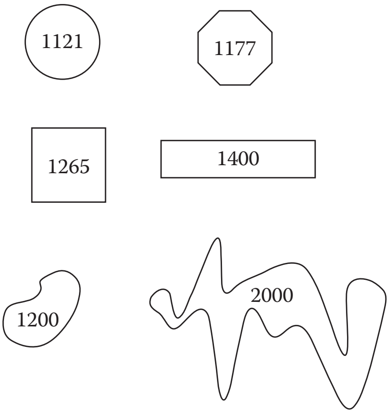

FIGURE 15.6 The more that a regular shape diverges from a circle the greater the edge per unit area and the less core that is available.

Edge density (edge length per unit area) can also be influenced by patch shape. Consider the 10 ha patches that all have the same area as shown in Figure 15.6. The more that a patch diverges in shape from a circle, the greater the edge that is represented per unit area. Patches shaped like amoebas have more edges than regular shapes. So when identifying stand boundaries, stands that are large and approximate a circle or hexagon in shape, will minimize edge and maximize *core* (interior) conditions. Patches that are small and irregularly shaped will minimize core and maximize edge. Core conditions are usually identified by considering the area of a patch some distance away from an edge, say 100 m. It should be clear by now that the distance away from an edge that constitutes a functional core varies from one species to another. For some species it might be 5 m, and for others 500 m. For species that are particularly edge-sensitive, the amount of core area in small or irregularly shaped patches can easily become zero (Figure 15.7). Of course, if we think about landscapes as gradients and not patches, then there is no need to think about a band or buffer on an edge, but rather a gradient of habitat quality across the edge.

The arrangement of patches on landscape can also influence edge conditions. Consider a set of patches in the pattern of a chessboard. If all the white squares are acceptable as habitat and the black ones are not, then edges are maximized. Now place all the white squares on one side of the

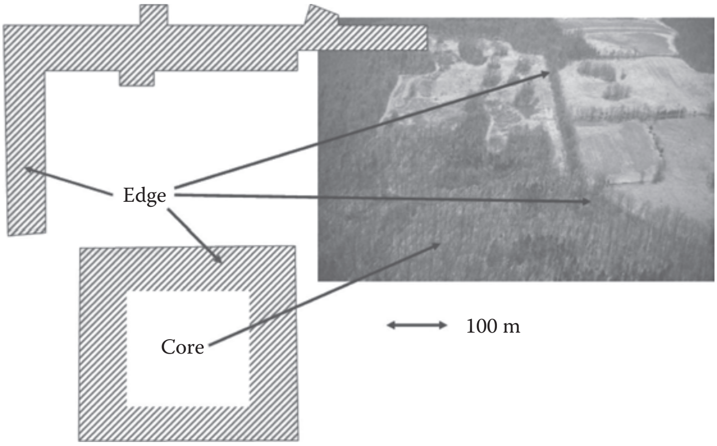

FIGURE 15.7 Depending on the functional width of an edge, then some patches can have no core area. Size, shape, and edge width dictate the amount of core.

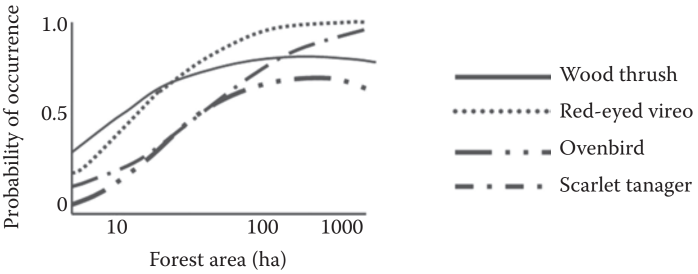

FIGURE 15.8 As the area of a forest patch increases, the probability of detecting forest interior bird species increases. For some species, very large patches are needed before there is a high probability of occurrence of these species. (Adapted and redrafted from Robbins, C.S., D.K. Dawson, and B.A. Dowell. 1989. *Wildlife Monographs* 103:1–34.)

chessboard and the black squares on the other side. By blocking patches of similar habitat quality you can increase overall patch size and minimize edge area. Pattern can also influence edge contrast. If a decision is made to minimize edges by systematically harvesting adjacent stands, using a system for clearcut regeneration across a watershed, then the contrast between recent clearcuts and various ages of regenerating clearcuts will be less abrupt. Alternatively, if we wanted to maximize induced edges using this system, we would disperse clearcuts throughout a watershed in a "staggered setting" approach, a technique commonly used on National Forests in the United States for years to improve edge conditions for game species and distribute the clearcut disturbances. The decisions of how to make large patches or small patches during management can be based on the area required by various species or by the area impacted by various disturbances. Even small disturbances can have significant effects on some forest interior species, because the area requirements for the species extend far beyond the territory size of the species, due to adverse edge effects. Consider four species of forest-interior birds from eastern United States (Figure 15.8). For some species, the patch area must be thousands of ha before there is a high degree of confidence that the species will be found in the patch. Since the territory sizes for these species are in the range of 1–10 ha, demographic processes associated with avoidance of edges and associations with core conditions are assumed to be largely responsible for these species being associated with such large contiguous forest patches. At least that is the case in landscapes where forests are interspersed among agricultural lands such as in eastern United States (Robbins et al. 1989). There seem to be less strong associations with large patch sizes for small neotropical birds in forested landscapes where older forests are interspersed with various ages of younger forests (Welsh and Healey 1993, McGarigal and McComb 1995). Agricultural lands provide a very stable *matrix* within which forested patches are embedded and may represent a context for the forests, which results in significant adverse edge effects that extend into the forested patches. In forested landscapes interspersed with various aged forest stands, these edge effects do not seem so significant for many forest-interior species, probably because stands are dynamic. Edge contrast can be ameliorated by rapid tree growth on some sites. On high-quality sites, forest structure and composition changes rapidly, minimizing the length of time that high contrast edges occur on the landscape.

HABITAT FRAGMENTATION

Habitat fragmentation is a landscape-level process in which a specific habitat is progressively subdivided into smaller, geometrically more complex, and more isolated fragments as a result of natural and/or human causes. It involves changes in landscape composition, structure, and function at many scales and is overlain on a mosaic created by changing landforms and natural disturbances. Habitat fragmentation is related to but different from habitat loss (Figure 15.9). Habitat can

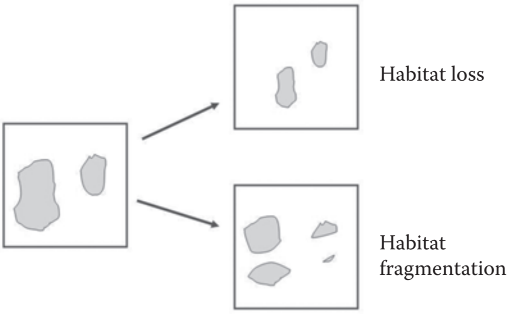

FIGURE 15.9 Habitat loss does not necessarily increase the isolation or geometry of patches, while fragmentation is a process that increases patch isolation and exacerbates edge effects. (Redrafted and adapted from Fahrig, L. 1999. *Forest Fragmentation: Wildlife and Management Implications*, Pages 87–95. Brill Press, Netherlands.)

be lost because of natural disturbances, human actions, or ecological succession. Loss can occur in a manner that erodes the edges of a large patch, such that habitat area declines, but the patch is still intact and it is not dissected into smaller, more isolated pieces. Alternatively, a large patch can be dissected by a road, utility right-of-way, or clearcut, and then another, and then another, until there are many smaller patches on the landscape and not just one large patch. Habitat area has declined, but, more importantly, habitat patches have become subdivided and more isolated from one another. This latter process is termed fragmentation; the effects of this process are clearly specific to a species. Fragmenting habitat for ovenbirds may be caused by reducing the size and connectedness of mature eastern hardwood forests. Fragmenting habitat for bobolinks may be caused by allowing forests to encroach upon grasslands. And fragmentation for both species may be caused by expanding housing developments and roads. The process of fragmentation is species-specific, though it is often generalized in the popular literature. Forest fragmentation: How often have you seen that term? But fragmenting a forest can be good, bad, or indifferent, depending on the structure and composition of the forest and the species with which you are concerned. Indeed, some forests are fragmented from natural disturbances on a regular basis and others rarely so. The effects of the loss of habitat, separate from the fragmentation of habitat, must be considered carefully to understand the potential impacts on animal and plant species (Wilson et al. 2009). There also is evidence of threshold effects in habitat loss, and isolation for some species of birds, suggesting that changing habitat area or isolation does not change habitat quality in a linear manner (Betts and Villard 2009, Betts et al. 2010).

HABITAT AREA: SPECIES–AREA RELATIONSHIPS

Forest fragmentation can occur from natural disturbances or human activities. Indeed, we would expect that many, if not all, species should be adapted to the frequency, severity, and size of natural disturbances in the landscapes where they occur. We often use this assumption as the basis for designing human disturbances in forests to minimize the risks to species, both known and unknown, through our management actions (Landres et al. 1999). Simply from the standpoint of supporting species richness (number of species in an area), we know that large patches of forest (or grassland) support more species than small patches of forest. All other things being equal, large oceanic islands support more species than small islands. There is typically an asymptotic relationship between area and species number (Figure 15.10). Hence the conventional wisdom, when considering identification of reserves designed to meet the needs of many species, is that large areas—areas where an asymptote in species-richness is reached—represent appropriate areas to "capture" the most species in a region. This approach to conservation of biodiversity is dependent

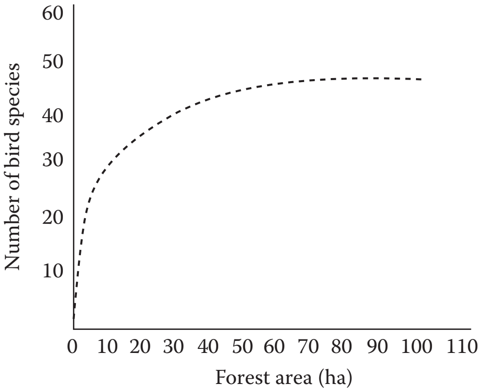

FIGURE 15.10 Example of a typical species-area relationship for forest birds among patches in a landscape. Species richness becomes asymptotic at large patch sizes.

on two spatial scaling properties: (1) the range of spatial scales represented following disturbance and regrowth across a landscape, and (2) the range of spatial scales represented by home ranges and populations of organisms occurring on a landscape.

As we have discussed already, natural disturbances of a particular severity typically occur over a range of sizes within a region or forest type. Less frequent disturbances tend to be larger and more severe. The combination of forest regrowth and disturbance produces a range, or domain, of spatial scales that are associated with the severity and frequency of a disturbance. The exact point within this domain, that any point on the landscape might experience, is dependent on many factors and is not deterministic but rather probabilistic. There is some probability that a disturbance will be of a particular size or severity, but we cannot predict exactly what it will be or when it will occur with certainty. Rather, it is this domain of sizes that we can predict, and it is the domain of sizes to which most species in the region should be reasonably well adapted to using. How those species react to the severity and size of the disturbance is largely dependent on the spatial domains represented by the suite of species occupying an area. For instance, if we look at the frequency of occurrence of species' home range sizes among all species in a region (Figure 15.11), it is typically a negative exponential distribution, with many species occupying very small portions of a landscape, and few species occupying large portions of a landscape. The spatial domain of the cumulative species

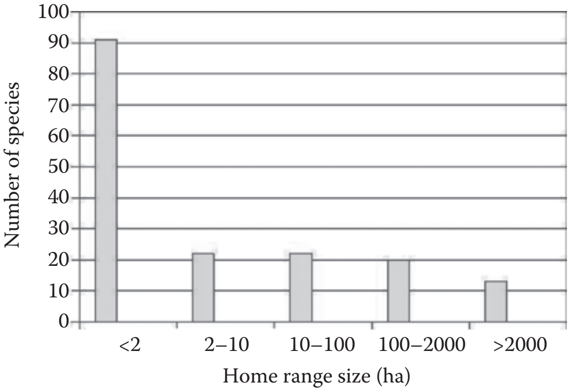

FIGURE 15.11 Frequency distribution of home range sizes for species in the northeastern United States. (Summarized from DeGraaf, R.M. and M. Yamasaki. 2001. *New England Wildlife: Habitat, Natural History, and Distribution*. University Press of New England, Hanover, NH, 496 pp.)

area requirements defines a domain of spatial scales that would need to be represented across large areas to meet the needs of the full suite of species. The domain of disturbance sizes in a landscape provides the template upon which the species can or cannot find the habitat areas and arrangements that meet the cumulative needs of the group of species. The interface between the spatial domains inherent in a landscape (from disturbances and regrowth) and the spatial domain of the animal community (from home ranges of multiple species) cause some landscapes to be better able to support a more full range of species than others. Now consider human impacts on landscape pattern and composition. As land-use developments, such as roads, housing, forest management, and agriculture, change the pattern of forests across a landscape, the domain of spatial scales represented in a forested landscape changes and the domain is often narrowed. Forest management occurs over a narrower range of spatial scales (fewer very small patches, fewer very big patches, Figure 15.12) than natural disturbances. The spatial scaling properties of the animals that use a landscape pattern that is constrained by land use may change somewhat in response to these new landscape configurations, but unless a species is preadapted to this new narrower range of conditions, it may find that its habitat availability has declined. This reduction in habitat for some species is caused by having a narrower range of patch sizes and arrangements than occurred prior to modern human intervention (Figure 15.12). Small patches may be less common because humans tend to homogenize stand conditions, making them easier to manage and producing uniform products within and among stands, unless we take actions to make stands heterogeneous (see Chapters 7, 8, and 9). Large patches are also less likely. Because of social constraints, we are unlikely to manage an entire 10,000-ha watershed using even-aged management to replicate a wildfire, but some species are well adapted to that forest condition at that spatial scale (especially if a complex early seral condition is provided). We often are managing forests and the animals that occur in them over a limited spatial domain. Those species adapted to conditions (stand types, edge densities, legacy material, etc.) occurring at smaller and larger spatial scales than those represented by management can be considered those most likely to be at risk of having decreased habitat quality (Figure 15.12). If we can identify those species, then we can take management actions to address their needs. Species needing large, complex, early successional patches, for instance, may have their needs met if even-aged systems with legacy retention are employed by clustering harvest units over time that collectively contribute to overall large patches, leaving late successional forests, also, in large patches. For those species that require small patches, then variable density planting and thinning or group selection systems using a variety of group sizes may help to address their needs. These silvicultural and harvest considerations must

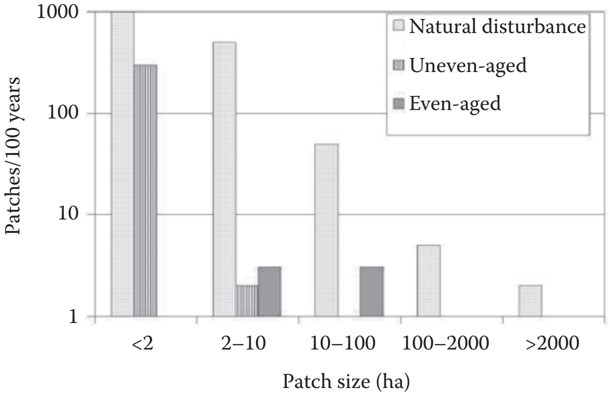

FIGURE 15.12 In this range of patch sizes one might expect over a 10,000 ha landscape under natural disturbance regimes and the range of conditions represented by even-aged and uneven-aged forest management approaches. Species associated with patch sizes under-represented by management may face risk unless the range of spatial scales of management is increased or reserves of various sizes are employed within which natural disturbances are allowed to occur.

be planned to ensure that a broader spatial representation is achieved over a landscape than would be achieved simply by maximizing timber profits. That is, planning to represent a broad spatial domain may come at an economic cost when managing a landscape because moving the landscape into an appropriate spatial domain may mean cutting stands earlier or later than would be done to maximize profits in order to achieve the desired patterns and reduce the risk of some species losing habitat availability.

Just as there are spatial domains of disturbance and regrowth, there also are temporal domains of disturbance and regrowth, and there are temporal domains of population demographics. Some species produce several generations in one year, and others produce several generations in decades or centuries. Consequently, the rate of change in forest structure and composition over a landscape, as well as the spatial patterns, can affect species differently. For instance, species adapted to prolonged forest recovery following a disturbance that retains significant legacy from the previous stand may find diminished habitat quality where forest managers are striving to minimize legacy retention and maximize the rate at which growing space is occupied by economically valuable trees. Vegetation management and density management can shorten the period of a diverse, early successional condition and reduce the opportunity for species to find and use this recently disturbed area. Further, intensive early stand management can minimize the time available for them to produce sufficient offspring to colonize new areas that grow into habitat elsewhere on the landscape over time. Similarly, species associated with post-rotation-aged forests may have limited opportunities to produce young. This is particularly a problem with k-selected species, which are species that reproduce late in life, produce few young, and reproduce infrequently. Long-lived species, such as tortoises and parrots, require some level of habitat stability over long time periods in order to meet their reproduction and survival requirements. If forest management or forest land use changes the duration of a particular seral stage, then habitat availability for species associated with habitat elements found in those stages can be reduced. Of particular concern are those species that are not only long-lived but also need to produce multiple generations to ensure population viability within a region.

One way of reducing the impact of changing the temporal domain of scale is to provide legacies from one forest condition to the next over large areas and allow some habitat elements to be represented over large areas over time (e.g., dead wood in managed forests), thereby buffering the diminished domains of scale represented among forest age classes. Attending to the needs of species that are long-lived or have multi-generational requirements to maintain viability may represent a cost to the resource manager not only in silvicultural activities and harvest planning, but also in a commitment to legacies of structures and patch types across managed landscapes. It is the intersecting domains of space and time in landscape composition and structure, which interface with the spatial and temporal domains of a collection of species occurring on the landscape, that must be coordinated to minimize the probability that some species will be placed at risk. This approach greatly complicates harvest planning but it is possible to find harvest-planning solutions to spatial problems such as these (Bettinger et al. 2001).

CASE STUDY: HABITAT AREA OR PATTERN?

In the early 1990s, Dr. Kevin McGarigal conducted a study that addressed the relative role of forest area vs. forest pattern in structuring bird communities in the Oregon Coast Range (McGarigal and McComb 1995). Subsequent work by Dr. Karl Martin also addressed associations with mammal and amphibian communities on these sites (Martin and McComb 2002, 2003). The work was set in the dynamic forests of the Oregon Coast Range and followed work by Robbins et al. (1989), Temple (1986), and others, who identified a number of area-sensitive bird species in eastern hardwood forests that seemed to be adversely affected by processes of forest fragmentation resulting from agricultural land uses and urbanization. Few studies had addressed fragmentation effects on vertebrates in managed forest landscapes at that time, and many of the findings regarding the effects of fragmentation in eastern hardwood forests were being used to design management strategies for forests in western coniferous forests. McGarigal and Martin wanted to see whether these same trends were consistent in forests that were fragmented by forest management, while controlling for habitat loss. The experimental design was to sample three replicates of 10 sub-basin (250–300 ha) conditions representing two dominant gradients in late seral forests: 0%–100% late-seral forest area with minimal fragmentation (remaining forest was in large blocks) and also sub-basins with a high level of late-seral forest fragmentation (remaining forest in many blocks) (Figure 15.13). But forests are not structured as simply as is represented in this experimental design. Patch shapes and arrangements vary considerably from one sub-basin to another so indicators of landscape structure and function were needed. Consequently, McGarigal and Marks (1995) developed an analytical computer program called FRAGSTATS to provide a huge number of landscape metrics to describe many aspects of patch conditions, sizes, shapes, connectedness, edge conditions, and core areas, among others. Using these metrics in their analyses allowed them to understand whether the animals were associated more with the composition of the landscapes (how much late-seral forest was available), or if pattern mattered. On the basis of over 100,000 observations of birds, mammals, and amphibians, several patterns emerged. For many bird species, habitat area matters. Of 15 species of birds that selected late-seral forests (based on use and availability), 11 were associated more with the *area* of late-seral forest than with its *configuration*; (more habitat was better than less). These included species such as brown creepers, pileated woodpeckers, and varied thrushes (McGarigal and McComb 1995). Five species of amphibians also were associated more with the area of a forest condition than its configuration, such as the southern torrent salamander (Martin and McComb 2003). And six species of mammals were more associated with patch area than configuration, including California red-backed voles, deer mice, creeping voles, Pacific shrews, and Pacific jumping mice (Martin and McComb 2002). None of the 14 mammal species captured were negatively associated with edges (Martin and McComb 2002).

But some species were clearly associated with configuration. Most species that exhibited an association with fragmented forests were more abundant in fragmented than unfragmented forests, unlike what was seen in many eastern hardwood forest studies. Species such as olive-sided flycatchers, deer mice, and Pacific jumping mice were positively associated with edges. Very few species were associated with a core area >100 m from an edge than with the edges; Pacific giant salamander was one of these core-associated species. As you would expect, there are species that likely would benefit from fragmentation of late seral western coniferous forests—and those that likely would not. The fact that landscape pattern (fragmented forests) seemed to be only modestly associated with the abundance of many of these species, and in most cases was more associated with fragmented than unfragmented forests, may seem counterintuitive but remember that these forests are dynamic. Harvested stands in these studies were regrowing. Plantations that had regrown even 20 years had reduced edge contrast and provided a matrix condition through which many species could once

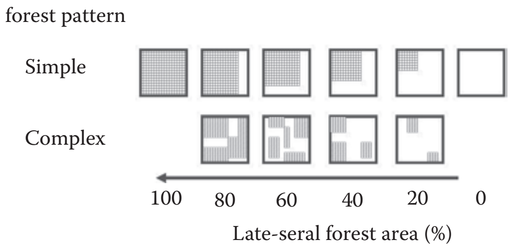

FIGURE 15.13 Experimental design used to assess the contributions of late-seral forest area and pattern to bird, mammal, and amphibian species in the Oregon Coast Range. (Redrafted from McGarigal, K. and W.C. McComb. 1995. *Ecol. Monogr.* 65:236–260. With permission from the Ecological Society of America.)

again disperse. Indeed, in landscapes where the matrix is static (e.g., agricultural lands) and the forest patches are isolated, the results of McGarigal and Martin might have been much different. It is also important to point out that McGarigal now is developing landscape metrics that measure gradients in landscapes rather than patches (McGarigal et al. 2009). If he were to be designing the project now, patch delineation would likely give way to gradient quantification (Cushman et al. 2010).

Further, animals dispersing across fragmented landscapes face different challenges in landscapes with little habitat available than when even marginal habitat is available between high quality patches. Despite the results reported above, there is reason to consider pattern effects on populations, especially under conditions of low habitat area (With 1999). That is the subject of our next chapter.

SUMMARY

Forested landscapes have structure, composition, and function. Function for each species varies, depending on how habitat patches are defined on the landscape and how they are connected across it. The scaling properties of a landscape are defined by the grain (the smallest unit of space that we find useful), the extent, or the outer boundaries of the landscape under consideration, and the context—the condition of the area surrounding the extent. Animals integrate patches of varying habitat quality across the complex mosaics of landscapes to meet their habitat needs. As landscape structure, composition, and function change, so will populations and the fitness of the species using the landscape.

Edges between successional stages (induced), or plant communities (inherent), represent zones in a landscape where the richness of animal species can be high, but adverse effects on forest-interior species are exacerbated. Predation, brood parasitism, spread of invasives, and altered microclimates along edges can lead to depressed fitness for forest-interior species.

Fragmentation is the process of breaking habitat patches into smaller, more complex, and more isolated pieces. This process is different from habitat loss, where habitat reduction may or may not be accompanied by increased isolation. In dynamic forest systems, where the matrix condition among habitat patches is continually changing, habitat loss is often a more serious issue than fragmentation. But once fragmentation has led to significant isolation of the remaining patches, then fragmentation effects may become apparent, especially if the matrix is inhospitable to the organism of interest.

Finally, it is important to realize that the conceptual framework and analytical approaches are changing when addressing habitat across landscapes. Scientists are now viewing landscapes as a set of gradients and seeing that associated measures of complexity, called surface metrics, may more accurately describe the complexity in landscape composition and pattern.

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