

PART 1

CONCEPTS

Chapter 2

BASICS OF LANDSCAPE ECOLOGY: AN INTRODUCTION TO LANDSCAPES AND POPULATION PROCESSES FOR LANDSCAPE GENETICISTS

Samuel A. Cushman,¹ Brad H. McRae,² and Kevin McGarigal³

¹*Forest and Woodlands Ecosystems Program, Rocky Mountain Research Station, United States Forest Service, USA*

²*The Nature Conservancy, North America Region*

³*Department of Natural Resources Conservation, University of Massachusetts, USA*

2.1 INTRODUCTION

Ecology is defined as the interaction of organisms and their environment (Tansley 1935) and the environments in which organisms live are spatially structured at a range of scales (Levin 1992). Therefore, the interactions that connect organisms with their environment are affected by the composition and structure of the landscape in which they live (Watt 1947). A foundational idea in ecology is that the strength of interaction

varies with location in the environment and with distance between individuals (Turner et al. 2001). Understanding the effects of location and distance on the interactions between organisms and between organisms and their environment is a key focus of **landscape** ecology (Wiens 1992). Landscape ecology focuses on the interactions of spatial patterns and ecological processes (Turner 1989). Given this emphasis on pattern–process relationships, much of the theory and methodology of landscape ecology focuses on how

12 Basics of landscape ecology

to characterize landscape heterogeneity, where it comes from, how it changes over time, and why it matters to ecological processes.

The emergence of landscape ecology was enabled by the confluence of several parallel developments over the past 40 years. The first is the recognition of the importance of broad-scale environmental issues. For example, habitat loss and fragmentation are widely seen as global drivers of a burgeoning extinction crisis (McKinney & Lockwood 1999), climate change is leading to dramatic reorganization of biological communities at broad scales (Thomas et al. 2004), and invasive species are having profound effects on ecosystems across the world (Mooney & Hobbs 2000). These broad-scale environmental challenges require solutions that are also at broad scales, which has motivated much landscape-level research and conservation planning. A second key in facilitating the development of landscape ecology is the emergence of scale and hierarchy concepts (Levin 1992). Landscape ecology focuses on the interaction of patterns and processes, and one of the key ideas is that both patterns and processes are scale-dependent (Wiens 1989). That is, each process acts at a characteristic scale in space and time and is affected by the structure and composition of the landscape at those characteristic scales (Fig. 2.1). A third key idea contributing to the emergence of landscape ecology is a transition from a view of ecosystems as internally homogeneous, discretely bounded, and equilibrial systems to one in which ecosystems are seen as spatially variable across scales and temporally dynamic (e.g., Watt 1947; Turner 1987). Many classical ideas in ecology and population genetics are based on simplified models of ecological systems in which spatial and temporal variation are ignored (Kareiva and Wennergren 1995). Landscape ecology seeks to inject space and time into the investigation explicitly and evaluate how the ecological processes and structure of the ecological system change as a result of spatial heterogeneity and temporal dynamics (Pickett & Cadenasso 1995). A critical fourth component in the emergence of landscape ecology is technological advances, particularly in remote sensing, computing, geographical information systems, and spatial statistical methods (Haines-Young et al. 2003; Sklar & Costanza 1991). These advances have enabled explicit consideration of spatial and temporal variability across scale in analysis that simply was not possible until very recently.

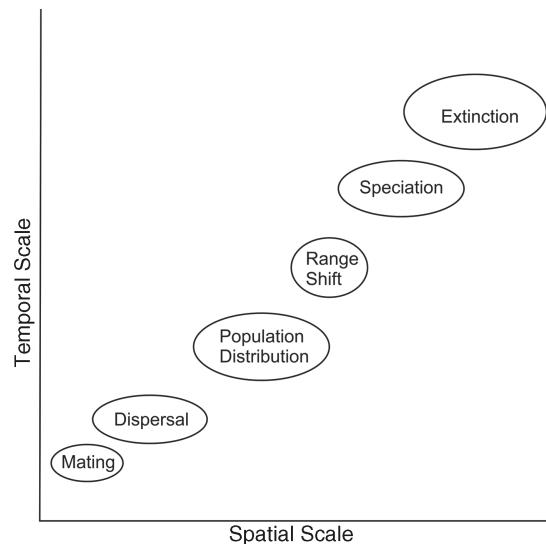


Fig. 2.1 Different population processes occur at different scales in space and time. Processes of mating among members of a population occur at short time scales and fine spatial scales relative to dispersal, which typically occurs over greater distances. The population distribution is typically larger in extent than mating and dispersal processes (spatial scale) and typically changes more slowly in time. The population extent may shift its range at longer time scales. Speciation and extinction events typically occur at longer time scales and coarser spatial scales.

2.2 HOW LANDSCAPES AFFECT POPULATION GENETIC PROCESSES

The habitats in which organisms live vary spatially across scales, and these patterns interact with organism perception and behavior to drive the higher-level processes of population dynamics, gene flow, and adaptive evolution (Johnson et al. 1992; Wiens et al. 1993). The structure and composition of the landscape are key drivers of population distribution and gene flow, and interact with individual genetic characteristics to affect fitness. In particular, a disruption in habitat continuity may interfere with ecological processes necessary for population persistence (Fahrig 2003). For example, habitat loss and fragmentation may create discontinuities (i.e., patchiness) in the distribution of critical resources (e.g., food, cover, water) and environmental conditions (e.g., microclimates). These discontinuities may inhibit movement and gene flow across the population or the

changes may result in reduced fitness, leading to population declines or adaptive evolution under directional selection. Although there are many ways that landscape structure and composition may affect population processes, they are dominated by: (1) area effects, (2) edge effects, and (3) isolation effects.

2.2.1 Area effects

One of the most important landscape-level influences on population processes is the effect that habitat extent has on gene flow and fitness. Habitat loss has consistently negative effects on biodiversity (Fahrig 2003), including reductions in species richness (Findlay & Houlahan 1997; Schmiegelow & Mönkkönen 2002; Steffan-Dewenter et al. 2002), declines in populations, and changes in species distributions (Bender et al. 1998; Sánchez-Zapata & Calvo 1999; Donovan & Flather 2002). Habitat loss changes the distribution of resources and can affect individual behavior and spatial activity patterns, changing the ability of the organism to acquire the resources needed to survive and reproduce (Mangel & Clark 1986; Wiens et al. 1993). For example, from an energetics perspective, if food resources become more patchily distributed, it may be more costly to acquire them (Mahan & Yahner 2000). In addition, moving between disjunct resource patches to acquire food resources may involve moving through suboptimal habitats that require higher energetic expenditures and expose individuals to higher rates of predation (Bergin et al. 2000) and reduce breeding (Kurki et al. 2000) and dispersal success (Belisle et al. 2001; With & Crist 1995; King & With 2002).

Most species require at least a minimum area of habitat in order to meet all life history requirements (e.g., Robbins et al. 1989). Theoretical studies predict a threshold habitat level below which the population cannot sustain itself (Fahrig 2002; Flather & Bevers 2002; Hill & Caswell 1999). The amount of habitat required for species persistence depends on species-specific behavioral and life-history characteristics (With & King 1999; Vance et al. 2003), and the effects of habitat loss on each species will depend on the interaction of its ecological requirements and capabilities with the degree of habitat loss in the surrounding landscape (McGarigal & Cushman 2002; Schmiegelow & Mönkkönen 2002; Fahrig 2003). For example, large-bodied, high-trophic-level species appear to be

particularly vulnerable to local extinction due to habitat loss (Gibbs & Stanton 2001). As habitat is lost in a landscape, the most area-sensitive species will be lost first. As the habitat loss continues, other species will drop out according to their minimum area requirements (e.g., Robbins et al. 1989; Bender et al. 1998; Flather & Bevers 2002). Thus, smaller patches generally contain fewer species than larger patches (Debinski & Holt 2000), and the set of species remaining in small patches is often a predictable subset of those found in large patches in the same region (Ganzhorn & Eisenbeiß 2001; Kolozsvary & Swihart 1999; Vallan 2000; Fahrig 2003). These area effects influence landscape genetic processes in several ways. First, as habitat is lost populations initially decline linearly with decreases in habitat extent, which results in reduction in effective population sizes, acceleration of genetic drift, and lower equilibrium heterozygosity and allelic richness. As habitat loss approaches the extinction threshold in some areas of the landscape, local populations may rapidly decline to extinction, resulting in gaps in distribution, which lead to attenuated gene flow, which creates spatial genetic structure and further reductions in heterozygosity and allelic richness. As the habitat area is further reduced beyond the extinction threshold the entire regional population will become extinct.

2.2.2 Edge effects

One of the strongest influences on population genetic processes is the effect of edges on organism movement and fitness. Edges are produced by natural discontinuities in geophysical factors (sometimes referred to as “inherent” edges), or by natural or anthropogenic disturbances (sometimes referred to as “induced” edges). These edges may be relatively permanent features of the landscape, for example, if they are produced by discontinuities in underlying abiotic factors (e.g., land–water interface), or transient features of a landscape, for example, if they are induced by disturbances (e.g., timber harvesting).

Depending on the ecology and life history of the species in question, edges can either inhibit or enhance movement and increase or decrease fitness (Kremsater & Bunnell 1999; Carlson & Hartman 2001; Laurance et al. 2001). Early wildlife management efforts were focused on maximizing edge habitat because it was believed that most species favored habitat conditions

14 Basics of landscape ecology

created by edges and that the juxtaposition of different habitats would increase species diversity (Leopold 1933). Indeed, this concept of edge as a positive influence guided land management practices for most of the 20th century. Recent studies, however, have suggested that changes in microclimate, vegetation, invertebrate populations, predation, brood parasitism, and competition along forest edges (i.e., edge effects) has resulted in the population declines of several vertebrate species dependent upon forest interior conditions (e.g., Strelke & Dickson 1980; Kroodsma 1982; Brittingham & Temple 1983). In fact, many of the adverse effects of forest fragmentation on organisms seem to be directly or indirectly related to these so-called negative edge effects.

One of the primary edge effects is the alteration of microclimate within habitat patches due to changes in the physical fluxes of radiation, wind, and water (Franklin and Forman 1987; Saunders et al. 1991; Baker & Dillon 2000). Following habitat loss, changes in these fluxes across the newly created edges can influence the microclimate of the remnant habitat patches (Saunders et al. 1991). Air temperatures at the edge of a forest remnant, for example, can be significantly higher than those found in either the interior of the remnant or the surrounding agricultural land (Geiger 1965; Kapos 1989). Similarly, with the conversion of natural vegetation to developed land uses, the entire pattern of momentum transfer over the landscape may be altered (Saunders et al. 1991). The wind profile does not fully equilibrate with the new land cover for some distance, perhaps for a distance as much as 100–200 times the height of the vegetation (Monteith 1975; Grace 1983). In addition, edges may allow below-canopy winds to penetrate the patch and modify relative humidity near the edge. Conversion of natural vegetation to developed land uses alters the rates of rainfall interception and evapotranspiration, and hence changes soil moisture levels (Kapos 1989). Altered surface and subsurface flows affect the timing and magnitude of peak flows (Hornbeck 1973) and the transport of soil and nutrients (Likens et al. 1970; Bormann et al. 1974). These watershed hydrological impacts influence the local moisture regimes along habitat edges.

One of the more obvious edge effects is increased rates of disturbance along edges, primarily as a result of increased exposure to wind (Franklin & Forman 1987; Saunders et al. 1991). Increased wind exposure at edges may result in damage to the vegetation, either through direct physical damage from pruning or

windthrow (Moen 1974; Grace 1977) or by increasing evapotranspiration with reduced humidity and increased dessication (Tranquillini 1979; Lovejoy et al. 1986). Several authors have noted that edges may have more stressed, dead, and downed trees than do adjacent forests (Geiger 1965; Chen et al. 1992). This condition is conducive to insect infestations, which can cause additional disturbance.

The combination of climatic and disturbance effects along edges often produces marked changes in vegetation structure and composition and structure. Changes in light, temperature, wind, and moisture regimes affect seedling establishment, growth, and survival (Wales 1972; Gates & Mosher 1981; Ranney et al. 1981; de Casenave et al. 1995). Some species benefit from the modified microclimate near edges, others do not (e.g., Chen et al. 1992; Zen 1995). Similarly, increased disturbance rates at edges favor certain species. Overall, the altered physical environment can exert considerable influence on the composition and structure of vegetation near edges. Plant species common at successional edges (in contrast to permanent edges caused by inherent differences between adjacent natural communities, e.g., forest–water edge) include species that benefit from disturbance, as well as shade-intolerant, mid- and early-succession vegetation and non-native species (Ranney et al. 1981; Lovejoy et al. 1986; Alverson et al. 1988). Vegetation structure near edges reflects these compositional changes, and is further modified by the high rates of physical disturbance. Consequently, vegetation near edges usually consists of a diverse mixture of species and structures and is often characterized by high foliage height diversity and abundant dead wood (both snags and logs).

The alteration of the abiotic and biotic environment near habitat edges can reduce the quality of the edge habitat for some animal species and increase it for others. This reduction in habitat quality may be due to a less favorable microclimate (i.e., resulting in higher energetic costs), less favorable physical structure, fewer available food resources, adverse interspecific interactions (e.g., increased competition, predation, or parasitism), or a combination of these. For example, Mills (1995) documented that voles in southwest Oregon were almost nonexistent near forest edges compared to forest interiors and attributed the difference to the lack of truffles (the vole's preferred food) near forest edges due to the drier microclimate. Unfortunately, despite the many studies documenting trends in species abundances and distributions near edges, few studies have

attempted to determine causes of the observed patterns (Kremsater & Bunnell 1999).

The several edge effects discussed above can influence spatial genetic processes in a number of ways. First, if edges act as barriers or filters reducing movement of organisms across the edge, this can create genetic substructure by blocking or reducing gene flow. This also will tend to increase the rate of genetic drift in the patches isolated by the edges, resulting in loss of genetic diversity across the subdivided population. In contrast, proximity to edges may facilitate movement of some species that are associated with those conditions, increasing gene flow across their populations. Second, increasing edge density will likely result in loss of habitat potential for species associated with interiors of large extensive habitat patches, leading to reduced local population sizes and loss of genetic diversity. Conversely, habitat capability for many species increases with edge density in the landscape, at least up to a point. For these species, increasing edge in the landscape would likely result in higher population densities, higher gene flow, and higher genetic diversity. Thus, the nature of the edge effect on population genetic structure will depend on whether the observed edges act as barriers or conduits for movement, or increase or decrease habitat capability for the organism in question.

2.2.3 Isolation effects

One of the ultimate drivers of spatial genetic structure in populations is the effect of landscape heterogeneity on movement patterns and resulting isolation of individuals and local populations. As heterogeneity increases in a landscape, movement of organisms will be affected, resulting in differing degrees of isolation depending on the abundance, distribution, and dispersal abilities of the species. When the landscape change results in a loss or fragmentation of habitat, and therefore supports fewer individuals (than the original contiguous habitat), there will be fewer local (within-patch) opportunities for intraspecific interactions. This may not present a problem for individuals (and the persistence of the population) if movement among patches is largely unimpeded by intervening habitats in the surrounding landscape and connectivity across the landscape can be maintained. However, if movement among habitat patches is significantly impeded, then individuals (and local populations) in remnant

habitat patches may become functionally isolated (McCoy & Mushinsky 1999; Rukke 2000; Virgos 2001; Bender et al. 2003; Tischendorf et al. 2003). The degree of isolation for any fragmented habitat distribution will vary among species depending on how they perceive and interact with landscape patterns (Dale et al. 1994; With & Crist 1995; Pearson et al. 1996; With et al. 1997); less vagile species with very restrictive habitat requirements and limited gap-crossing ability will likely be most sensitive to isolation effects (e.g. Marsh & Trenham 2001; Rothermel & Semlitsch 2002).

Local populations can become functionally isolated in several ways. First, the edge of the occupied patch may act as a filter or barrier that impedes or prevents movement, thereby disrupting emigration and dispersal from the patch (Wiens et al. 1985). Some evidence for this exists for small mammals (e.g., Wegner & Merriam 1979; Chasko & Gates 1982; Yahner 1986). Second, the distance from remnant habitat patches to other neighboring habitat patches may influence the likelihood of successful movement of individuals among habitat patches. Again, the distance at which movement rates significantly decline will vary among species depending on how they scale the environment. Therefore, a 100 m-wide agricultural field may be a complete barrier to dispersal for small organisms such as invertebrates (e.g., Kareiva 1987) or amphibians (Rothermel & Semlitsch 2002; Marsh et al. 2004), yet be quite permeable for larger and more vagile organisms such as birds. Lastly, the composition and structure of the intervening landscape mosaic may determine the permeability of the landscape to movements (known as landscape “resistance”; see Chapter 8). A landscape may be composed of a variety of continuous gradients, discrete patches, or networks of linear elements (such as roads or hydrological networks). Each of these elements may differ in its resistance to movement, facilitating movement through certain elements of the landscape and impeding it in others (e.g., Adriansen et al. 2003; Cushman et al. 2006; Spear et al. 2010). Regardless of how local populations within a landscape become functionally isolated, whether it is due to properties of the edges themselves, the distance between patches, or properties of the intervening landscape, the end result is the same – fewer individual movements across the landscape. This, in turn, can lead to genetic differentiation as a function of cumulative movement cost (isolation-by-resistance; IBR) and lead to loss of genetic diversity through drift in

16 Basics of landscape ecology

small isolated subpopulations (Charlesworth & Charlesworth 1987).

2.3 DEFINING THE LANDSCAPE FOR LANDSCAPE GENETIC RESEARCH

2.3.1 What is a landscape?

From an ecological perspective a landscape is a system of interacting ecological patterns and processes at any scale. Spatially, a landscape can be considered to be an area that is spatially heterogeneous in at least one factor of interest (Turner 2005). From an organism's perspective a landscape can be considered to be a heterogeneous distribution of resources and conditions, such as those that define its ecological niche, at a scale relevant to its ecology. A key point is that a landscape is not necessarily defined by its size. Rather it is defined by being a spatially heterogeneous area at an **extent** and resolution relevant to the phenomenon under consideration. In landscape genetics the phenomenon under consideration is usually the genetic structure of a population and the processes that govern it, such as gene flow or adaptive evolution (e.g., Manel et al. 2003; Segelbacher et al. 2010). Thus in landscape genetics the extent of the landscape may be defined by the extent occupied by the focal population and its structure may be defined by the ecological factors that drive the population process of interest (such as gene flow or selection). Given that the appropriate definition of a landscape will vary depending on the ecological system

and objectives of research, there are several key steps in defining the landscape appropriately for any given research project. These include defining a meaningful spatial extent for the landscape, choosing an appropriate conceptual model of landscape structure, selecting proper **thematic content** and **thematic resolution**, and selecting a proper spatial **grain**.

There are a range of conceptual models of landscape structure that are widely adopted in landscape ecological research (Fig. 2.2). For some questions landscape structure can be represented by a point pattern of element occurrences (Fig. 2.2a), which indicate the location of entities of interest, such as organisms or particular environmental features, in the landscape. Alternatively, when the extent and pattern of linear features, such as hydrological or road networks, are relevant, a landscape may be represented as a linear network (Fig. 2.2b). Commonly in past landscape ecology research landscapes have been represented as mosaics of different patch types, each representing a distinct ecological condition (Fig. 2.2c). Alternatively, in many cases landscape conditions are best represented as gradients that continuously vary across the study area, such as elevation, climate, or density of vegetation (Fig. 2d). In landscape genetics research the distribution of genetic samples (representing individuals or populations) is frequently represented as a point pattern or a graph matrix (Fig. 2.2e). The landscape in landscape genetic analysis may be represented by linear networks, patch mosaics, gradients, or a combination of these, depending on the nature of the system and the question at hand. The focus of landscape genetic

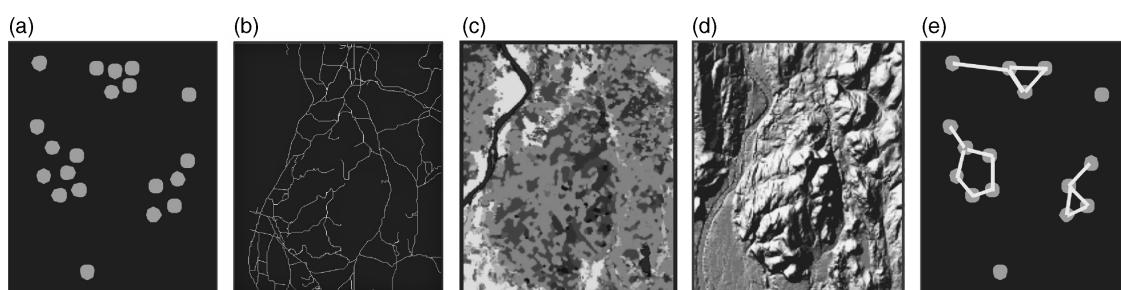


Fig. 2.2 Conceptual models of landscape structure. The structure of a landscape can be represented in various ways. For example, the distribution of point elements (a) might be a suitable landscape model for a system in which the location of entities is the only factor that is important. Conversely, a linear network model (b) might be appropriate when the question involves connectivity of a hydrological network or the influences of a road network on fragmenting terrestrial habitats. A landscape mosaic model (c) could be chosen when the research goal is to assess the effects of different categorical land cover types on gene flow or selection. A gradient model (d) would be appropriate when gene flow or selection processes are affected by continuously varying attributes of a landscape such as elevation, density of vegetation or human population density. Landscape genetics studies sometimes represent spatial locations of genetic samples, with or without graph edges connecting them (e). (For a color version of this figure, please refer to the color plates section.)

research is associating differences in the genetic characteristics of individuals or populations at point locations (Fig. 2.2a) with the structure and connectivity of the landscape in which they reside (Fig. 2.2a to d).

2.3.2 Thematic content

It is a considerable challenge to determine how to represent the spatial structure of the environment in a way that is relevant to the population process under study. The choice of what attributes of environmental variation to represent (thematic content) can have immense implications for landscape genetic analysis. Consider a mountainous landscape in the US Rocky Mountains. There are many landscape features that one might choose to characterize, including elevation, forest cover, soil depth, geological parent material, climate, human landuse, roads, water sources, and other factors (e.g., Fig. 2.3). How does one choose which factors to represent in a model of landscape structure to use in landscape genetic studies? Ideally, the research team has selected a system and study organism based on prior knowledge that enables *a priori* development of research hypotheses. For example, if the researcher hypothesizes that gene flow of a particular species is related to elevation, forest cover, and roads then these factors would be reasonable choices to include as thematic content in the **landscape definition**. The apparent structure of the landscape is fundamentally dependent on the attributes selected to be represented thematically, and finding meaningful relationships between genetic processes and landscape patterns depends on correctly including the landscape features that most strongly affect the genetic process of interest.

2.3.3 Thematic resolution

Once factors to include have been selected, one must then choose how to represent them in terms of thematic resolution. Thematic resolution refers to the functional form (for continuous variables) or classification scheme (for categorical variables) used to define the values of a variable. For example, if one selected elevation as a factor of interest, would one choose to represent its effect on gene flow as linearly increasing with increasing elevation (Fig. 2.4a) or nonlinearly increasing, perhaps as a Gaussian function (Fig. 2.4c). Gene flow is usually most related to **functional connectivity** between locations.

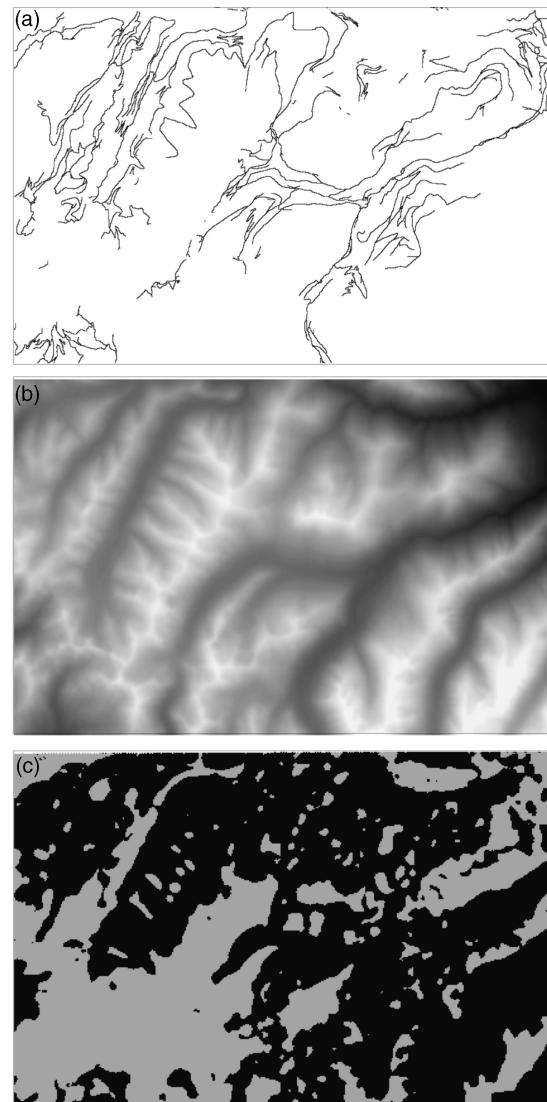


Fig. 2.3 The thematic content of a landscape is the factors or variables represented spatially. For example, a landscape genetics study might hypothesize that roads fragment the population (a), or that gene flow is higher at low elevations than at high elevations (b), or that fitness is high in closed canopy forest but low in non-forest (c). It is critical to carefully select the thematic content of the landscape model to match the *a priori* hypotheses chosen to meet the analysis objective.

Predictions of functional connectivity can be made by calculating least-cost paths across a map representing hypothesized resistance to movement (e.g., red lines in

18 Basics of landscape ecology

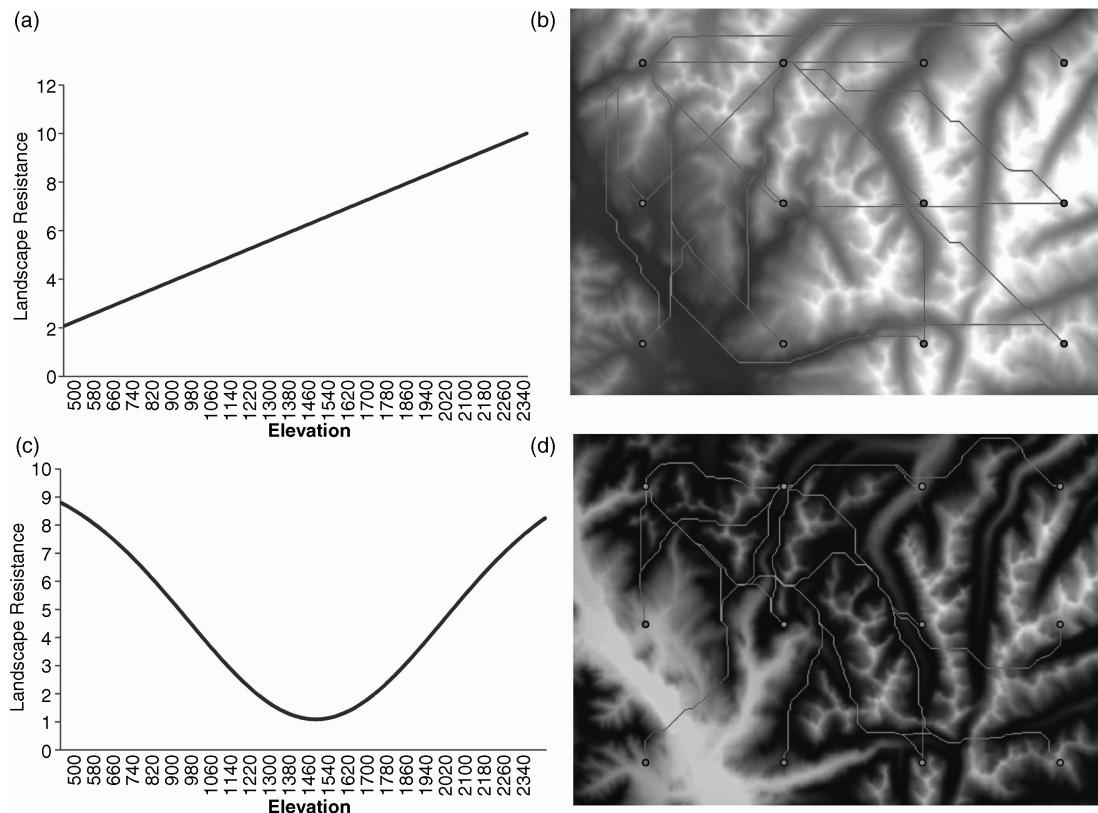


Fig. 2.4 The thematic resolution is the resolution and functional form at which each factor included in the thematic content is represented. For example, the effect of elevation on a population process could be represented in various ways. For example, resistance to gene flow could increase linearly with elevation (a). In this case landscape resistance would be low in the valley areas (dark) and high on ridges (white) (b). The least-cost routes (lines) among a network of individuals (dots) would minimize cumulative cost by preferentially following low-elevation paths (b). Conversely, resistance to gene flow might be lowest at middle elevations (c). In this case resistance to gene flow would be lowest at intermediate elevations and higher in the deepest valleys and on the highest ridges (c), and least-cost routes connecting a network of individuals would preferentially follow paths that avoid low and high elevations (paths in d). Notably, even though (b) and (d) both have the same thematic content (elevation) and address the same question (gene flow), they produce very different predictions of the pattern and degree of connectivity among individuals. (For a color version of this figure, please refer to the color plates section.)

Fig. 2.4). If gene flow were related to elevation as a Gaussian function (as in Fig. 2.4d), but one used a linear function (as in Fig. 4b) to represent its effect, it is likely that the results would be misleading given that predicted connectivity among points is very different in these two representations of elevation effects. Similarly, suppose that one selected forest cover as a variable of interest; how would it be mapped for analysis? One could represent the effects of forest cover as four classes of different forest types (Fig. 2.2a), or as three classes

of different successional stages (Fig. 2.5b), or as a combination of the four classes and three seral stages (12 cover-seral classes as in Fig. 2.5c). If gene flow were governed by seral stage (as in Fig. 2.5b) but forest cover were represented as cover types (as in Fig. 2.5a) it is likely that the analysis would not find a relationship (or produce a misleading relationship) as these maps have very different spatial patterns and produce substantially different predictions of the connectivity among locations (lines in Fig. 2.5a to c).

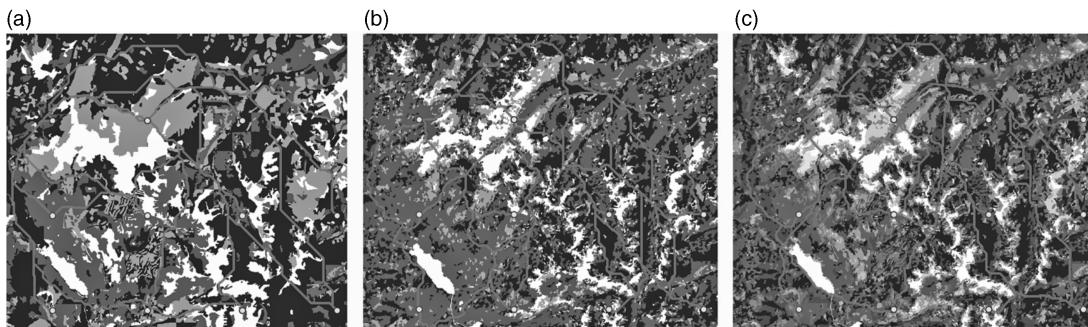


Fig. 2.5 In a mosaic model of landscape structure and when the chosen thematic content is forest cover, there are a number of ways to represent the thematic resolution of forest in a landscape. For example, one could represent the effect of forest cover on a population process as four classes of different forest types (a), or as three classes of different successional stages (b), or as a combination of the four cover types and three seral stages (c). A network of individuals is shown as yellow dots and the least-cost paths connecting them are shown as red lines. The location of these least-cost routes and the relative cost of movement among pairs of points differ notably between these three thematic resolutions of forest cover. (For a color version of this figure, please refer to the color plates section.)

2.3.4 Spatial extent and grain

Given a choice of a particular variable to represent and its thematic resolution, the next critical question is over what extent and at what spatial grain should it be mapped for analysis? *Extent* is the area within the landscape boundary and defines the population for the analysis. *Grain* is the size of the individual units of observation. For example, a fine-grained map might represent information in 0.1 ha units, whereas a coarse-grained map might resample this information to 1 ha or 10 ha size units. Extent and grain define the upper and lower limits of resolution of a study and inferences about scale-dependency are constrained by the extent and grain of the data (Wiens 1989). One cannot reliably extrapolate beyond the extent of the sampled population, nor can one infer a pattern–process relationship finer than the grain of the data (Fig. 2.6). In practice grain and extent in landscape genetic studies are usually dictated by the available spatial data for a study area and the distribution of collected genetic samples. However, just as a mismatch of choice of what variables to measure or the thematic resolution at which to measure them can distort or mask the true ecological relationships, incorrect specification of grain and extent can strongly affect landscape genetic analyses (e.g., Anderson et al. 2010; Cushman & Landguth 2010; Short Bull et al. 2011), although improperly specified grain and extent may often have less influence in landscape genetic analysis than misspecification of thematic content and

resolution (McRae et al. 2008; Cushman & Landguth 2010; Koen et al. 2010). For example, Fig. 2.7 shows how predicted connectivity among a set of source points changes in a landscape as a function of changing grain of the map, holding extent, thematic content, and thematic resolution constant.

2.3.5 *A priori* hypotheses should guide landscape definition

Ideally, one would *a priori* develop a suite of hypotheses regarding the potential relationships between thematic content, thematic resolution, grain and extent, and the process under study. These topics are explored in more detail in Chapters 5 and 8 of this book. The relevant point here is that choices regarding thematic content and thematic resolution have a large influence on the strength and nature of observed relationships in landscape genetics research (e.g. Cushman & Landguth 2010; Shirk et al. 2010; Wasserman et al. 2010) and that great care must be taken to make appropriate choices as to what landscape features to include in an analysis and how to represent them in terms of thematic resolution and spatial scale. These choices should be guided by *a priori* knowledge of the process and targeted hypotheses about potential pattern–process relationships. One does not need to have perfect knowledge of the process in advance and sophisticated methods have been developed to explore large hypothesis spaces and seek optimized results (e.g., Shirk et al.

20 Basics of landscape ecology

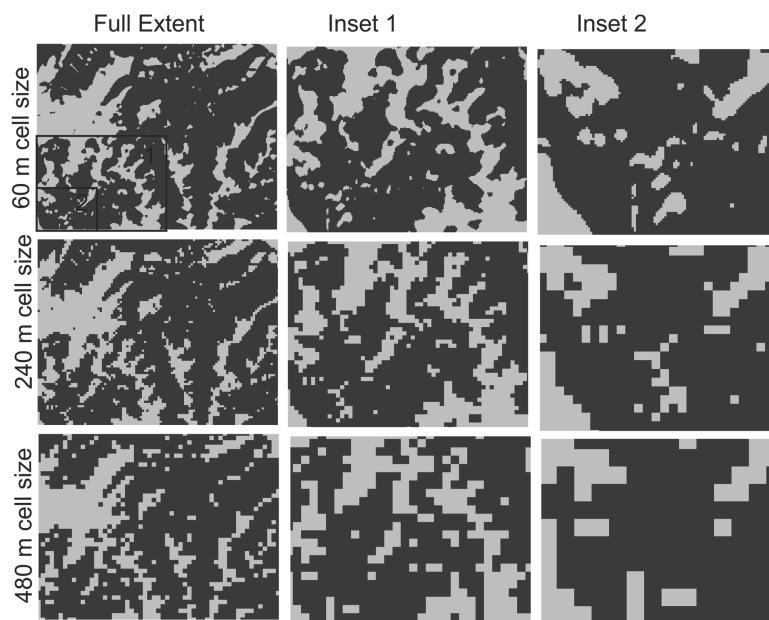


Fig. 2.6 Illustration of the effects of changing grain and extent on landscape composition. This figure shows a two-class mosaic of forest and non-forest (e.g., mosaic model, forest cover as thematic content, binary mapping of forest (black) and non-forest (gray) as thematic resolution). The effects of different grains are shown in the rows of the nine-panel figure, with 60 m cell size in the top row, 240 m cell size in the middle panel, and 480 m cell size in the bottom row. The effects of different extents are shown in columns of the figure, with a “full extent” shown in the first column and two lesser window extents shown in columns 2 (“inset 1”) and 3 (“inset 2”). The extents of these inset landscapes are shown in numbered boxes in the first panel. The changing patterns and extent of forest and non-forest across the panels show that landscape structure is highly sensitive to both the grain and extent of the analysis.

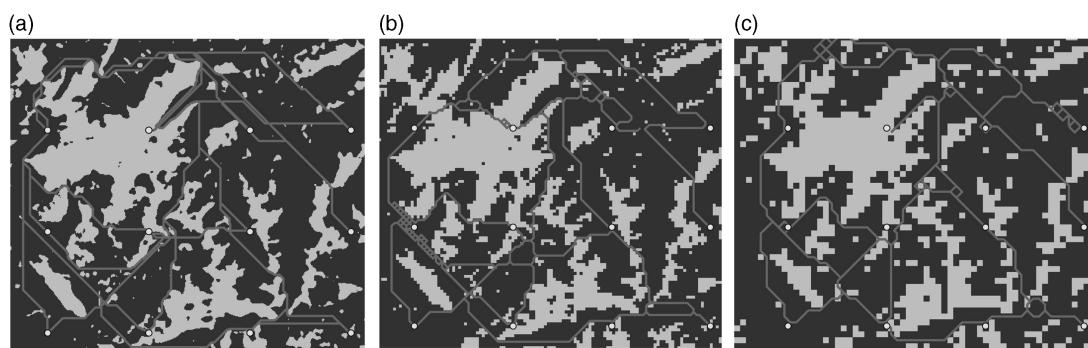


Fig. 2.7 Effect of changing the grain on predicted connectivity patterns. This figure shows how changing the grain of a two-class mosaic of forest and non-forest affects predicted connectivity among a network of individuals. Individuals are shown as points and the least-cost paths connecting all combinations of individuals are shown as lines. The routes and relative cost among pairs of individuals change as the grain of the landscape map changes. (For a color version of this figure, please refer to the color plates section.)

2010; Wasserman et al. 2010). However, care must be exercised in proposing what variables, what thematic resolution, and what scales to analyze.

2.4 DEFINING POPULATIONS AND CHARACTERIZING DISPERSAL PROCESSES

Equally important to correctly defining the thematic content, thematic resolution, and spatial scale of the landscape for analysis is delineating the populations under study and characterizing their dispersal processes. Population connectivity is the net result of three factors: (1) the structure and resistance of the landscape, (2) the distribution and density of the population, and (3) the dispersal of the organism under study (Cushman & Landguth 2012). Correctly defining the landscape enables the study to correctly address issue (1) above, but issues (2) and (3) are equally important. Distribution and density are important because if a population is uniformly spread and occurs at a high density then there will likely be high genetic connectivity and high internal rates of movement regardless of the structure of the landscape. Conversely, if the population is very fragmented in its distribution and occurs at low density then gene flow will be primarily driven by patterns of occurrence in the landscape. Similarly, if a species has very high dispersal ability and can move through a wide range of land cover types then landscape heterogeneity will have relatively less influence on movement and gene flow than for a species with limited dispersal ability (e.g., Bohanak 1999; Govindaraju 1988; Landguth et al. 2010a). In the sections below we will describe three important models of population structure and discuss their implications for gene flow processes and landscape genetic analyses.

2.4.1 Panmictic populations

Much of classical population genetics theory is based on an idealized model in which populations are assumed to be discretely bounded and internally panmictic. When there is no non-random mating, mutation, selection, random genetic drift, gene flow, or meiotic drive both allele and genotype frequencies in a population remain constant from generation to generation (Hartl & Clark 1997). All real populations are likely to violate one or more of these assumptions. The effects of this will

depend on which assumptions are violated. Non-random mating will result in deviations from Hardy–Weinberg proportions. A common cause of non-random mating is inbreeding, which causes an increase in homozygosity for all genes. Another cause is lack of panmixia driven by higher probability of mating with proximal individuals as a function of isolation-by-distance (IBD) or isolation-by-resistance. This is very commonly observed in landscape genetic studies. In addition, genetic migration provides genetic connectivity among two or more populations through long-distance dispersal. In general, genetic migration results in more homogeneous allele frequencies among the populations. In the presence of migration among populations Hardy–Weinberg proportions will normally not be observed. Third, genetic drift in small populations can cause random change in allele frequencies due to sampling effects. Genetic drift is not just an issue in small populations. In populations that are under strong isolation-by-distance or isolation-by-resistance, drift will tend to lead to relatively rapid loss of genetic diversity within local genetic neighborhoods (e.g., Wright 1943; Rousset 1997; Landguth et al. 2010a). In most real populations non-random mating, migration and drift have large influences on the genetic structure of the population and the discretely bounded, panmictic model of populations therefore is useful only as an ideal model with which to compare the real structure of populations. Several alternative models of population structure have been developed to more accurately reflect the effects of spatial structure of the landscape on non-random mating, migration, and drift.

2.4.2 Metapopulations

Metapopulations are literally populations of populations connected by dispersal (Levin 1974; Hanski & Gilpin 1991). Metapopulation theory has been formalized in a number of alternative models (Harrison 1991, 1994; Harrison & Taylor 1997), which largely differ in the rate and direction of individual movement among habitat patches. At its simplest, the theory holds that within each habitat patch the population has a finite probability of extinction, and likewise each patch has a particular colonization rate based on the number of occupied patches in the metapopulation (Fig. 2.8a). More sophisticated versions of the metapopulation concept involve spatially-explicit representation of the size, shape, and location of habitat patches, which allows for agent-based

22 Basics of landscape ecology

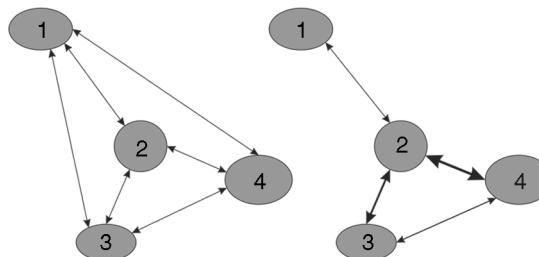


Fig. 2.8 Two depictions of metapopulation representation of a population structure. (a) A simple, spatially-unstructured metapopulation in which all populations are equally connected and exchange migrants at equal rates regardless of size and proximity. (b) A spatially-explicit metapopulation in which the expected rate of exchange among pairs of populations is a function of both population size and proximity. Arrows represent the rate of migration among pairs of populations. In (a) the arrows connect all pairs of populations and are all of equal “weight”, indicating an equal rate of exchange among all populations. In (b) arrows do not connect some populations that are farther apart than the maximum dispersal ability of the species (e.g. populations 1–3, 1–4), and the rate of exchange is highest between populations 2 and 4 because they are closest in proximity and because 4 is the largest population. Conversely, the rate of exchange between 1 and 2 is lowest because they are the pair of populations that is farthest apart and both populations are relatively small.

analysis of individual movement among patches to account for the effects of spatial structure of the landscape mosaic (Fig. 2.8b). In both versions of the metapopulation concept, populations in particular patches continually go extinct, but the metapopulation as a whole persists so long as the colonization rate is equal to the extinction rate. Metapopulations subject to high local extinction rates, but with correspondingly high rates of recolonization, have a high population turnover, but persist as long as the opposing rates are equal. Metapopulation dynamics reflect the rates of local extinctions and recolonizations as determined by interpatch movement and factors affecting these processes. Individual movement between patches is perhaps the most important defining feature of a metapopulation. The theory predicts that subdivision and isolation of populations caused by fragmentation can lead to reduced dispersal success and patch colonization rates, which may result in a decline in the persistence of the local populations and an enhanced probability of regional extinction for the entire metapopulation (e.g., Lande 1987; With & King 1999). Specifically, increased population isolation increases extinction risk by reducing demographic and genetic input from immigrants and reducing the chance of recolonization after extinction (Lande 1988; Schoener & Spiller 1992; Gulve 1994). In population and landscape genetics, metapopulation concepts of population structure are often represented by the island and stepping-stone models, in which local populations are assumed to be ideal, panmictic Wright–Fisher systems that are connected by dispersal among them.

2.4.3 Gradient populations

The metapopulation model essentially preserves the core characteristics of the ideal panmictic population model. Specifically, each of the subpopulations is generally considered to have no internal structure. That is, within a subpopulation mating is assumed to be random. The model essentially represents a network of ideal populations linked by migration. In many situations this model fails to reflect real population structure. For example, populations of many plants and animals cannot readily be delineated into “patches” that approximate ideal panmictic subpopulations. Often populations are continuously distributed across extensive areas, spanning distances far larger than the dispersal ability of the individuals within it. In such situations it is often impossible to define boundaries to delineate “subpopulations” and the extent of the population is such that the assumption of non-random mating will be grossly violated. In such cases it is better to adopt a “gradient” concept of population structure (e.g., Wright 1943; Endler 1973; Templeton 1981; Cushman et al. 2010; Wasserman et al. 2010).

Very often the probability of mating with any particular individual or dispersing to any particular destination is a function of the distance that individual or destination is from the subject. This is the essential characteristic of the concept of isolation-by-distance, that mating choices or dispersal destinations are related to distance (Wright 1943). In landscape genetics mating and dispersal are often influenced by the spatial

structure of the landscape, such that there is non-uniform probability of movement through different land cover types. In this case mating and dispersal probabilities will be affected by the intervening landscape between the origin and destination as embedded in the concept of landscape resistance (see Chapter 8).

Isolation-by-distance or isolation-by-resistance processes can create strong spatial genetic population structure as a result of non-random neighborhood mating, non-random dispersal, and elevated genetic drift in local genetic neighborhoods (e.g., Wright 1943; Endler 1973; Landguth et al. 2010b). One signature of this spatial genetic structure is the range of the genetic correlogram. A correlogram plots the correlation of one variable with itself as a function of the lag between the two observations. For example, in landscape genetics one might calculate the Mantel correlogram, showing the correlation of genetic distance among individuals as a function of the cost-distance between them (Borcard & Legendre 2012; Fig. 2.9).

The correlogram in Fig. 2.9 shows that the genetic distance between individuals increases as the cost distance between them increases, reflecting local non-random mating, and local dispersal. At short distances there is positive correlation between individuals, indicating that individuals that are separated by short cost distances are likely to be genetically similar, as a result of sharing a high proportion of alleles because

they reside in the same genetic neighborhood (Wright 1943). The correlogram shows that at longer cost distances the genetic correlation decreases to zero and then becomes negative. This negative correlation indicates that individuals separated by long cost distances (e.g., greater than ~60,000 in the correlogram shown in Fig. 2.9) are likely to be more genetically dissimilar than average across the full population, reflecting a low proportion of shared alleles because they reside in different genetic neighborhoods that do not directly exchange dispersers or mates.

These distance and cost-based processes result in populations that differ in many critical respects from either the classical panmictic model or the metapopulation model. In the panmictic model, any individual drawn from the population has the same probabilities of having any particular combination of alleles and degree of heterozygosity, as the population is assumed to be “well-mixed”. In contrast, in a gradient population the alleles an individual will carry and its heterozygosity are highly dependent on its location within the population (e.g. Wright 1943). The movement ability, behavior, and population density of the organism in interaction with the structure of landscape resistance will determine the strength and pattern of internal genetic structure. Importantly, this internal genetic structure is non-transitive. The transitive law of logic states that if object 1 has some relationship to 2 and 2

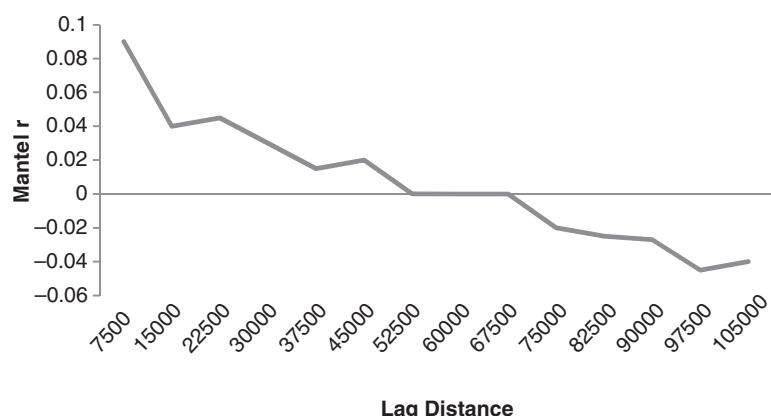


Fig. 2.9 Mantel correlogram showing the change in correlation between the genetic distance and cost distance. The *y* axis is the Mantel correlation among individuals and the *x* axis is the cost distance between them. The correlogram shows that at short cost distances (up to 45,000 cost units) there is significantly positive correlation, indicating that individuals tend to be genetically similar when they are separated by relatively small cost distances. Conversely, at cost distances beyond ~60,000 cost units the correlation is negative, indicating that individuals separated by large cost distances tend to be genetically dissimilar.

24 Basics of landscape ecology

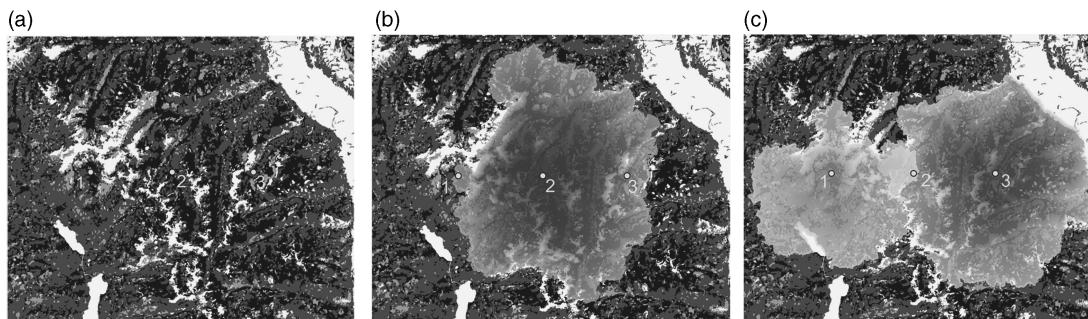


Fig. 2.10 Depiction of genetic neighborhoods in a continuously distributed population on a resistance surface. The gray-scale background is a landscape resistance model in which gene flow is facilitated by a mature closed canopy forest; the resistance increases as the forest cover becomes open and is highest in non-forest cover types. The three numbered yellow dots represent the locations of three individuals taken from a continuous population that is distributed across the map. The blue patch surrounding point 2 in (b) is a dispersal kernel that originates on the location of individual 2 and extends outward to a maximum of 20,000 cost units. If this species had a genetic neighborhood extent of 20,000 cost units, this blue patch would indicate the extent of the genetic neighborhood centered on the location of individual 2. Both individuals 1 and 3 are within this genetic neighborhood (e.g., they are both covered by the blue dispersal kernel originating at individual 2). However, given that the dispersal kernel value is higher (darker blue) at the location of individual 3 than at the location of individual 1 (which is right on the edge of the kernel), one would predict higher genetic similarity between individuals 2 and 3 than between individuals 2 and 1, if gene flow is governed by the landscape features depicted in the resistance surface. In (c) the genetic neighborhood extent (20,000 cost units) is shown surrounding each of individuals 1 and 3. These two neighborhood kernels both overlap individual 2, but they do not overlap each other. That is, the genetic neighborhood extent surrounding individual 1 does not include individual 3 and vice versa. This shows the non-transitive nature of continuously distributed populations governed by isolation-by-distance or resistance. The extent of a local population is a function of each location and there are often no discrete boundaries between genetic neighborhoods. (For a color version of this figure, please refer to the color plates section.)

has the same relationship to 3, then 1 and 3 share that relationship as well. This applies to panmictic populations, such that if individual 1 and 2 are in the same population and individual 2 and 3 are in the same population, then we can deduce that 1 and 3 are in the same population and all share the same probability profile for allelic composition and heterozygosity (e.g., Fig. 2.10a). However, in a gradient population this is not the case. One may choose to define local populations in the gradient concept by the extent of the local neighborhood of genetically correlated individuals (e.g., Epperson 1993). Figure 2.10b shows that individuals 1 and 3 are in the same local population as individual 2 based on this definition, as their local genetic neighborhood kernels overlap the location of individual 2. However, individuals 1 and 3 are not in the same genetic neighborhood and so by this definition they are not in the same local population (Fig. 2.10c). All three individuals could be expected to have non-random genetic differences from one another as a result of local non-random mating, dispersal, and drift.

2.5 PUTTING IT TOGETHER: COMBINATIONS OF LANDSCAPE AND POPULATION MODELS

Depending on the ecological system, study organism, and objectives of analysis, there are a large combination of different landscape models and population types that could be appropriate for a given landscape genetic study (Table 2.1). It is important to think carefully about designing landscape analysis *a priori* in ways that are appropriate given the study species, the nature of its population, and the type of population process under study. Table 2.1 delineates some of the common combinations of landscape model, spatial population model and population process model for landscape genetic studies of gene flow. For example, row 1 in Table 2.1 represents a landscape model of a classic, discrete, isolated, panmictic population in a homogeneous landscape. The second row adds the effect of spatial pattern to this model, in which habitat patches are connected to various degrees to a large mainland source population. This landscape model would be appropriate when

Putting it together: combinations of landscape and population models 25

Table 2.1 Conceptual overview of different models for representing landscapes, spatially structured populations, and gene flow. Note that all landscape models can include linear landscape features such as roads, rivers, etc., that might pose barriers to population connectivity and gene flow.

| Data type used for landscape model | Landscape model | Spatial population model | Gene flow model |
|---|--|--|---|
| Categorical: habitat–non-habitat | Single (isolated) habitat fragment/patch | Single (closed) population; classic population ecological model | Single, panmictic population |
| Categorical: habitat–non-habitat | Small “island” population connected by dispersal to large “mainland” population | Island–mainland | Island–mainland |
| Categorical: habitat–non-habitat | Multiple habitat patches imbedded within a matrix of homogeneous non-habitat | Multiple (sub)populations with varying degrees of connectivity, which are largely determined by size of patches and geographical distance among them; classic metapopulation model | Stepping-stone/ isolation-by-distance (IBD) among populations |
| Categorical: habitat–corridor–non-habitat | Multiple habitat patches imbedded within a matrix of homogeneous non-habitat, connected by habitat corridors | Multiple (sub)populations with varying degrees of connectivity, which are largely determined by presence/length of corridors among patches | Stepping-stone/ isolation-by-distance (IBD) among populations |
| Continuous/ categorical: habitat matrix | Multiple habitat patches imbedded within a heterogeneous matrix varying quality | Multiple (sub)populations with varying degrees of connectivity, which are largely determined by the quality of the heterogeneous matrix among patches | Isolation-by-resistance (IBR) among populations |
| Continuous: landscape gradient | Heterogeneous matrix of varying quality; discrete habitat patches cannot be delineated | Subpopulations cannot be delineated; continuously distributed individuals | Isolation-by-resistance (IBR) among individuals |

the study population exhibits an island–mainland structure, for example. The third row represents a situation where there is no clear mainland population and the species is distributed in a mosaic of subpopulation patches that are linked to various degrees by dispersal as functions of patch size and distance among them. In this situation a stepping-stone isolation-by-distance gene flow model would be appropriate. The fourth row is the same as the third, but with

the addition of corridors linking some of the subpopulations. The fifth row represents a situation where gene flow is affected by multiple habitat features, including perhaps a combination of categorical and continuous landscape variables, and connectivity among populations is determined by the cumulative cost of movement through this complex matrix. A population-level isolation-by-resistance model would be appropriate in this situation. The sixth row is like

26 Basics of landscape ecology

the fifth, except that subpopulations cannot be delineated among continuously distributed individuals, and an individual-based isolation-by-resistance framework is appropriate.

2.6 FRAMEWORKS FOR DELINEATING LANDSCAPES AND POPULATIONS FOR LANDSCAPE GENETICS

It should be clear from the previous sections that assessing the influences of landscape structure on adaptive evolution or gene flow involves complex processes involving many components. Some of the issues are conceptual and involve establishing clear objectives and perspectives on the hypothesized factors that influence these processes and the scales at which they operate. Other issues are technical and have significant implications for the computation and interpretation of measures of spatial structure of the landscape and its association with population genetic processes. A thorough understanding of these issues is prerequisite to the effective application of the protocol that follows. In this section, we present a five-step protocol for quantifying landscape structure for landscape genetic analysis (Fig. 2.11). The protocol presented is not a cookbook with precise step-by-step instructions. Rather, it is a general process outlining broad steps and important considerations. The details of the analysis, that is, the decisions made at each step in the process, must be tailored to the specific context of the application.

2.6.1 Step 1: establish analysis objectives

Ultimately, the analysis must be guided by well-formulated objectives. Thus, the first step is to establish the analysis objectives. In landscape genetics research we typically are interested in one or more of the following questions:

- What are the factors that drive gene flow in a population?
- What are the environmental factors that determine patterns of genetic diversity across the population?
- What are the environmental factors that are related to adaptive variation in a population?

The choice of which of these questions are of interest will have fundamental influence on the analytical

approaches that are appropriate (see Wagner & Fortin 2013; Chapter 5). Chapter 5 presents a detailed framework for selecting and implementing statistical modeling approaches depending on the objectives of a landscape genetic analysis. Equally important to proper selection of statistical methods, however, is proper definition and analysis of landscape structure.

2.6.2 Step 2: define the landscape

Once the analysis objectives have been established, the next step is to define the landscape in a manner that is relevant to the target species. This involves establishing the spatial extent of the analysis, establishing a model of the landscape structure (including choosing the thematic content and resolution), and establishing a relevant spatial grain and data model for the analysis.

Define the extent of the landscape

The first step in defining the landscape is to define the extent of the landscape and delineate its boundary. This is often a difficult task because the relevant ecological boundaries often do not correspond to the superimposed administrative and/or analysis boundaries. To the extent possible, the extent of the landscape should be meaningful ecologically given the scale at which the target population operates. For example, the local range of the focal species or of the local population or metapopulation may be suitable as the basis for delineating the landscape. In many cases, however, there will be other practical considerations that must be taken into account. For example, the landscape extent may have to correspond to particular administrative or ownership parcels given logistics or access. At a minimum, the scope and limitations of the analysis given these scaling considerations should be made explicit.

Establish a model of the landscape structure

The second step is to establish a digital model of the landscape structure. It is preferable that *a priori* ecological knowledge has guided the selection of the research subject and objectives for the analysis. For example, in landscape genetics, usually *a priori* hypotheses should focus on factors that are likely to drive gene flow or adaptive variation in the target species. It is critically important to establish a model of landscape structure that reflects these hypotheses and enables evaluation of

Frameworks for delineating landscapes and populations for landscape genetics 27

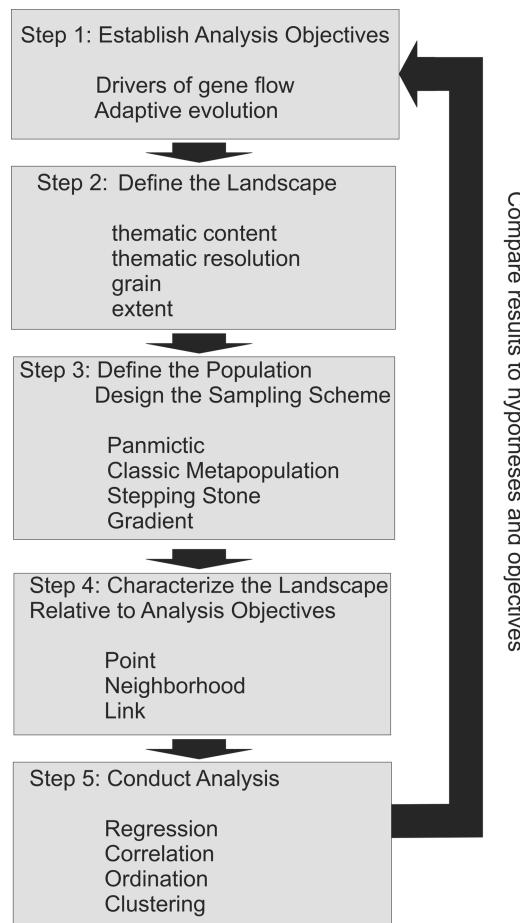


Fig. 2.11 Schematic of a five-step protocol for quantifying landscape structure for landscape genetic analysis. The first step is to establish the objectives of the analysis, such as identifying the drivers of gene flow or the landscape variables that drive selection and develop *a priori* hypotheses about how landscape features and patterns of these features may affect these processes. The second step is to define the landscape appropriately given the analysis objectives. This involves deciding on the thematic content, thematic resolution, grain and extent at which to represent the landscape variables identified in step 1 as potential drivers of the population process of interest. The third step is to define the structure of the study population and design and implement an appropriate sampling scheme to collect genetic data from that population. Different sampling designs are likely to be appropriate when the population is structured as a classic metapopulation, a stepping-stone spatially-structured metapopulation or a continuous gradient population. The fourth step is to characterize the structure of the landscape relative to the analysis objectives. The appropriate way to characterize landscape structure will depend on whether the objectives suggest point-, neighborhood-, or link-based analysis. For analysis of gene flow link-based analysis will generally be the most appropriate, in which the researcher quantifies the connectivity between each pair of sampled individuals or populations (such as the cumulative cost distance or current flow between them). For analyses of adaptive evolution, analysis will likely need to both consider link-based gene flow and point- or neighborhood-level effects of landscape composition on selection. The fifth step is to conduct the analysis associating genetic patterns to landscape patterns in a manner appropriate to address the proposed hypotheses. This is likely to involve regression, correlation, ordination, or clustering analyses. The final step is to compare the results of the analysis with the hypotheses and analysis objectives.

28 Basics of landscape ecology

a range of alternative hypotheses. Depending on the system, focal species, and study objectives a range of models of landscape structure could be appropriate, including linear networks, patch mosaics, or landscape gradients. In addition to correctly deciding whether a network, mosaic or gradient model of landscape structure is appropriate, it is important to carefully decide on the thematic content and resolution at which these features will be represented. This is a broad topic, the full treatment of which is beyond the scope of this chapter, and readers are referred to Chapter 8 for a more in-depth discussion of the process of defining landscape models relative to landscape genetics research. However, a few brief examples here will help illustrate some generally important concepts. If a patch mosaic model is chosen, it is important to decide on the features to be categorized (thematic content; e.g., vegetation cover, elevation classes, or land management designations) and the levels over which they will be categorized (thematic resolution; e.g., how many different classes of vegetation cover). Similarly, if a gradient model is selected to represent the landscape, one needs to decide what continuous environmental variables will be included in the analysis (thematic content; e.g., elevation gradient, precipitation gradient, or canopy cover gradient), and the functional form of relationships hypothesized between these gradients and the response variable (thematic resolution; e.g., linear, unimodal, or logarithmic).

Establish a relevant grain of analysis

The last step in defining the landscape is to define a relevant grain (or minimum mapping unit) and digital data model. In some cases, these decisions will be guided by technical considerations owing to the source of the data and the data processing software available. In most cases, a raster data model will be desirable. Additionally, the grain of the data should represent a balance between the desire for accurate calculations of landscape composition and configuration, computational efficiency, and the desire to scale patterns appropriately for the chosen landscape extent. On the one hand, the grain should be kept as fine as possible to ensure that small and narrow, yet meaningful, features of the landscape are preserved in the data model. On the other hand, the grain should be increased in relation to the extent so that unnecessary detail is not confounded with the important coarse-scale patterns over large spatial extents.

2.6.3 Step 3: define the population and design the sampling scheme

Once the landscape has been defined relative to objectives, it is important to give equal consideration to the distribution and structure of the study population and to decide how genetic data should be sampled from that population to obtain reliable inferences about relationships between population genetic processes and landscape structure (Chapter 4). There are several important considerations in this step. First, the pattern of population distribution and extent will have large impacts on the genetic processes at play and their interaction with landscape structure. It is important to have reliable knowledge about the extent and distribution of the population. It is particularly important to evaluate whether the study area encompasses an entire population or whether the population extends beyond the boundaries. It is ideal to select a study area of sufficient extent that it encloses a closed population, which allows for more rigorous assessment of population genetic conditions and avoids the edge and boundary effects. However, in most real world landscape genetics studies subject populations extend often far beyond the limits of the study area that can be sampled. It is important to think carefully about the implications of this for the sampling design, analysis approach, and interpretation of results. It is also important to consider whether the population consists of continuously distributed individuals, a territorial mosaic, or local subpopulations linked by dispersal in a metapopulation. These different “population structures” will have a direct influence on the population genetic processes and their interactions with landscape structure, and it is important to think carefully *a priori* about what these are and how they may affect the processes in question, and thus what sampling and analytical approaches are appropriate. Finally, once the extent and structure of the population have been considered, it is important to design an appropriate sampling scheme to collect spatially-referenced genetic data. Spatially-referenced genetic data are the response variable for landscape genetic analysis, and meaningful results are fundamentally dependent on the sampling scheme used for collecting these genetic data. The complex decision process for designing a sampling scheme is beyond the scope of this chapter, and we refer readers to Chapter 4 for details. However, given the importance of this topic we make a few recommendations. First, the appropriate sampling design will depend on both the

landscape model selected (and the thematic content, thematic resolution, grain, and extent) and the population structure present (continuous or metapopulation). The sampling scheme will also depend on whether the objectives are to identify the factors that control neutral gene flow, identify the environmental variables driving adaptive evolution, or both. For example, if the study is intended to identify the factors driving gene flow in a continuous population, and one hypothesizes that gradients in elevation drive landscape resistance to movement, it might be wise to develop a sampling strategy that ensures that a large number of individuals are sampled across the study area, with spatial stratification to ensure equal representation of locations across the elevation gradient. Conversely, if the goal is to identify the environmental variables that drive adaptive evolution in a metapopulation, a suitable sampling strategy might be to sample some number (perhaps 20–30) individuals in each of a large number of subpopulations that vary across the environmental gradients hypothesized to provide selection pressure.

2.6.4 Step 4: characterize the landscape relative to analysis objectives

Once the landscape has been defined, the population structure described, and the locations of genetic samples selected, it is necessary to analyze the structure of the landscape relative to the locations of the genetic samples in a manner that is appropriate given the objectives of the project. This analysis will provide the independent (predictor) variables for the analysis, and thus is a critically important part of developing the data set for any landscape genetics project. Depending on the study species, ecological system, and research objective, the pertinent measurements are likely to be node-based, neighborhood-based, or link-based (Wagner & Fortin 2013; Chapter 5). When the objectives of the research are to identify the factors that drive neutral gene flow then generally link-based measures of landscape structure will be appropriate (Wagner & Fortin 2013; Chapter 5). Link-based analyses are based on the landscape attributes that lie between sampling points, rather than the characteristics of the points themselves. This is the appropriate framework for analyses of gene flow because gene flow is governed by the connectivity of the landscape *between* points rather than the attributes of the landscape *at* points. There are a large number of methods commonly used to calculate relevant variables

for link-based analyses, most of which are based on the concepts of cost distance (Adriansen et al. 2003) or circuit theory (McRae 2006). When the objective is related to gene flow neighborhood-based measures of landscape structure may be relevant. For example, instead of basing the analysis on pairwise cost distances among points, an analysis could predict genetic differentiation based on the connectivity of the local neighborhood using measures such as centrality (Estrada & Bodin 2008), patch connectivity indices developed in metapopulation ecology (Moilanen & Hanski 2006), and gravity models (Murphy et al. 2010). In such situations the landscape analysis would involve calculating the relevant neighborhood connectivity metric given the structure and composition of the landscape surrounding each of the sampled locations. When the analysis objective involves identifying relationships between adaptive variation and environmental gradients, the analytical framework will usually be based on point and neighborhood analysis of landscape conditions. This is because when an environmental feature drives directional selection of certain alleles we would expect the frequency of those alleles in any local population to be related to the environmental conditions at or around that site. Relevant landscape analyses to develop variables for an analysis of this kind of question might include sampling of the environmental variable at the sampled location, or perhaps the mean and variability of that environmental variable within differing neighborhood extents surrounding that location. In addition, in some situations the spatial pattern of environmental features may influence the strength and direction of selection. In such cases, calculating landscape pattern metrics (McGarigal et al. 2002) for variables represented as patch mosaics and surface metrics (McGarigal & Cushman 2005; McGarigal et al. 2009) within differing neighborhood extents surrounding the sampled sites may also be important, depending on the hypotheses being tested.

2.6.5 Step 5: conduct analysis

The final step in the analysis is to conduct statistical modeling to associate the genetic structure among the sampled locations to the environmental conditions in the landscape at, around, or between those locations. The methods available to analyze these pattern–process relationships are beyond the scope of this chapter, and we refer the readers to Chapter 5 for presentation of a synthetic framework to guide selection and

30 Basics of landscape ecology

implementation of statistical analysis in landscape genetics. The point we want to raise here is that the success of any analytical methods applied to landscape genetic data will fundamentally depend on correct decisions made in each of the four steps described above. Meaningful objectives and clear *a priori* hypotheses must guide careful delineation of landscape extent, thematic content, thematic resolution and grain of analysis, which must be followed by appropriate sampling design to collect genetic data (response variables) and spatial analysis to characterize the landscape structure at, around, or between those sampling locations (predictor variables) in a manner that provides a robust data set for analysis.

2.7 CURRENT CHALLENGES AND FUTURE OPPORTUNITIES

In addition to the inherent challenge of correctly matching data collection, landscape definition, and analyses, there are several issues that pose particular current challenges, as well as future opportunities, in landscape genetics research. One of the most challenging tasks in landscape genetic analysis is to resolve the potential difficulties posed by time lags and past population histories. Many methods currently used in landscape genetics are based on associating genetic differences among populations or individuals with the structure of the landscape at, around, or between those locations. There are several apparent problems related to temporal scale in this effort, such as time lags for the genetic structure of the population to respond to landscape changes (e.g., ghosts of landscape past; Landguth et al. 2010b). Also, different population histories, especially patterns of range expansion or contraction from previous refugia, can create genetic patterns in the current landscape that may mimic the effects of isolation-by-distance and resistance, or directional selection along environmental gradients.

There are a number of analytical challenges that have yet to be resolved which complicate analysis of pattern–process relationships in landscape genetics. For example, this chapter focused on the sensitivity of landscape genetic analysis to thematic content, resolution, grain, and extent of the landscape, but it remains a challenge to decide how to best represent different landscape variables. We argued that *a priori* knowledge should guide these decisions, but often there is insufficient knowledge to make informed choices. A

number of efforts have been made to develop predictions of optimal or functional grain, thematic content and thematic resolution (e.g., based on simulations, see Chapter 6) and to develop modeling frameworks that enable the evaluation of a large number of competing hypotheses (e.g., Shirk et al. 2010; Chapter 5).

One of the greatest challenges and opportunities for landscape genetics is the development of theories and methods to study adaptive evolution in complex spatial environments. In adaptive landscape genetics it is not just the landscape extent between locations that matters, but also the local environment (e.g., Wagner & Fortin 2013). Selection is expected to be driven by local or neighborhood environmental conditions, while the effects of this selection will only be expressed as measurable genetic differentiation when gene flow is sufficiently restricted (such as in isolated subpopulations or along gradients of isolation-by-distance or isolation-by-barriers (IBB); e.g., Neimiller et al. 2008; Nosil et al. 2008; Yang et al. 2013). Understanding how to combine the effects of selection and gene flow in complex landscapes remains an area of nascent study with much additional work to be done. Thus far, simulation modeling (e.g., Chapter 6) has provided the strongest framework for exploring spatially dependent selection in its interaction with gene flow in affecting adaptive evolution of populations (e.g., Landguth & Balkenhol 2012; Landguth et al. 2012).

The review and protocol presented in this chapter suggest that correctly delineating and analyzing landscape heterogeneity for a given landscape genetic question is not a trivial matter. In many past applications researchers have not carefully considered thematic content, thematic resolution, grain, and extent of their landscape model prior to analysis. Too often researchers take the spatial data that are available without considering the implications the scale and content of those data have for analysis. Our most important message in this chapter is for researchers to carefully tailor genetic sampling, landscape definition, and analysis to the question, system, and organism under study. We hope that the concepts and protocol proposed in this chapter will facilitate this.

REFERENCES

- Adriansen, F., Chardon, J.P., De Blust, G., Swinnen, E., Gulnick, H., & Matthysen, E. (2003) The application of “least-cost” modeling as a functional landscape model. *Landscape and Urban Planning* **64**, 223–47.

- Alverson, W., Waller, D.M., & Solheim, S.L. (1988) Forests too deer: edge effects in northern Wisconsin. *Conservation Biology* **2**, 348–58.
- Anderson, C.D., Epperson, B.K., Fortin, M.J., Holderegger, R., James, P., Rosenberg, M.S., & Spear, S. (2010) Considering spatial and temporal scale in landscape-genetic studies of gene flow. *Molecular Ecology* **19**, 3565–75.
- Baker, W.L. & Dillon, G.K. (2000) Plant and vegetation responses to edges in the southern Rocky Mountains. In Knight, R.L., Smith, R.W., Buskirk, S.W., Romme, W.H., & Baker, W.L. (ed.), *Forest Fragmentation in the Southern Rocky Mountains*. University Press of Colorado, Boulder.
- Bélisle, M., Desrochers, A., & Fortin, M.J. (2001) Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* **82**, 1893–904.
- Bender, D.J., Contreras, T.A., & Fahrig, L. (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* **79**, 517–33.
- Bender, D.J., Tischendorf, L., & Fahrig, L. (2003) Evaluation of patch isolation metrics for predicting animal movement in binary landscapes. *Landscape Ecology* **18**, 17–39.
- Bergin, T.M., Best, L.B., Freemark, K.E., & Koehler, K.J. (2000) Effects of landscape structure on nest predation in roadsides of a midwestern agroecosystem: a multiscale analysis. *Landscape Ecology* **15**, 131–43.
- Bohonak, A.J. (1999) Dispersal, gene flow and population structure. *Quarterly Review of Biology* **44**, 21–45.
- Borcard, D. & Legendre, P. (2012) Is the Mantel correlogram powerful enough to be useful in ecological analysis? A simulation study. *Ecology* **93**, 1473–81.
- Bormann, F.H., Likens, G.E., Siccamo, T.C., Pierce, R.S., & Eaton J.S. (1974) The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. *Ecological Monographs* **44**, 255–77.
- Brittingham, M.C. & Temple, S.A. (1983) Have cowbirds caused forest songbirds to decline? *BioScience* **33**, 31–5.
- Carlson, A. & Hartman, G. (2001) Tropical forest fragmentation and nest predation – an experimental study in an Eastern Arc montane forest, Tanzania. *Biodiversity and Conservation* **10**, 1077–85.
- Charlesworth, D. & Charlesworth, B. (1987) Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* **18**, 237–68.
- Chasko, G.G. & Gates, J.E. (1982) Avian habitat suitability along a transmission line corridor in an oak-hickory forest region. *Wildlife Monographs* **82**, 1–41.
- Chen, J., Franklin, J.F., & Spies, T.A. (1992) Vegetation response to edge environments in old-growth Douglas-fir forests. *Ecological Applications* **2**, 387–96.
- Cushman, S.A. & Landguth, E.L. (2010) Scale dependent inference in landscape genetics. *Landscape Ecology* **25**, 967–79.
- Cushman, S.A. & Landguth, E.L. (2012) Multi-taxa population connectivity in the Northern Rocky Mountains. *Ecological Modeling* **231**, 101–12.
- Cushman, S.A., McKelvey, K.S., Hayden, J., & Schwartz, M.K. (2006) Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. *The American Naturalist* **168**, 486–99.
- Dale, V.H., O'Neill, R.V., Southworth, F., & Pedlowski, M. (1994) Modeling effects of land management in the Brazilian Amazonia settlement of Rondonia. *Conservation Biology* **8**, 196–206.
- Debinski, D.M. & Holt, R.D. (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology* **14**, 342–55.
- de Casenave, J.L., Pelotto, J.P., & Protomastro, J. (1995) Edge-interior differences in vegetation structure and composition in a chaco semiarid forest, Argentina. *Forest Ecology and Management* **72**, 61–9.
- Donovan, T.M. & Flather, C.H. (2002) Relationships among North American songbird trends, habitat fragmentation and landscape occupancy. *Ecological Applications* **12**, 364–74.
- Endler, J.A. (1973) Gene flow and population differentiation studies of clines suggest that differentiation along environmental gradients may be independent of gene flow. *Science* **179**, 243–50.
- Epperson, B.K. (1993) Recent advances in correlation studies of spatial patterns of genetic variation. In: Hecht, M.K., MacIntyre, R.J., & Clegg, M.T. (eds.), *Evolutionary Biology*. Springer.
- Estrada, E. & Bodin, Ö. (2008) Using network centrality measures to manage landscape connectivity. *Ecological Applications* **18**, 1810–25.
- Fahrig, L. (2002) Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecological Applications* **12**, 346–53.
- Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics*, pp. 487–515.
- Findlay, C.S. & Houlahan, J. (1997) Anthropogenic correlates of species richness in southeastern Ontario wetlands. *Conservation Biology* **11**, 1000–9.
- Flather, C.H. & Bevers, M. (2002) Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *The American Naturalist* **159**, 40–56.
- Franklin, J.F. & Forman, R.T.T. (1987) Creating landscape configuration by forest cutting: ecological consequences and principles. *Landscape Ecology* **1**, 5–18.
- Ganzhorn, J.U. & Eisenbeiß, B. (2001) The concept of nested species assemblages and its utility for understanding effects of habitat fragmentation. *Basic and Applied Ecology* **2**, 87–99.
- Gates, J.E. & Mosher, J.A. (1981) A functional approach to estimating habitat edge width for birds. *The American Midland Naturalist* **105**, 189–192.
- Geiger, R. (1965) *The Climate near the Ground*. Harvard University Press, Cambridge, MA.

32 Basics of landscape ecology

- Gibbs, J.P. & Stanton, E.J. (2001) Habitat fragmentation and arthropod community change: carrion beetles, phoretic mites and flies. *Ecological Applications* **11**, 79–85.
- Govindaraju, D.R. (1988) Relationship between dispersal ability and levels of gene flow in plants *Oikos* **52**, 31–5.
- Grace, J. (1977) *Plant Response to Wind*. Academic Press, London.
- Grace, J. (1983) *Plant–Atmosphere Relationships: Outline of Studies in Ecology*. Chapman & Hall, London.
- Gulve, P.S. (1994) Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. *Ecology* **75**, 1357–67.
- Haines-Young, R., Green, D.R., & Cousins, S.H. (eds.) (2003) *Landscape Ecology and Geographical Information Systems*. CRC Press, London.
- Hanski, I. & Gilpin, M. (1991) Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**, 3–16.
- Harrison, S. (1991) Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society* **42**, 73–88.
- Harrison, S. (1994) Metapopulations and conservation. In: Edwards, P.J., May, R.M., & Webb, N.R. (eds.), *Large-Scale Ecology and Conservation Biology*. Blackwell, Oxford.
- Harrison, S. & Taylor, A.D. (1997) Empirical evidence for metapopulation dynamics. In: Hanski, I.A. & Gilpin, M.E. (eds.), *Metapopulation Biology: Ecology, Genetics and Evolution*. Academic Press, San Diego, CA.
- Hartl, D.L. & Clark, A.G. (1997) *Principles of Population Genetics*. Sinauer associates Inc., Sunderland.
- Hill, M.F. & Caswell, H. (1999) Habitat fragmentation and extinction thresholds on fractal landscapes. *Ecology Letters* **2**, 121–7.
- Hornbeck, J.W. (1973) Storm flow from hardwood-forested and cleared watersheds in New Hampshire. *Water Resources Research* **9**, 346–54.
- Johnson, A.R., Wiens, J.A., Milne, B.T., & Crist, T.O. (1992) Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology* **7**, 63–75.
- Kapos, V. (1989) Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology* **5**, 173–85.
- Kareiva, P. (1987) Habitat fragmentation and the stability of predator–prey interactions. *Nature* **326**, 388–90.
- Kareiva, P. & Wennergren, U. (1995) Connecting landscape patterns to ecosystem and population processes. *Nature* **373**, 299–302.
- King, A.W. & With, K.A. (2002) Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? *Ecological Modeling* **147**, 23–39.
- Koen, E.L., Garroway, C.J., Wilson, P.J., & Bowman, J. (2010) The effect of map boundary on estimates of landscape resistance to animal movement. *PLoS One* **5**, e11785.
- Kolozsvary, M.B. & Swihart, R.K. (1999) Habitat fragmentation and the distribution of amphibians: patch and landscape correlates in farmland. *Canadian Journal of Zoology* **77**, 1288–99.
- Kremsater, L. & Bunnell, F.L. (1999) Edge effects: theory, evidence and implications to management of western North American forests. In: Rochelle, J.A., Lehmann, L.A., & Wiesniewski, J. (eds.), *Forest Fragmentation: Wildlife and Management Implications*. Brill, Leiden, The Netherlands, pp. 117–53.
- Kroodsma, R.L. (1982) Edge effect on breeding forest birds along a power-line corridor. *Journal of Applied Ecology* **19**, 361–70.
- Kurki, S., Nikula, A., Helle, P., & Linden, H. (2000) Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology* **81**, 1985–97.
- Lande, R. (1987) Extinction thresholds in demographic models of territorial populations. *The American Naturalist* **130**, 624–35.
- Lande, R. (1988) Genetics and demography in biological conservation. *Science* **241**, 1455–60.
- Landguth, E.L. & Balkenhol, N. (2012) Relative sensitivity of neutral versus adaptive genetic data for assessing population differentiation. *Conservation Genetics* **13**, 1421–6.
- Landguth, E.L., Cushman, S.A., Murphy, M.A., & Luikart, G. (2010a) Relationships between migration rates and landscape resistance assessed using individual-based simulations. *Molecular Ecology Resources* **10**, 854–62.
- Landguth, E.L., Cushman, S.A., Schwartz, M.K., McKelvey, K.S., Murphy, M., & Luikart, G. (2010b) Quantifying the lag time to detect barriers in landscape genetics. *Molecular Ecology* **19**, 4179–91.
- Landguth, E.L., Cushman, S.A., & Johnson, N.A. (2012) Simulating natural selection in landscape genetics. *Molecular Ecology Resources* **12**, 363–8.
- Laurance, W.F., Pérez-Salícrup, D., Delamônica, P., Fearnside, P.M., D'Angelo, S., Jerozolinski, A., Pohl, L., & Lovejoy, T.E. (2001) Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* **82**, 105–16.
- Leopold, A. (1933) *Game Management*. Charles Scribners, New York.
- Levin, S.A. (1974) Dispersion and population interactions. *The American Naturalist* **108**, 207–28.
- Levin, S.A. (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* **73**, 1943–67.
- Likens, G.E., Bormann, F.H., Johnson, N.M., Fisher, D.W., & Pierce, R.S. (1970) Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. *Ecological Monographs* **40**, 23–47.
- Lovejoy, T.E., Bierregaard, R.O. Jr., Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown, K.S. Jr., Powell, A.H., Powell, G.V.N., Schubart, H.O.R., & Hays, M.B. (1986) Edge and other effects of isolation on Amazon forest fragments. In Soule, M.E. (ed.), *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates Inc., Massachusetts.

- Mahan, C.G. & Yahner, R.H. (2000) Effects of forest fragmentation on behaviour patterns in the eastern chipmunk (*Tamias striatus*). *Canadian Journal of Zoology* **77**, 1991–7.
- Manel, S., Schwartz, M.K., Luikart, G., & Taberlet, P. (2003) Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology and Evolution* **18**, 189–97.
- Mangel, M. & Clark, C.W. (1986) Towards a unified foraging theory. *Ecology* **67**, 1127–38.
- Marsh, D.M. & Trenham, P.C. (2001) Metapopulation dynamics and amphibian conservation. *Conservation Biology* **15**, 40–9.
- Marsh, D.M., Thakur, K.A., Bulka, K.C., & Clark, L.B. (2004) Dispersal and colonization through open fields by a terrestrial, woodland salamander. *Ecology* **85**, 3396–405.
- McCoy, E.D. & Mushinsky, H.R. (1999) Habitat fragmentation and the abundances of vertebrates in the Florida scrub. *Ecology* **80**, 2526–38.
- McGarigal, K. & Cushman, S.A. (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* **12**, 335–45.
- McGarigal, K. & Cushman, S.A. (2005) *The Gradient Concept of Landscape Structure. Issues and Perspectives in Landscape Ecology*. Cambridge University Press, Cambridge.
- McGarigal, K., Cushman, S.A., Neel, M.C., & Ene, E. (2002) FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps [Online]. Available at: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.
- McGarigal, K., Tagil, S., & Cushman, S.A. (2009) Surface metrics: an alternative to patch metrics for the quantification of landscape structure. *Landscape Ecology* **24**, 433–50.
- McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* **14**, 450–3.
- McRae, B.H. (2006) Isolation by resistance. *Evolution* **60**, 1551–61.
- McRae, B.H., Dickson, B.G., Keitt, T.H., & Shah, V.B. (2008) Using circuit theory to model connectivity in ecology, evolution and conservation. *Ecology* **89**, 2712–24.
- Mills, L.S. (1995) Edge effects and isolation: red-backed voles on forest remnants. *Conservation Biology* **9**, 395–403.
- Moen, A.N. (1974) Turbulence and visualization of wind flow. *Ecology* **55**, 1420–4.
- Moilanen, A. & Hanski, I. (2006) Connectivity and metapopulation dynamics in highly fragmented landscapes. In Crooks, K.R. & Sanjayan, M. (Eds.), *Connectivity Conservation*. Cambridge University Press, Cambridge, UK.
- Monteith, J.L. (1975) *Vegetation and the Atmosphere*. Academic Press, London.
- Mooney, H.A. & Hobbs, R.J. (eds.) (2000) *Invasive Species in a Changing World*. Island Press, Washington.
- Murphy, M.A., Evans, J.S., & Storfer, A. (2010) Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology* **91**, 252–61.
- Neimiller, M.L., Fitzpatrick, B.M., & Miller, B.T. (2008) Recent divergence with gene flow in Tennessee cave salamanders (Plethodontidae: *Gyrinophylus*) inferred from gene genealogies. *Molecular Ecology* **17**, 2258–75.
- Nosil, P. (2008) Speciation with gene flow could be common. *Molecular Ecology* **17**, 2103–6.
- Pearson, S.M., Turner, M.G., Gardner, R.H., and O'Neill, R.V. (1996) An organism-based perspective of habitat fragmentation. In: Szaro, R.C. and Johnston, D.W. (eds.), *Biodiversity in Managed Landscapes: Theory and Practice*. Oxford University Press, New York.
- Pickett, S.T.A. & Cadenasso, M.L. (1995) Landscape ecology: spatial heterogeneity in ecological systems. *Science* **269**, 331–4.
- Ranney, J.W., Bruner, M.C., & Levenson, J.B. (1981) The importance of edge in the structure and dynamics of forest islands. In Burgess, R.L. & Sharpe, D.M. (eds.), *Forest Island Dynamics in Man-Dominated Landscapes*. Springer-Verlag, New York.
- Robbins, C.S., Dawson, D.K., & Dowell, B.A. (1989) Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildlife Monographs* **103**, 1–34.
- Rothermel, B.B. & Semlitsch, R.D. (2002) An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibian. *Conservation Biology* **16**, 1324–32.
- Rousset, F. (1997) Genetic differentiation and estimation of gene flow from F-statistics under isolation-by-distance. *Genetics* **145**, 1219–28.
- Rukke, B.A. (2000) Effects of habitat fragmentation: increased isolation and reduced habitat size reduces the incidence of dead wood fungi beetles in a fragmented forest landscape. *Ecography* **23**, 492–502.
- Sánchez-Zapata, J. & Calvo, J.F. (1999) Raptor distribution in relation to landscape composition in semi-arid Mediterranean habitats. *Journal of Applied Ecology* **36**, 254–62.
- Saunders, D., Hobbs, R.J., & Margules, C.R. (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5**, 18–32.
- Schmiegelow, F.K. & Mönkkönen, M. (2002) Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecological Applications* **12**, 375–89.
- Schoener, T.W. & Spiller, D.A. (1992) Stabilimenta characteristics of the spider *Argiope argentata* on small islands – support of the predator-defense hypothesis. *Behavioral Ecology and Sociobiology* **31**, 309–18.
- Segelbacher, G., Cushman, S.A., Epperson, B.K., Fortin, M.J., Francois, O., Hardy, D.J., Holderegger, R., Taberlet, P., Waits, L.P., & Manel, S. (2010) Applications of landscape genetics in conservation biology: concepts and challenges. *Conservation Genetics* **11**, 375–85.
- Shirk, A.J., Wallin, D.O., Cushman, S.A., Rice, C.G., & Warheit, K.I. (2010) Inferring landscape effects on gene flow: a new model selection framework. *Molecular Ecology* **19**, 3603–19.

34 Basics of landscape ecology

- Short Bull, R.A., Cushman, S.A., Mace, R., Chilton, T., Kendall, K.C., Landguth, E.L., Schwartz, M.K., McKelvey, K., Allen-dorf, F.W., & Luikart, G. (2011) Why replication is important in landscape genetics: American black bear in the Rocky Mountains. *Molecular Ecology* **20**, 1092–107.
- Sklar, F.H. & Costanza, R. (1991) The development of dynamic spatial models for landscape ecology: a review and prognosis. In: Turner, M.G. & Gardner, R.H. (eds.), *Quantitative Methods in Landscape Ecology: The Analysis and Interpretation of Landscape Heterogeneity*. Springer-Verlag.
- Spear, S.F., Balkenhol, N., Fortin, M.J., McRae, B.H., & Scribner, K.I.M. (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Molecular Ecology* **19**, 3576–91.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., & Tscharntke, T. (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* **83**, 1421–32.
- Strelke, W.K. & Dickson, J.G. (1980) Effect of forest clearcut edge on breeding birds in Texas. *Journal of Wildlife Management* **44**, 559–67.
- Tansley, A.G. (1935) The use and abuse of vegetational concepts and terms. *Ecology* **16**, 284–307.
- Templeton, A.R. (1981) Mechanisms of speciation – a population genetic approach. *Annual Review of Ecology and Systematics* **12**, 23–48.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., & Williams, S.E. (2004) Extinction risk from climate change. *Nature* **427**, 145–8.
- Tischendorf, L., Bender, D.L., & Fahrig, L. (2003) Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecology* **18**, 41–50.
- Tranquillini, W. (1979) *Physiological Ecology of the Alpine Timberline*. Springer-Verlag, Berlin.
- Turner, M.G. (ed.) (1987) *Landscape Heterogeneity and Disturbance*. Springer-Verlag.
- Turner, M.G. (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* **20**, 171–97.
- Turner, M.G. (2005) Landscape ecology: what is the state of the science?. *Annual Review of Ecology, Evolution, and Systematics* 319–44.
- Turner, M.G., Gardner, R.H., & O'Neill, R.V. (2001) *Landscape Ecology in Theory and Practice: Pattern and Process*. Springer.
- Vallan, D. (2000) Influence of forest fragmentation on amphibian diversity in the nature reserve of Ambohitantely, highland Madagascar. *Biological Conservation* **96**, 31–43.
- Vance, M.D., Fahrig, L., & Flather, C.H. (2003) Effect of reproductive rate on minimum habitat requirements of forest-breeding birds. *Ecology* **84**, 2643–53.
- Virgos, E. (2001) Role of isolation and habitat quality in shaping species abundance: a test with bayers (*Meles meles* L.) in a gradient of forest fragmentation. *Journal of Biogeography* **28**, 381–9.
- Wagner, H.H. & Fortin, M.J. (2013) A conceptual framework for the spatial analysis of landscape genetic data. *Conservation Genetics* **14**, 253–61.
- Wales, B.A. (1972) Vegetation analysis of north and south edges in a mature oak-hickory forest. *Ecological Monographs* **42**, 451–71.
- Wasserman, T.N., Cushman, S.A., Schwartz, M.K., & Wallin, D.O. (2010) Spatial scaling and multi-model inference in landscape genetics: *Martes americana* in northern Idaho. *Landscape Ecology* **25**, 1601–12.
- Watt, A.S. (1947) Pattern and process in the plant community. *Journal of Ecology* **35**, 1–22.
- Wegner, J.F. & Merriam, G. (1979) Movements by birds and small mammals between a wood and adjoining farmland habitats. *Journal of Applied Ecology* **16**, 349–57.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology* **3**, 385–97.
- Wiens, J.A. (1992) What is landscape ecology, really? *Landscape Ecology* **7**, 149–50.
- Wiens, J.A., Crawford, C.S., & Gosz, J.R. (1985) Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* **45**, 421–7.
- Wiens, J.A., Stenseth, N.C., van Horne, B., & Ims, R.A. (1993) Ecological mechanisms and landscape ecology. *Oikos* **66**, 369–80.
- With, K.A. & Crist, T.O. (1995) Critical thresholds in species' responses to landscape structure. *Ecology* **76**, 2446–59.
- With, K.A. & King, A.W. (1999) Extinction thresholds for species in fractal landscapes. *Conservation Biology* **13**, 314–26.
- With, K.A., Gardner, R.H., & Turner, M.G. (1997) Landscape connectivity and population distributions in heterogeneous environments. *Oikos* **78**, 151–69.
- Wright, S. (1943) Isolation-by-distance. *Genetics* **28**, 114–38.
- Yahner, R.H. (1986) Microhabitat use by small mammals in even-aged forest stands. *The American Midland Naturalist* **115**, 174–80.
- Yang, J., Cushman, S.A., Yang, J., Yang, M., & Bao, T. (2013) Effects of climatic gradients on genetic differentiation of *Caragana* in the Ordos Plateau, China. *Landscape Ecology* **28**, 1729–41.
- Zen, M.C. (1995) Growth and morphological development of Douglas-fir and western hemlock on forest edges in the Alberni Valley. MSc thesis, University of Washington, Seattle, WA.