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**Introduction**

The discipline of landscape ecology emphasizes the causes and consequences of spatial pattern on the functioning of populations, communities, and ecosystems. Nature is generally not homogenous with respect to ecological properties. Those properties include gradients in abiotic factors, such as the temperature, moisture, and the abundance of required resources; and biotic factors, such as the presence of predators, pathogens, and competing species. This spatial heterogeneity exists at multiple scales of space and time. The term "landscape" evokes patterns over a broad scale, such as the view from an airplane or satellite extending over several square kilometers and including the mosaic of forests, grasslands, wetlands, agricultural fields, and urban areas seen below (Figure 1). This mosaic and the diversity of habitats therein is the setting where species make their living. The spatial pattern of habitats determines how species and their populations are distributed across this view from above. The influence of spatial pattern is also important at finer scales. Studies in landscape ecology have illustrated how the spatial pattern of resources at the scale of 1 m² altered the habitat use by beetles and ants (Wiens and Milne, 1989; Wiens et al., 1993). "Scale" is an important concept in landscape ecology because the influence of spatial patterns often depends on the scale in which they are observed and measured. It is common to measure spatial heterogeneity at multiple scales in order to best discern which scales are important for a given ecological phenomenon (e.g., Price et al., 2005). No matter what scale is studied, the spatial pattern of resources alternatively provides opportunities for population spread and increase, limits and constrains population growth, or threatens the persistence of some species.

**Basic Concepts and Terminology about Population Dynamics**

A population is a group of interbreeding organisms that produce viable, fertile offspring; under the biological species concept, members of a population belong to a single species. Localized breeding groups are also known as "demes." In a typical landscape, the suitable habitat for most species exists in a patchy pattern (Figure 1), so patches of habitat usually define the location and boundaries of demes.

Ecologists are interested in the number of individuals in a population (that is, population size classically denoted by the letter N). The change in N through time (dN/dt) is population dynamics. Population size changes by the demographic processes of birth, immigration, death, and emigration (BIDE). This BIDE model of population growth is

$$dN/dt = \text{Births} + \text{Immigrants} - \text{Deaths} - \text{Emigrants}.$$  

Populations in which immigration and/or emigration occurs are considered to be open populations and are connected to other demes by the movement of individuals. The distances between demes influence the frequency of these deme-to-deme movements. Movements may happen regularly for the population but occur infrequently during the life cycle of an individual. Movements often take the form of dispersal from the natal site to a different habitat patch. Dispersal lessens the probability of competition and interbreeding with parents and siblings, especially when the population in the natal patch is small. Analyses of population viability and genetic diversity emphasize effective population size ($N_e$), which is the number of individuals actually participating in breeding. In most populations, $N_e < N$ because some individuals are unsuccessful in attracting a mate, reproductively immature, or of postreproductive age.
Population Dynamics in Landscapes

The number of individuals in a population, \( N \), is limited by available resources. The limiting resource(s) may include food or nest sites for animals, or moisture, sunlight, and/or soil nutrients for plants. Suitable habitats are the locations and conditions that provide these resources. Given that resources are finite, \( N \) has a maximum value that is sustainable. Ecologists use the term carrying capacity \((K)\) to refer to the maximum \( N \) that a given environment can support over the long term. The logistic growth equation is a simple model of population dynamics learned by most students of ecology:

\[
\frac{dN}{dt} = rN \left( \frac{K - N}{K} \right)
\]

The value \( dN/dt \) represents change in \( N \) over a unit of time (\( t \)), and \( r \) is the intrinsic rate of increase, which is a measure of per capita population growth:

\[
r = \frac{\text{births} - \text{deaths}}{N}
\]

Assumptions of this model include a closed population (i.e., there is no immigration or emigration) and that \( r \) and \( K \) are constants. Other ecological forces that could influence population growth, such as predation or competition, are not included. The logistic growth model implies that a population attains equilibrium with resources in its environment. The continuous form of this model produces graphs of \( N \) against time as an S-shaped curve in which the population grows until \( N = K \) and then \( N \) remains constant at that value. The assumptions of the logistic growth model are rather restrictive, and very few if any populations in nature would fulfill all of them. Nevertheless, it expresses a central premise that populations are limited by availability of resources and the amount of habitat in the landscapes where they live. Furthermore, landscape ecologists study how the spatial arrangement of habitat patches can alter population dynamics.

Landscape-level changes in habitat abundance and spatial pattern affect population dynamics. Data on populations of grassland birds in North America provide evidence of how changes in habitat availability alter population size. At the continental scale, the abundance of bird species that require grassland habitats has been declining since the mid-1900s in...
Figure 2 Change in abundance for grassland birds at (a) continental scale for eastern North America and (b) regional scale for Illinois. (a) Data for Eastern meadowlark (Sturnella magna) and field sparrow (Spizella pusilla) provided by United States Geological Survey (USGS) North American Breeding Bird Survey, http://www.mbr-pwrc.usgs.gov/bbs/bbs.html. Solid line is mean estimate, with dashed lines showing 95% credible interval. (a) and (b) Reprinted from Herkert JR (2007) Evidence for a recent Henslow’s Sparrow population increase in Illinois. Journal of Wildlife Management 71: 1229–1233, with permission from Wiley.

Populations, Jewell and Arcese (2008) linked the population growth rates of the sparrows indirectly to landscape-level patterns of land use (Figure 3). Rates of brood parasitism by cowbirds (Molothrus ater) reduced sparrow reproduction, and cowbird abundance was strongly correlated with land uses such as urban and agricultural lands with livestock grazing. These land uses created areas where parasitism rates were so high that local reproduction in sparrow populations could not replace individuals lost to mortality (i.e., \( r < 0 \)). Their results suggest that these populations were maintained by immigration from areas with lower parasitism rates rather than by local reproduction.

Simulation models are often employed to explore the effects of landscape patterns on population dynamics. Spatially explicit models can simulate the occupancy of specific locations as well as the demographic rates characteristic of populations at those locations. Such models allow the researcher to test hypotheses about population dynamics in the complex settings of real and theoretical landscapes. These models are especially useful for studying the impacts of various scenarios of landscape change on populations. Pearson et al. (1999) examined how management options related to forest clearing would affect habitats, and therefore the abundances, of a suite of native species. Complex population processes such as survival, reproduction, and movement of individuals can be represented in spatially explicit models. For example, Holdo et al. (2011) used a model to study the impact of road construction that would interfere with migratory movements of the Serengeti wildebeest (Connochaetes spp.; Figure 4). Their simulations suggest that this barrier to movement could reduce wildebeest population by one-third because these animals would be less able to migrate to the most productive foraging sites. Locations of the most productive sites shift in location seasonally, and the road interfered with the animals’ ability to track and migrate to those sites. Moreover, the road was predicted to divide a single wildebeest population into two separate subpopulations.
Although the overall abundance of required resources is of great importance for populations, the patchiness and spatial arrangement of habitat types have the potential to complicate population dynamics in landscapes. Demographic rates, such as survival and reproduction, may be affected by patch size and shape. Movements between patches can be influenced by the distance between patches and other spatial features. Therefore, an understanding of how population dynamics play out in space is important for research and management.
Landscape Structure and Population Dynamics

Landscape ecologists are interested in spatial patterns. For populations, the overall abundance of habitat and its spatial distribution have a strong influence on the genetic structure and population dynamics of species. The concepts of patch, matrix, and corridor are useful for understanding how populations are influenced by the spatial structure of landscapes (Figure 5). For the time being, assume that patches are recognizable as discrete areas of similar habitat and that all habitat patches contain suitable habitat with enough resources to sustain a population. (This assumption of discrete, homogeneous patches will be relaxed later.) The unsuitable habitats found between habitat patches comprise the landscape matrix. Corridors are linear strips of habitat that connect patches and facilitate the movements among patches (Figure 5). The number, sizes, shapes, and spatial arrangement of habitat patches, as well as the presence of corridors, impose a spatial structure on the species that occupies them.

Several terms contain the word “structure.” The spatial distribution of habitat may be referred to as “patch structure” when applied to a specific habitat type or as “landscape structure” when applied to the spatial pattern of all habitat types in the landscape. The term “population structure” refers to the spatial distribution of breeding groups (i.e., demes) and the rates of exchange of individuals, via emigration and immigration, among these groups. Much of the problem of analyzing population dynamics at the landscape level relates to understanding the influence of landscape (or patch) structure on population structure.

Patches, Matrix, and Corridors

The patch structure of a landscape influences the dynamics of populations living therein because patch structure affects the spatial distribution of individuals and their movements (Saunders et al., 1991). Patch size is one of most important qualities of landscape structure because it is directly related to local population size. Larger patches have a greater abundance of resources and will support a greater \( N \) over the long term (i.e., the patch’s carrying capacity), whereas smaller patches support fewer individuals. Immigration and emigration are affected by the distance between patches and the intervening landscape matrix. When patches are far from one another, the chance of successful movement between them is reduced. Dispersing animals can suffer mortality from hazards of predation, starvation, or accident while crossing the unsuitable matrix. The dispersal mechanisms of plant seeds may fail to deliver them to distant patches, and dispersing animals may not find a suitable patch.

Corridors connect patches and facilitate interpatch movements. Similarly, small habitat patches (i.e., habitat fragments) scattered throughout the matrix can act as “stepping stones” to promote movement between large patches. Intertape distances between these fragments are small, and the habitat fragments provide temporary refuge for the dispersing animal before crossing the next gap. Likewise, these fragments may be too small to support a plant population over the long term, but temporary populations can produce seeds capable of colonizing nearby patches. The effectiveness of corridors and stepping stones for movement can be altered by characteristics of the landscape matrix (Baum et al., 2004; Vergara, 2011).

Figure 5  Schematic diagram of patch–matrix–corridor model. In this example, a centrally located core patch is surrounded by smaller satellite patches. Individuals from the population of the core patch disperse to the satellite patches, which support smaller populations that frequently go extinct. Linear corridors or closely spaced habitat fragments (stepping stones) facilitate movement among patches.
Characteristics of the landscape matrix may facilitate or hinder movement. Habitats in the matrix may be harsh or benign relative to the resource needs of individual species. The matrix may contain barriers to movement. The barriers include natural features such as rivers or mountains and human constructed features such as roadways, agricultural fields, and urban areas. The relative ease or difficulty of movement through the landscape matrix is called its permeability. The spaces between habitat patches, filled by the matrix, are called gaps. A species’ ability to move across this space is called its gap-crossing ability. Gap-crossing ability and matrix permeability for a given species in a particular landscape depend on the life-history characteristics, habitat needs, and vagility of the species as well as the matrix itself (Chardon et al., 2003; Baguette and Van Dyck, 2007). For example, a bird can readily fly across 100-m wide plowed agricultural field, but that same field is a barrier to a salamander, which risks predation or death by desiccation during an attempt to cross it.

**Landscape Context**

The suitability and uses of particular habitat patches may be affected by landscape context. The matrix and landscape-level abundance of similar habitats alter the abundance of a species at the patch scale (Radford and Bennett, 2007). When a given habitat type is abundant in the broader landscape, then it is more likely to see occupancy or visits to small patches (Pearson, 1993; Lewis et al., 2011). This effect has been documented in mobile animals, such as mammals, flying insects, and birds, which readily move between patches. Landscape context affects plant population dynamics by altering pollination services and rates of seed predation (Steffan-Dewenter et al., 2001). The abundance and diversity of habitats in the broader matrix affect the probability that pollinators or seed predators will visit a given patch. Some animal species depend on a variety of habitat types during their lives and the ability to move among them. These species may be especially sensitive to landscape context. For example, some amphibians require wetlands for breeding but then disperse to upland habitats after the breeding season (Pillsbury and Miller, 2008). Such species require different habitat types in different seasons or different parts of their life cycles. Therefore, a mix of patch types that provide supplementary or complementary resources (sensu Dunning et al., 1992) must be considered when assessing habitat quality and quantity at patch and landscape scales. By altering rates of immigration and emigration, landscape context can affect the genetic diversity and divergence among populations (Blevins et al., 2011).

**Quantifying Landscape Structure and Connectivity**

Spatial metrics provide a means of quantifying the spatial arrangement of habitat. The most straightforward metrics focus on the statistical distribution of patch sizes. First, the landscape is classified into suitable versus unsuitable habitat (i.e., a binary landscape), and the areas of suitable patches are tallied. Then the “number of patches,” “mean patch size,” and “size of the largest patch” are useful for comparing landscapes with similar amounts of habitat but having a different spatial arrangement of habitat. Other metrics can measure more complex aspects of spatial pattern such as the shape of patches. These metrics incorporate a ratio of perimeter-to-area for patches. Compact shapes, such as circular or square patches, have a lower perimeter-to-area ratio, whereas elongated patches or those with complex shapes have a greater perimeter-to-area ratio. The metric of “contagion” (e.g., Riitters et al., 1996) measures the intermixing of habitat types, which is correlated with number of patches as well as patch size and shape. There are many spatial metrics available, and many are correlated with each other (Hargis et al., 1998). No single metric will measure all of the important aspects of spatial pattern. The best choices will be those metrics that measure the qualities of landscape structure predicted to influence the population processes under study. One of the most important qualities is habitat connectivity, which measures the ease of moving between habitat patches.

Landscape ecologists have developed a variety of metrics for measuring the connectivity of landscapes (Kindlmann and Burel, 2008). These metrics incorporate the interpatch distances, area of habitat at various distances from the focal habitat, and the presence of stepping stones and corridors (Leidner and Haddad, 2011). A proximity index rates the relative amount and distance to suitable habitat for single patches (Gustafson and Parker, 1994). Deciding which among the available metrics is the best choice for any given species remains challenging. Furthermore, connectivity has been treated as both independent and dependent variables in landscape ecology research (Goodwin, 2003). When considered an independent variable, connectivity was considered a structural aspect of the landscape under study. These studies often compared the performance of populations living in landscapes having different patch structures. When treated as a dependent variable, connectivity was a function of various species responses to pattern in the same landscape. A highly mobile species, such as a bird or large mammal, can easily move between patches, but a sedentary organism or nonflying invertebrate will find the same landscape disconnected (or fragmented) if it cannot readily move among patches. Thus, sensitivity to habitat loss and fragmentation depends on species’ habitat needs and life-history traits (Driscoll and Weir, 2005; Sutton and Morgan, 2009).

**Landscape Structure, Population Viability, and Conservation**

Conservation biology naturally considers the effects of landscape structure on population structure and population viability. Therefore, there is a close and complementary connection between the disciplines of Conservation Biology and Landscape Ecology. The conservation of any species depends on the maintenance of viable populations, and the patch structure of landscapes affects population viability at both the patch and landscape level.

**Population Viability in Small Patches**

Population viability is strongly related to effective population size ($N_e$) and genetic diversity, two characteristics that are linked. Small populations suffer from demographic stochasticity and reduced genetic diversity. Populations in landscapes...
in which small isolated patches predominate show less genetic diversity overall than populations in unfragmented landscapes (e.g., butterfly (Collier et al., 2010) and toad (Allentoft et al., 2009)). Moreover, population sizes in small patches fluctuate to a greater degree because of demographic stochasticity, which is the fluctuation in \( N_0 \), birthrates, and death rates through time. They also fluctuate as a result of environmental stochasticity, which is variation in demographic rates from unpredictable events related to factors such as weather. Such fluctuations create a greater chance of extinction and expose the population to loss of diversity because of genetic drift and population bottlenecks.

The viability of populations in small patches is reduced because of limited genetic diversity. Small populations contain less genetic diversity because there are fewer individuals. In addition, genetic drift and inbreeding further reduce genetic diversity over time. Genetic drift is the random change in allele frequencies because of sampling error in the process of mating. Over the long term, drift ultimately leads to the loss of alleles when their frequencies randomly reach zero. Levels of heterozygosity, a common way of measuring genetic diversity, are positively associated with population growth and persistence (Hanski and Saccheri, 2006). Individuals with higher levels of heterozygosity typically have higher survival and reproductive rates than individuals with less heterozygosity (Colman et al., 1998). This phenomenon is called heterozygote advantage or heterosis. Heterozygosity declines as alleles are lost and the population becomes fixed for one allele. Similarly, inbreeding reduces heterozygosity among offspring when related individuals breed, and inbred populations have a greater chance of extinction (Saccheri et al., 1998). Inbred offspring have lower levels of heterozygosity and have a greater chance of being homozygous for deleterious recessive alleles. This reduced fitness is termed “inbreeding depression.”

In small populations, the choice of mates is directly related to \( N_0 \) and matings among related individuals will inevitably occur. The primary conclusion is that small populations have lower genetic diversity and stochastic processes of genetic drift, inbreeding, and population bottlenecks will further reduce genetic diversity over time.

The predominance of small patches in fragmented landscapes can affect demography and behaviors. Small populations may suffer reduced population growth rates because of social factors called Allee effects. Allee (1931) suggested that some species have a minimum viable population (MVP) size. Birth and death rates are density-dependent, and recruitment drops to unsustainable levels below a certain \( N \). For example, fertilization rates in flowering plant may depend on visitation rates by pollinating insects, but a minimum density of individual plants is needed to attract the necessary numbers of pollinators (Hackney and McGraw, 2001). When \( N_0 \) or densities are too low, recruitment rates decline because of low fertilization rates. Likewise, vulnerability to predators can increase in some animal groups. Flock size and herd size are correlated with the ability to detect predators and thereby reduce predation risk for the individual (Lima and Dill, 1990). Allee effects are apparent when survival and reproductive rates are positively correlated with population density and density is below the threshold for density-dependent population regulation (i.e., the carrying capacity). However, care should be taken not to confuse these effects with the negative effects of small population size such as inbreeding (Stephens et al., 1999). In fragmented landscapes, the small patches may support too few individuals needed to accrue the positive benefits of population size and/or density. For animals, patterns of behaviors such as movements can be altered by habitat fragmentation. For example, Mitrovich et al. (2009) found differences in the home range overlap and movements and crowding for the coachwhip (Masticophis flagellum), a large snake, in small patches relative to large patches. Movements of large highly mobile mammals may be affected, too. Seasonal movement behaviors of white-tail deer (Odocoileus virginianus) varied with the mean size and number of patches in a landscape in the midwestern USA (Grovenburg et al., 2011). Deer in landscapes with many large patches tended to be sedentary residents, whereas those in landscapes with small patches were more likely to be migratory.

The genetic and demographic problems of small populations interact synergistically in a phenomenon referred to as an extinction vortex (Gilpin and Soule, 1986). When \( N_0 \) falls, genetic diversity is lost because of the phenomena of bottlenecks, drift, and inbreeding. Reduced genetic diversity causes drops in population growth, reducing mean fitness because genetic diversity is correlated with the levels heterozygosity in individuals and the population as a whole. In small populations that have lost a significant amount of genetic diversity, low or negative growth rates further reduce \( N \), which results in greater loss of genetic diversity. Moreover, reduced genetic diversity limits the ability of the population to adapt, via natural selection, to changes in its environment. Therefore, small populations are more sensitive to environmental change than large populations having more diversity. This combination of interacting processes eventually threatens the small population with extinction.

What population size qualifies a small population? Although the most accurate answer will depend on the life history of specific species, the “50/500” rule of thumb from conservation biology (Franklin, 1980) provides a useful starting point when detailed life-history information is lacking. This rule states that isolated demes with an effective population size (\( N_e \)) greater than 500 will be relatively safe from the dangers of the loss of genetic diversity. These risks progressively increase as \( N_e \) declines from 500 toward 50. At \( N_e < 50 \), all combined forces of the extinction vortex act on the population, and extinction may be inevitable without management intervention. Thus, a \( N_e > 50 \) is needed for short-term population viability and \( N_e > 500 \) needed for long-term viability. The “50/500” rule was based on goal of maintaining genetic diversity (Franklin, 1980). Shaffer (1981) outlined the concept known as the minimum viable population. Estimates of a MVP include three parameters: a \( N_u \) a probability of extinction (or persistence), and a specific time period. For example, “An MVP for any given species in any given habitat is the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes” (Shaffer 1981, p. 132). When incorporating the dangers of demographic and environmental stochasticity, the minimum \( N_e \) should be in the range of thousands rather than hundreds (Traill et al., 2010).
Some scientists criticize the notion of general guidelines for MVPs, arguing that the minimum $N_e$ for long-term persistence must be determined on a species-by-species basis (Flather et al., 2011). Population viability and MVP will be affected by the unique combination of species’ traits, including its phylogeny, life history, resource needs, habitat availability, population structure and demography, and environmental threats (both natural and human caused) within the context of the landscape where it lives. For landscape-level conservation efforts, it should be more profitable to identify and address the specific causes of population declines (Caughley, 1994) rather than focus on maintaining a minimum number of individuals. Nevertheless, an estimate of MVP can be useful for labeling species as being at risk of extinction, motivating policy makers and managers to take appropriate actions, and setting a target population size for restoration efforts.

**Immigration and Rescue Effects**

Despite the problems described in the previous section, small populations are frequently observed in nature and seem to persist over the long term. Their persistence can be explained by the fact that these populations are open and connected to other demes in the landscape via the movement of individuals. Population biologists commonly refer to these movements as “immigration” (into) and “emigration” (from) when in reference to a specific deme.

Immigration has several benefits to a small population and some risks. Immigrant individuals can increase genetic diversity if they bring alleles that are absent or rare in the deme. Even infrequent or low levels of immigration are sufficient to restore genetic diversity lost to genetic drift (Slatkin, 1985). Immigrants provide a form of gene flow. The interpatch transport of gametes, such as pollen for flowering plants, is another example of gene flow. Moreover, immigrants provide a form of population growth when local recruitment rates are low (see BIDE model in the section Basic Concepts and Terminology about Population Dynamics). Thus, immigration can periodically rescue a population from the negative effects of demographic stochasticity and loss of genetic diversity, but there are significant risks associated with the movement of individuals. “Outbreeding depression” occurs when immigrants introduce genetic traits that are poorly suited for the local environmental conditions. Offspring expressing these traits will have reduced fitness, and the mean fitness of the population will be lower until natural selection eliminates these traits. If immigration of these traits persists, then the mean fitness and population growth rate will be determined by a balance between immigration and selection. A second risk is the introduction of pathogens and parasites carried by immigrants.

**Preserving Habitat at Landscape Level: The SLOSS Debate**

Conservation biologists have debated the best strategy for preserving habitat for threatened and endangered species. If the total area of habitat that can be protected is limited, then what is the best scheme for distributing that habitat in space? The essence of this question is whether to protect the same acreage of habitat in “single large or several small” (i.e., the acronym SLOSS) patches. There are advantages and disadvantages for both choices (Diamond et al., 1976). A single large preserve provides habitat to support the largest possible population. If $N_e$ is sufficiently large, then this choice will avoid the problems of small populations discussed previously. However, the danger of a single habitat patch is that some environmental catastrophe such as a hurricane or fire or an introduced virulent pathogen could extirpate the entire species. If the species is spread across several smaller patches sufficiently separated in space, then the chance of a catastrophic event affecting all of them is less than if they are confined to a single patch. For the “several small” strategy to be viable, the demes of respective patches must be large enough to avoid the extinction vortex, or the populations must be open to movement between patches in order to accrue the benefits of immigration. The movement of immigrants may be natural or facilitated by human management in the form of translocations of individuals.

Land management around preserved patches may include the preservation of corridors to connect patches and facilitate movements among them. Corridors likewise have their relative advantages and disadvantages (Haddad et al., 2011), and their effectiveness depends on the natural history of the target species (Gilbert-Norton et al., 2010). Species that are dispersal-limited or have difficulty crossing the landscape matrix receive the greatest benefits corridors. For animals, corridors of low-quality habitat can enhance movement among habitat patches even if populations cannot persist within the corridor itself (Haddad and Tewksbury, 2005).

**Landscape Ecology and Metapopulation Dynamics**

Most populations in nature have a patchy distribution because of patchiness of their habitat, and population structure is determined by the exchange of individuals (e.g., immigration and emigration) among patches. If the rates of exchange are high and frequent, such as by a highly mobile species, then there is simply one population occupying multiple patches. If exchanges among patches are very infrequent or nonexistent, then each patch has a distinct and separate population. An intermediate level of exchange would include regular movements among patches by dispersing individuals moving from their natal site to another patch. This amount of exchange characterizes metapopulations.

The dynamics of open populations persisting in a patchy landscape often take the form of a metapopulation. A metapopulation is a network of individual demes connected by the processes of immigration and emigration. Metapopulation dynamics exist when species have demes in discrete habitat patches. Each deme has a finite probability of extinction, but extinction events are not synchronized in time across space. Empty patches are common, but none of them are too isolated to be recolonized from an extant deme. Thus, a metapopulation exhibits turnover in the occupancy of patches that is a function of local extinctions and recolonizations (Hanski, 1999). McCullough (1996) provides examples of metapopulation ecology applied to problems of wildlife conservation.
Metapopulation theory has been an important tool for helping ecologists think about population dynamics in fragmented landscapes, but detecting metapopulations and parameterizing metapopulation models from field data is still challenging (Driscoll, 2007). The incidence function model of (Hanski et al., 1996b) has been one of the most useful because it requires only patch occupancy data. By monitoring how many and which patches are occupied over time, ecologists can relate the probability of occupancy to patch size, shape, and isolation. Alternative techniques include analyses of genetic structure to infer the relative isolation of habitat patches and the frequency of immigration among them (Wang et al., 2008).

Sources and Sinks

In the simplest case of population structure, the size of patches and the quality of habitat contained within them is similar, but this case is likely uncommon in nature. In a metapopulation spread over several habitat patches, variation in population growth rates can exist because of patch-specific differences in habitat quality, interspecific interactions, or other ecological factors. Pulliam (1988) described the situation in which some patches have intrinsic rates of increase \( r = \text{birthrate} - \text{death rate} \) greater than 0 – that is, local birthrates exceed local death rates. These patches were termed “sources” because local population growth will produce an excess of individuals. The local population growth exceeds the patch’s carrying capacity, and these excess individuals must emigrate; if not, then feedbacks from local resource limitation will reduce growth rates. In the same metapopulation, other patches called sinks have \( r < 0 \) because the local birthrate is less than the death rate. If isolated from other populations, extinction is inevitable for sink populations. However, sinks can persist in the context of a metapopulation because excess individuals from source patches can immigrate into sinks. These sinks receive a demographic subsidy and are able to persist because the sum of \( (\text{births} + \text{immigrants} - \text{deaths}) \geq 0 \).

The knowledge of source and sink patches is critical for understanding how a particular metapopulation functions. This understanding is important for landscape-level conservation efforts in which choices are made about the protection (or allowing the destruction) of some fraction of the existing patches. If a critical number of the sources patches are lost, then the entire metapopulation will collapse (Hanski and Ovaskainen, 2002). Unfortunately, patch occupancy alone is not a reliable indicator of the source/sink status of individual patches. The hard work of estimating demographic rates must be undertaken to fully understand this aspect of population dynamics.

Core and Satellite Model

In conservation planning, the “core and satellite model” of habitat protection has been used at the landscape level (Shen et al., 2008; Snep and Ottburg, 2008). This model envisions critical habitat distributed in patches varying in area and quality. Core patches support the largest \( N_c \) and populations that persist through time. Core populations may act as demographic sources, and their greatest value to the broader metapopulation is to produce emigrants destined for satellite populations (Runge et al., 2008). Small patches located near the periphery of the core patches support small satellite populations that periodically go extinct. Satellite populations depend on immigrants from the core patches to avoid extinction or for recolonization after local extinction. Satellite populations may be demographic sinks or simply have a small \( N_s \), that is vulnerable to the problems of small populations.

Landscape Change, Habitat Fragmentation, Edge Effects, and Extinction Debt

Landscape changes, particularly those caused by human land uses, can alter the abundance and connectivity of suitable habitat. Habitat fragmentation results when habitat loss converts a landscape dominated by large connected patches of habitat to one in which habitat exists in small, disconnected fragments. Fragmentation of native habitats is happening on a global scale (Riiters et al., 2000). This phenomenon affects habitat quality as well as its quantity and spatial distribution. Consequently, fragmentation affects the spatial structure of populations. The effects of fragmentation can be conceptually separated into the effects of (1) reduced patch size and (2) increased patch isolation. The processes of habitat loss and fragmentation often occur concurrently, but Fahrig (2003) argued that their effects need to be considered independently to best understand the consequences of landscape change on populations and communities.

In fragmented landscapes, the effects of small patch size are confounded with edge effects. Small fragments have more edge, which can alter habitat quality. Small habitat patches have a greater edge-to-interior ratio because of simple geometry. As the area of a circle \( (\pi \times \text{radius}^2) \) decreases, the perimeter of a circle \( (2 \times \pi \times \text{radius}) \) decreases more slowly. Circles and squares are simple, compact shapes in which length and width are approximately equal. Habitat fragments of elongated and complex shapes have a greater amount of perimeter compared to the area. The patch perimeter or “edge” is the boundary between the habitat of the patch and the landscape matrix, and the ecological conditions at the patch edge can be modified by the conditions in the matrix (Matlack, 1993). For example, consider a forest patch in a matrix of agricultural fields. The edges of forest are drier, warmer, windier, and receive more sunlight than locations deep in the interior of the forest patch. These altered conditions are termed “edge effects” and may extend some distance into the forest patch. Edge effects also include differences in the biotic interactions. For example, predation rates may be greater near edges. The “interior habitat” – sites within the patch but some minimum distance from the patch boundary – is considered free of edge effects. Some species are sensitive to the differences between edges and interiors. So-called “edge-sensitive” or “interior-dependent” species avoid edges or experience lower survival and/or reproductive rates in edges. As fragment size decreases, the edge-to-interior ratio increases; edge-sensitive species have less and less interior habitat for use. Below a particular patch size, interior habitat is absent because edge effects penetrate to all regions of the small patch. Therefore, interior-dependent
species are absent from the smallest patches that are dominated by edge-tolerant species (Banks-Leite et al., 2010). Although the example of forest habitat was discussed here, edge effects also exist for grasslands and other nonforest habitats (Renfrew et al., 2005).

The response of populations to the process of habitat loss and fragmentation may lag behind the changes in habitat quantity and quality. For example, some edge-sensitive species may persist in habitat fragments in spite of the loss of interior habitat. This lag occurs because individuals survive in small patches but long-term recruitment rates drop below mortality rates. Thus, small patches are occupied and some reproduction may be occurring, but not enough for long-term population persistence. In addition, the metapopulation dynamics may be disrupted by the overall loss of participating patches or the loss of a critical patch, and the metapopulation collapses (Hanski et al., 1996a). Eventually, these species will go extinct in this landscape, but extinction is delayed by the presence of long-lived individuals and some low levels of reproduction. This delay is termed “extinction debt” (Hanski and Ovaskainen, 2002; Honnay et al., 2005), and it depends on the life history of species affected by habitat fragmentation (Piqueray et al., 2011). Krauss et al. (2010) reviewed data for a variety of species living in fragmented grasslands of Europe. They found that long-lived perennial plant species were more likely to exhibit extinction debt than short-lived, mobile species such as butterflies. For species exhibiting extinction debt, their distribution on the landscape is better explained by past habitat patterns than by the distribution and quality of habitat in the contemporary landscape.

Environmental Gradients and Habitat Heterogeneity at Multiple Scales

The concept of source and sink populations (Pulliam, 1988) raised awareness of how variation in demographic performance among patches affects the occupancy of individual patches as well as the landscape-wide distribution of a population. The spatial arrangement of patches is important because sink patches may persist only if they are within the dispersal window of at least one demographic source (Foppen et al., 2000). In the original models of source and sink metapopulations, within-patch conditions were considered homogeneous, but this situation is seldom typical in real landscapes. Spatial heterogeneity within patches may affect demographic rates and population dynamics at fine scales.

For large patches, spatial heterogeneity in habitat quality may create source–sink dynamics among sites within the patch. Environmental heterogeneity can create a mosaic of sites having higher and lower rates of survival, reproduction, and recruitment (Meekins and McCarthy, 2001). Within-patch heterogeneity can be especially high when patches are defined by a coarse-level criterion, such as land-cover type, and fine-scale heterogeneity is ignored. Fine-scale heterogeneity in temperature, moisture, soil nutrients, etc. may be correlated with occurrence of individuals (Palmer, 1990; Fraterrigo et al., 2006) and demographic rates (Meekins and McCarthy, 2001). If habitat quality is strongly correlated with fine-scale edaphic conditions (or some other measure of resource abundance for such food availability), then these conditions may be used to estimate the demographic potential of a given site (Seydack et al., 2000; Ecke et al., 2002; Gonzalez-Megias et al., 2005; Flinn, 2007). Although not separated into discrete patches, source-sink dynamics can occur among the sites within patches. The demographic rates associated with an entire patch will be a function of the average habitat quality of its embedded sites. Landscape ecologists, with their appreciation for issues of scale, are well-equipped to study the relative effects of within-patch, among-patch, and landscape heterogeneity on population dynamics.

Changing patterns of biodiversity in changing landscapes illustrate how spatial patterns at different scales interact with population processes. In portions of Europe and North America, forests are expanding following agricultural abandonment. New forest patches are developing from abandoned farmland via the process of secondary succession; this new habitat is also called postagricultural forest. The spatial arrangement of old forest patches is of great importance for native herbaceous plant species that depend on forest habitats. At the landscape scale, the abundance and proximity of “ancient forests” (not cleared for agriculture) is correlated with the patterns of plant diversity among recovering forest patches (Matlack, 1994a, b). The ancient forests preserved a pool of forest plant species during the time period of heavy agricultural use in the landscape (Pearson et al., 1998). During the period of recovery after the peak of agriculture, these species are able to disperse from the ancient forests to the new forest patches. Moreover, life-history traits influence the establishment and persistence of populations (Vellend, 2003; Flinn and Vellend, 2005) in particular patches. Verheyen et al. (2003) studied the distribution of forest herbaceous plant species in these postagricultural forests and their landscapes. They found that recovery after disturbance is a two-stage process in which the dispersal and colonizing ability of a species is initially most important in establishing populations in new forest patches. Next, after a species had colonized a new forest patch, habitat quality and niche specialization of the species influenced abundance and persistence within patches (also Pearson and Fraterrigo, 2011). The distribution of dispersal limited plant species was not correlated with habitat quality at the landscape scale because these species simply could not reach isolated forest patches. In other words, habitat fragmentation negated any effects of varying habitat quality for these postagricultural forests in the initial phase of recovery. Habitat quality became important only if and when a species reached a patch. This process takes many years to play out and will affect forest biodiversity for a century or more of recovery (Vellend et al., 2007).

Continuous Habitat Variability in Landscapes

The patch–matrix–corridor approach to characterizing spatial pattern is useful for landscapes in which patches exist as discrete readily identifiable units, and there are greater differences among patches than within them. However, in many landscapes, habitat variation occurs along environmental gradients that change relatively slowly across space (Figure 6). In such a landscape, drawing a definite boundary to denote habitat
patches is nearly impossible because suitability varies in a complex and continuous manner across space. In mountainous landscapes, topography creates gradients in temperature, moisture, and light related to elevation, aspect, slope, and terrain shape (Figure 6). Instead of maps of discrete patches of suitable and unsuitable habitat, these landscapes are best represented by maps showing continuous variation in habitat quality (Thompson et al., 2006; Franklin, 2009).

Quantifying the spatial pattern of habitats in these landscapes is challenging (Dorner et al., 2002). The statistical characteristics of this continuous variation can be quantified using a range of statistical techniques including blocking, spectral analysis, measures of spatial autocorrelation (Turner et al., 1991), or surface metrics (McGarigal et al., 2009). Patterns of habitat heterogeneity can change between fine and coarse scales, and these analyses can identify the particular spatial scale(s) in which spatial pattern and population processes are linked (Fortin and Dale, 2005). To be useful, the analysis should be approached from an organism-based perspective; that is, landscape structure can be understood by relating environmental gradients to the tolerances and resource needs of individual species (Cushman et al., 2010) and to population processes such as dispersal ability and sizes of home ranges. The influence of environmental gradients in determining species distributions and community composition has long been recognized by the ecologists. However, the theory and analytical techniques for studying populations in these types of landscapes is still under development.

**Figure 6** Map of predicted soil moisture as an example of continuous variation in habitat quality. Soil moisture is influenced by topography shown by 10-m contour lines as well as slope, aspect, and surrounding landforms. Drier sites are found on ridges and peaks, whereas wetter sites are located in ravines and valleys. This map was developed using a digital elevation model to calculate a topographic relative moisture index (Parker, 1982). (Reproduced with permission from Simon SA, Collins TK, Kaufman GL, McNab WH, and Ulrey CJ (2005) Ecological zones in the Southern Appalachians: First Approximation. Asheville, NC: US Department of Agriculture, Southern Research Station. Forest Service Research Paper SRS-41). Map shows 50-m grid cells.

**Landscape Structure and Interspecific Interactions**

Interspecific interactions are important determinants of population dynamics, and landscape structure can influence these interactions. All species interact with predators, parasites, competitors, and so on as the biotic portion of their environment. In breeding birds of forests, nest predation rates are affected by both landscape-level and within-patch habitat patterns (Lloyd et al., 2005). Predation rates increase as patch sizes decline and the landscape-wide abundance of nonforest
habitats increases. Moreover, landscape structure influences the movement patterns of different predator species so that the risk of encountering a specific predator species depends on the precise location in the landscape (Bergin et al., 2000). Conversely, spatial complexity can promote coexistence between predators and prey. “Refugia” are habitats (or microhabitats) where prey are relatively safe from predators. When predators are abundant, refugia prevent them from driving their prey to extinction.

Spatial heterogeneity is one of the principal explanations for the coexistence of competing species (Amarasekare, 2003) in community ecology. Coexistence can be achieved by niche partitioning when species specialize on different habitats or resources. Habitat heterogeneity within and among patches promotes coexistence. Spatial structure and heterogeneity through time are also necessary for the coexistence by the competition–colonization trade-off (Tilman, 1994). In this mechanism, competing species differ in their competitive abilities and ability to colonize new habitat patches. The superior competitors have low colonizing abilities, and the better colonizers are poor competitors. Disturbance periodically kills off local populations of the superior competitor, and for a brief time those sites or patches are empty. The superior colonizer (but poor competitor) quickly occupies the empty sites and holds them until the superior competitor arrives. Regular, localized disturbances permit coexistence by continually providing habitat for the poor competitor (e.g., Debout et al., 2009). Coexistence is possible when the landscape is a shifting mosaic of disturbed patches and sites at different stages of recovery from prior disturbances (Figure 7). Disturbance and its effects on landscape structure through time are a recurring research theme in landscape ecology.

Summary

Landscape ecology is concerned with the causes and consequences of spatial pattern in nature at multiple spatial scales. Spatial pattern in habitats and resources influences the growth, persistence, and decline of populations. The patch–matrix–corridor model of describing spatial heterogeneity is a useful conceptual model that is directly applicable to populations. Species frequently exhibit a patchy distribution in landscapes as a function of the spatial arrangement of their habitats. This landscape-level pattern (i.e., the landscape structure) determines how populations are organized in

Figure 7 Illustration of a landscape as a shifting mosaic of sites in different stages of recovery from disturbance. In the schematic (a), sites fully recover from disturbance after 60 years of recovery. A landscape in the Pisgah National Forest in North Carolina (b) is a mosaic of forest stands of various ages as measured by time since the year of stand origin. This pattern is a consequence of natural disturbances and human land uses such as timber management.

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[Image 76x390 to 531x708]
local breeding groups and how frequently individuals move between these groups. This population structure in turn affects population dynamics. Landscape structure, in combination with life-history traits of a species, determines whether that species exists as a single large population, as a metapopulation of demes connected by movement of individuals, or as a collection of separate isolated populations. An understanding of population structure reveals the conservation challenges facing many species. In landscapes in which habitat is highly fragmented, isolated populations in small patches face a number of problems ranging from loss of genetic diversity to edge effects. Thus, the landscape ecology of populations is related to conservation. Some landscapes exhibit continuous variation in habitat quality, and the patch–matrix–corridor model is not directly applicable. Techniques for describing habitat heterogeneity at multiple scales are available, but understanding how this type of variation affects population dynamics is more challenging.

See also: Habitat Loss and Fragmentation. Metapopulations

References


