Chapter 12

APPLICATIONS OF LANDSCAPE GENETICS TO CONNECTIVITY RESEARCH IN TERRESTRIAL ANIMALS

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12.1 INTRODUCTION

This chapter focuses on applications of landscape genetics for understanding connectivity of terrestrial animal populations. We start with a general introduction covering unique characteristics and challenges of the terrestrial study system, followed by an overview of common research questions addressed in terrestrial animals using neutral markers in landscape genetics. These common research questions include detecting and defining barriers, identifying corridors, examining source-sink dynamics, and detecting and predicting animal responses to environmental change. Based on this overview, we highlight limitations of current research approaches and present case studies that have specifically dealt with some of these limitations when testing ecological hypotheses about gene flow in heterogeneous landscapes. Finally, we end the chapter with future directions and current knowledge gaps for terrestrial animal landscape genetic studies.

12.2 GENERAL OVERVIEW OF TERRESTRIAL ANIMAL STUDY SYSTEMS AND RESEARCH CHALLENGES

Landscape genetic studies have focused on terrestrial animals more than any other taxonomic group (Storfer et al. 2010). This is not surprising given the inclusion of “land” in the name of the discipline and the usefulness of landscape genetics as a method to infer animal movement, a key process in ecology and conservation. Many aspects of landscape genetic studies are well
suited for applications related to terrestrial animals. Landscape genetics usually requires a model of the continuous environment, and such GIS models are most widely available for terrestrial systems (Chapter 2). This has allowed for a more realistic representation of the heterogeneity present in terrestrial landscapes, whereas it is much more difficult to represent the heterogeneity in aquatic systems using typical remote sensing methods. The ability to incorporate existing GIS data into studies of animal population connectivity has benefited researchers greatly. In addition, landscape genetics has enabled effective research on animals that are secretive or difficult to study using traditional mark-recapture or radio telemetry methods (e.g., Schwartz et al. 2009). Furthermore, landscape genetic studies provide some of the best case studies of how contemporary habitat alteration is affecting population processes such as connectivity in terrestrial species, ranging from insects (e.g., Keyghobadi et al. 2005a), amphibians (e.g., Funk et al. 2005; Murphy et al. 2010a, 2010b; Spear et al. 2012), reptiles (e.g., Stow et al. 2001; Clark et al. 2010), birds (e.g., Pavlacky et al. 2009), and mammals (e.g., Epps et al. 2005; Vignieri et al. 2005; Wasserman et al. 2012).

12.2.1 Comparison of terrestrial animal studies with other systems

Landscape genetics research focused on terrestrial animals has a number of unique aspects compared to aquatic systems or terrestrial plant species. The terrestrial landscape can be depicted as a combination of linear elements, mosaics of categorical patch types (Forman 1995), and gradients of continuously varying ecological factors (McGarigal and Cushman 2005; Chapter 2). The patterns of these factors interact with organism behavior to affect population processes, such as mating and dispersal. The functional connectivity of a landscape depends on how the pattern of the environment interacts with behavioral responses and movement abilities of the species to drive population processes.

Terrestrial systems are generally depicted as two-dimensional patterns, which is in contrast to many marine and lacustrine systems, in which hydrodynamic fluxes occur in three dimensions, and riverine systems, which are often depicted as networks of one-dimensional links. This in principle can make analysis of terrestrial landscapes simpler than marine systems and more complicated than riverine networks, simply as a function of the dimensionality of the pattern–process relationships. Temporal dynamics also are very different between typical terrestrial and aquatic systems. Functional connectivity in terrestrial environments is often more constrained, occurs at a finer scale, and changes at a slower rate than connectivity across marine environments (Carr et al. 2003; also see Chapter 13). In many ways, this can make it easier to develop strong statistical models in terrestrial landscape genetic studies if sufficient spatial data are available, as the scale of sampling is more likely to match the scale of the gene flow process. In contrast, studies of seascape genetics often have detected very little genetic structure across broad areas (Selkoe et al. 2010; Schunter et al. 2011), due in part to the combination of long-distance transport of gametes and larva by currents and temporal dynamics that are rapid relative to population turnover. In the terrestrial system, the dynamics of landscape change are generally slower than population processes, enabling the effects of landscape change to be recorded in changes in the genetic structure of populations. However, in many instances rates of change in terrestrial landscapes exceeds the equilibration time of population genetic processes, requiring non-equilibrium methods to analyze current rates of gene flow.

The vast scales, high-frequency dynamics, and typically immense numbers of gametes and larva in marine systems create processes that are essentially “large number problems” in the sense of statistical mechanics and the Boltzmann equation (Boltzmann 1872), in which the overall statistical behavior of the entire system is highly predictable as the outcome of millions of microscale interactions. Terrestrial systems, however, are more often in the range of “middle number problems”, where there are often too many interacting individuals and entities to effectively model the mechanistic interactions of the entire system, but too few to average away the individual interactions in a statistical mechanics approach, and dynamics are too slow to collapse them as “noise” and too frequent to ignore and model as a static system. As a result, terrestrial landscape genetic analysis is often a “complex systems” problem, in which researchers attempt to reduce complexity by adopting spatially-explicit approaches to represent the location, movement, and interactions of individuals within populations as functions of the spatial structure of the landscape. This presents a number of conceptual and technical challenges for analysis. For instance, a researcher using resistance modeling (see Chapter 8) typically has to parameterize a multivariate resistance surface in a terrestrial system, whereas following oceanographic currents or stream lengths may be sufficient in an aquatic system (although many aquatic systems do
have multiple environmental influences; Chapter 13). Finally, the slower rate of change in functional connectivity in the terrestrial environment introduces the challenge of accounting for temporal lags.

Animals and plants also differ with respect to landscape influence on genetic structure in several ways (also see Chapter 11). The most obvious difference is that individual plants are stationary whereas animals are mobile. The second major difference is that gene flow in terrestrial animals occurs through the transport of gametes by the individual, whereas movement of gametes in plants typically occurs independent of the individual plant through seed and pollen. Therefore, modeling plant gene flow might require a simultaneously modeling of both gametes. On the other hand, the field of adaptive landscape genetics is much more amenable to plants due to their sessile nature (see Chapter 9).

### 12.2.2 Methodological and study design challenges often faced by terrestrial researchers

An important methodological issue that is often faced by researchers investigating landscape genetics of terrestrial animals is whether to sample an individual or population level (see Chapter 2). Historically, population-level sampling was typical due to its compatibility with population genetic theory, and because groups of individuals could often be tied to discrete terrestrial units, such as ponds or forest patches. However, many species do not occur in discrete population clusters and analysis at the individual level may be more appropriate because artificially imposing clusters may bias results (Schwartz & McElvee 2009). Recent simulation and empirical work has also shown that population-based analysis may be replaced by individual-based analyses for organisms with patchy distributions, which can allow researchers to increase the number of patches sampled (Prunier et al. 2013). The choice of an individual or population level of analysis has important implications for sampling design and data analysis (Chapter 2 and Chapter 3). The number of terrestrial animal studies using individual-based analyses is increasing since this sampling approach provides a more comprehensive coverage of the landscape and thus better captures landscape heterogeneity. Another important consideration and challenge in sampling design is obtaining a balanced sample of male and female individuals. Multiple studies have demonstrated that habitat use and dispersal patterns can differ by sex and that the more philopatric sex is often more strongly affected by land conversion, roads, and other forms of habitat fragmentation (e.g., Stow et al. 2001; Proctor et al. 2005; Amos et al. 2014; Paquette et al. 2014; Elliot et al. 2014a, 2014b).

The complex, often indirect, relationship of animal movement with gene flow is another challenge (Bohonak 1999). Animal movement occurs for multiple reasons, many of which are not related to gene flow. Thus, models used to account for landscape influence in a genetic study must recognize that only a subset of movements are relevant when using empirical movement data to identify key landscape variables (see Chapter 8). Furthermore, genetic data may not always be appropriate to direct conservation actions such as movement corridors if the types of movement the actions need to facilitate are not tied to mating or reproduction (i.e., migration). These concerns highlight the importance of understanding the study system and conducting landscape genetic studies with well-designed objectives that can investigate multiple processes.

When analyses are based on individuals, another challenge in many terrestrial animal studies is the fact that most animal species are not stationary, so that the location where an animal is sampled may not represent typical movements or actual places where genetic exchange has occurred (Graves et al. 2012). Thus, locations of genetic samples obtained for terrestrial animals are usually associated with a higher degree of spatial uncertainty than sampling locations for plants. Uncertainty in sampling locations is of the greatest concern in highly heterogeneous landscapes in which organisms might be briefly located or drawn to suboptimal habitats, a challenge that is particularly relevant for wide-ranging species such as large mammals. A simulation study in a binary landscape concluded that, in most cases, location uncertainty was unlikely to significantly alter landscape genetic results (Graves et al. 2012). Of course, the impacts of all of these issues are dependent on the scale of sampling, and on the spatial distribution and dispersal capabilities of the species under study. This is discussed in more detail elsewhere (see Chapter 2), but is an important consideration in many of the case studies we highlight.

### 12.2.3 Research focus of current studies

Most landscape genetic studies of terrestrial animals have focused on assessing the influence of landscape permeability on gene flow using neutral loci. Understanding landscape effects on movement and gene flow
is crucial in ecology, evolution, and conservation, and landscape genetic approaches are particularly well suited for understanding effective dispersal (Broquet & Petit 2009; Baguette et al. 2013). Consequently, typical landscape genetics research questions for connectivity of terrestrial animals include detecting barriers, identifying corridors, examining population dynamics, and predicting the response to environmental change. In the following sections, we present an overview of representative studies that have addressed these broad questions. We chose not to conduct a metareview of all landscape genetic papers, as was done in Storfer et al. (2010), but instead highlight examples across multiple taxonomic groups of terrestrial animals.

12.3 DETECTING BARRIERS AND DEFINING CORRIDORS

12.3.1 Detecting barriers

The detection of landscape barriers using population genetic data has been a long-standing goal in landscape genetics (Storfer et al. 2007, 2010). Multiple studies have evaluated the effectiveness of different methodological approaches for detecting barriers (Landguth et al. 2010; Safner et al. 2011; Blair et al. 2012) including traditional population genetic metrics (Chapter 3), clustering and assignment methods (Chapter 7), and boundary detection methods (Chapter 3). The most powerful and accurate methods detected in these simulation studies were Bayesian clustering methods (Safner et al. 2011; Blair et al. 2012) and Mantel tests of individual-based genetic distance (Landguth et al. 2010). Overall, these methods were particularly successful when effective population size was low, the species had limited vagility, and the barrier had restricted gene flow for multiple generations.

Landscape genetic studies of terrestrial wildlife have identified a number of both natural and anthropogenic barriers to movement and gene flow (Table 12.1). Across taxonomic groups of species, rivers have frequently been identified as a barrier (Blanchong et al. 2008; Côté et al. 2012; Lugon-Moulin & Haussser 2002; Coulon et al. 2006; Mockford et al. 2007; Cullingham et al. 2009; Robinson et al. 2012). Major ridgelines have been identified as barriers to gene flow in amphibians (Funk et al. 2005; Murphy et al. 2010b), snakes (Manier and Arnold 2006), turtles (Mockford et al. 2007) and small mammals (Zalewski et al. 2009). Conversion of grasslands and forest to agriculture and grazing has been identified as a barrier to gene flow for insects (Marchi et al. 2013), birds (Lindsay

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<th>Unit of analysis*</th>
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<tbody>
<tr>
<td>Banks et al. (2005)</td>
<td>Antechinus agilis</td>
<td>ind, pop</td>
<td>Pine plantations barrier to gene flow</td>
</tr>
<tr>
<td>Blanchong et al. (2008)</td>
<td>Odocoileus virginianus</td>
<td>pop</td>
<td>River was barrier to gene flow</td>
</tr>
<tr>
<td>Bush et al. (2011)</td>
<td>Centrocercus urophasianus</td>
<td>ind</td>
<td>River and agricultural region were barriers to gene flow</td>
</tr>
<tr>
<td>Carmichael et al. (2007)</td>
<td>Canis lupus</td>
<td>ind, pop</td>
<td>Genetic structure was explained by differences in habitat types</td>
</tr>
<tr>
<td>Côté et al. (2012)</td>
<td>Procyon lotor</td>
<td>pop, ind</td>
<td>River was partial barrier to gene flow</td>
</tr>
<tr>
<td>Coulon et al. (2006)</td>
<td>Capreolus capreolus</td>
<td>ind</td>
<td>Region with canals, highway, and river restricted gene flow</td>
</tr>
<tr>
<td>Cullingham et al. (2009)</td>
<td>Procyon lotor</td>
<td>ind</td>
<td>Rivers are barrier to gene flow and restricts spread of rabies</td>
</tr>
<tr>
<td>Cushman &amp; Lewis (2010)</td>
<td>Ursus americanus</td>
<td>ind</td>
<td>Development, roads, and low forest cover restricted movements</td>
</tr>
<tr>
<td>Epps et al. (2005)</td>
<td>Ovis canadensis nelsoni</td>
<td>pop</td>
<td>Highways, canals and developed areas act as barriers to gene flow</td>
</tr>
<tr>
<td>Funk et al. (2005)</td>
<td>Rana luteiventris</td>
<td>pop</td>
<td>Ridgelines and elevational differences were barriers to gene flow</td>
</tr>
</tbody>
</table>
et al. 2008; Bush et al. 2011), amphibians and reptiles (Stow et al. 2001; Johansson et al. 2005; Row et al. 2010), and mammals (Banks et al. 2005; Paquette et al. 2014). Unsuitable natural habitat can also be a significant barrier to gene flow and movement. For example, dry grassland habitat has been shown to fragment salamander populations (Rittenhouse & Semlitsch 2006), and savanna habitats can fragment lemur populations that depend on forested habitat (Radespiel et al. 2008). Anthropogenic landscape features such as roads and other human development have been identified as barriers across several taxonomic groups,

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<tbody>
<tr>
<td>Geffen et al. (2004)</td>
<td>Canis lupus</td>
<td>pop</td>
<td>Differences in climate and habitat type restrict gene flow</td>
</tr>
<tr>
<td>Johansson et al. (2005)</td>
<td>Rana temporaria</td>
<td>pop</td>
<td>Agricultural fields were barrier to gene flow.</td>
</tr>
<tr>
<td>Kuehn et al. (2007)</td>
<td>Capreolus capreolus</td>
<td>pop</td>
<td>Transportation network barrier to gene flow</td>
</tr>
<tr>
<td>Lindsay et al. (2008)</td>
<td>Dendroica chrysoparia</td>
<td>pop</td>
<td>Agricultural lands were barrier to gene flow.</td>
</tr>
<tr>
<td>Marier &amp; Arnold (2006)</td>
<td>Anaxyrus boreas, Thamnophis elegans, Thamnophis sirtalis</td>
<td>pop</td>
<td>Escarpment was barrier for T. elegans and T. sirtalis</td>
</tr>
<tr>
<td>Marchi et al. (2013)</td>
<td>Bembidion lampros</td>
<td>pop</td>
<td>Agricultural fields were barrier to gene flow</td>
</tr>
<tr>
<td>Mockford et al. (2007)</td>
<td>Emydoidea blandingii</td>
<td>pop</td>
<td>Mountains and rivers are the strongest barriers to gene flow</td>
</tr>
<tr>
<td>Murphy et al. (2010)</td>
<td>Rana luteiventris</td>
<td>pop</td>
<td>Gene flow restricted with increased topographic complexity</td>
</tr>
<tr>
<td>Paquette et al. (2014)</td>
<td>Procyon lotor</td>
<td>ind</td>
<td>Agricultural fields were barrier to gene flow for females.</td>
</tr>
<tr>
<td>Perez-Espona et al. (2008)</td>
<td>Cervus elaphus</td>
<td>pop</td>
<td>Greatest barrier was sea lochs and roads, while mountain slopes and forests also restricted gene flow</td>
</tr>
<tr>
<td>Proctor et al. (2005)</td>
<td>Ursus arctos</td>
<td>ind, pop</td>
<td>Highway and associated development barrier to gene flow</td>
</tr>
<tr>
<td>Radespiel et al. (2008)</td>
<td>Microcebus ravelobensis</td>
<td>ind, pop</td>
<td>Open savannah and a major road was a barrier</td>
</tr>
<tr>
<td>Riley et al. (2006)</td>
<td>Canis latrans, Lynx rufus Odocoileus virginianus</td>
<td>ind, pop</td>
<td>Highway barrier to gene flow in both species</td>
</tr>
<tr>
<td>Robinson et al. (2012, 2013)</td>
<td></td>
<td>ind</td>
<td>Highways and rivers restrict movement of Odocoileus virginianus and spread of chronic wasting disease</td>
</tr>
<tr>
<td>Row et al. (2010)</td>
<td>Mintoinus gloydi</td>
<td>ind, pop</td>
<td>Agricultural lands were barrier to gene flow</td>
</tr>
<tr>
<td>Sacks et al. (2004)</td>
<td>Canis latrans</td>
<td>ind</td>
<td>Genetic structure was explained by difference in habitat types</td>
</tr>
<tr>
<td>Stow et al. (2001)</td>
<td>Egeria cunninghami</td>
<td>ind, pop</td>
<td>Forests cleared for grazing were a barrier to gene flow, with females more strongly affected than males</td>
</tr>
<tr>
<td>van der Wal et al. (2012)</td>
<td>Cervus canadensis</td>
<td>ind</td>
<td>Roads were a barrier to gene flow</td>
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<tr>
<td>Wasserman et al. (2010)</td>
<td>Martes americana</td>
<td>ind</td>
<td>Genetic structure was explained by elevation and hypothesized to relate to differences in vegetation and snowpack.</td>
</tr>
<tr>
<td>Zalewski et al. (2009)</td>
<td>Neovison vison</td>
<td>ind, pop</td>
<td>Mountain range was barrier to gene flow</td>
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*ind, individual; pop, population.
including carnivores (Proctor et al. 2005; Riley et al. 2006; Cushman & Lewis 2010), ungulates (Epps et al. 2005; Coulon et al. 2006; Kuehn et al. 2007; Perez-Espona et al. 2008; Robinson et al. 2012) and amphibians (Murphy et al. 2010a). For example, highways were found to be the principle factor driving genetic differentiation in a population of mountain goats (Shirk et al. 2010).

In addition, climate gradients and habitat differences have been shown to be cryptic barriers to gene flow possibly because of species’ environmental tolerance limits or natal imprinting (Sacks et al. 2004; Geffen et al. 2004; Carmichael et al. 2007; Wasserman et al. 2010). Cryptic climatic and habitat barriers are of elevated importance because of the difficulty in observing them and the likelihood that global scale changes in climatic and land cover will lead to major shifts in how these factors affect species distribution, abundance, genetic diversity and gene flow (e.g. Wasserman et al. 2012, 2013).

The identification of barriers to gene flow can also provide important information for the management of invasive species and disease in the terrestrial environment (Storfer et al. 2007, 2010; Segelbacher et al. 2010). Landscape genetic models can help predict the geographic nature of disease spread and barriers can quarantine disease within a limited geographic area (Rees et al. 2008; Biek & Real 2010). For example, highways have been shown to restrict the spread of chronic wasting disease in white-tailed deer (Odocoileus virginianus; Robinson et al. 2012, 2013) and the spread of bovine tuberculosis in elk (Cervus Canadensis; van der Wal et al. 2012). Rivers have been documented as barriers to the spread of chronic wasting disease in white-tailed deer (Blanchong et al. 2008; Robinson et al. 2013) and rabies in raccoons (Cullingham et al. 2009; Côté et al. 2012; Paquette et al. 2014).

### Evaluating and designing corridors

One important, but relatively rare, application of landscape genetic methods is to evaluate the effectiveness of current corridors (Table 12.2). In an early examination

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<tr>
<td>Angelone &amp; Holderegger (2009)</td>
<td><em>Hyla arborea</em></td>
<td>population</td>
<td>Conservation measures have increased connectivity of breeding ponds within valleys, although one valley had greater connectivity</td>
</tr>
<tr>
<td>Braunisch et al. (2010)</td>
<td><em>Tetrao urugallus</em></td>
<td>individual</td>
<td>Used landscape genetic associations to design corridors based on groups of “MLP” paths</td>
</tr>
<tr>
<td>Cushman et al. (2009, 2013)</td>
<td><em>Ursus americanus</em></td>
<td>individual</td>
<td>Mapped potential corridors using a genetically optimized resistance surface</td>
</tr>
<tr>
<td>Dixon et al. (2006)</td>
<td><em>Ursus americanus</em></td>
<td>individual</td>
<td>Population assignments indicated asymmetric migration between two main patches</td>
</tr>
<tr>
<td>Epps et al. (2007)</td>
<td><em>Ovis canadensis</em></td>
<td>population</td>
<td>Incorporation of slope and anthropogenic barriers allow modeling of dispersal corridors that matched genetic migration estimates</td>
</tr>
<tr>
<td>Mech &amp; Hallett (2001)</td>
<td><em>Clethrionomys gapperi</em>, <em>Peromyscus maniculatus</em></td>
<td>population</td>
<td>For <em>C. gapperi</em>, highest genetic distance in isolated sites, intermediate in sites connected by corridors, and lowest in continuous forest. No difference for <em>P. maniculatus</em></td>
</tr>
<tr>
<td>Paetkau et al. (2009)</td>
<td><em>Rattus fuscipes</em>, <em>Rattus leucopus</em></td>
<td>individual</td>
<td>Use and occupation of the corridor was higher for <em>Rattus fuscipes</em> than for <em>Rattus leucopus</em> and movements were asymmetrical</td>
</tr>
<tr>
<td>Wells et al. (2009)</td>
<td><em>Junonia coenia</em></td>
<td>population</td>
<td>Higher genetic diversity and lower <em>F</em>&lt;sub&gt;st&lt;/sub&gt; in connected patches</td>
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of the effectiveness of forest corridors for small mammals, Mech and Hallett (2001) evaluated the genetic connectivity of red-backed vole (*Clethrionomys gapperi*) and deer mouse (*Peromyscus maniculatus*) populations in continuous forest, isolated forest patches, and forest patches connected by forested corridors. They found that genetic distance increased from smallest to largest in contiguous, corridor, and isolated landscapes for the red-backed vole, a closed-canopy specialist, but genetic distances for the deer mouse, a habitat generalist, were not significantly different across treatments. Dixon et al. (2006) used non-invasive genetic sampling of black bears to obtain microsatellite genotypes that could be used to evaluate the effectiveness of a regional corridor in Florida. Using assignment test approaches (Chapter 7), they demonstrated that dispersal and gene flow were occurring primarily south to north within the corridor. A similar approach was used to evaluate whether a newly established corridor in Australia was being utilized by two native small mammals, the bush rat (*Rattus fuscipes*) and the Cape York rat (*Rattus leucopus*) and revealed that use of the corridor was higher for the bush rat than for Cape York rat (Paetkau et al. 2009).

In a study of the declining European tree frog (*Hyla arborea*) in Switzerland, Angelone and Holderegger (2009) evaluated the effectiveness of conservation efforts to establish stepping stones of habitat (i.e., ponds) to provide structural and functional connectivity. The application of assignment test approaches indicated that dispersal and gene flow was occurring among the newly established ponds and establishing a network of interconnected populations. Genetic approaches have also been used to demonstrate the effectiveness of corridors for maintaining genetic diversity, gene flow, and fitness in an open-habitat specialist butterfly, *Junonia coenia* (Wells et al. 2009).

Many review papers have highlighted the potential of landscape genetic methods for designing corridors (Storfer et al. 2007, 2010; Segelbacher et al. 2010; Sork & Waits 2010), but relatively few empirical studies have been conducted (Table 12.2). A study of desert bighorn sheep (*Ovis canadensis nelsoni*) was one of the first to test the effectiveness of different least-cost GIS models and to identify dispersal corridors using the best-fitting models (Epps et al. 2005, 2007). Similar approaches were used to identify optimal corridor regions for black bears (*Ursus americanus*; Cushman et al. 2009, 2013), American marten (*Martes americana*; Wasserman et al. 2013), and wolverine (*Gulo gulo*) in the northern Rocky Mountains of the United States (Schwartz et al. 2009). Another good example of landscape genetic approaches for defining corridors is the work of Braunisch et al. (2010) to quantify landscape permeability for capercaillie in the Black Forest of Germany. The authors calculated pairwise relatedness for 213 individuals and found that relatedness was positively correlated with the proportion of coniferous and mixed forest and negatively correlated to forest edges, roads, settlements, and agricultural land. The authors then used this information to identify the location of corridors crucial to preserving connectivity among habitat patches.

### 12.4 Evaluating Population Dynamics

Understanding source-sink dynamics (Pulliam 1988) and the impact of habitat quality on production and attraction of migrants is important in corridor and reserve design. Landscape genetic approaches have good potential for identifying source and sink habitats by identifying asymmetric gene flow with coalescent approaches (Beerli & Felsenstein 2001) and assignment tests (Paetkau et al. 1995; Wilson & Rannala 2003; Faubet & Gaggiotti 2008; Holderegger & Gugerli 2012). For example, Andreasen et al. (2012) used Bayesian clustering (Chen et al. 2007) and Bayesian assignment test (Faubet & Gaggiotti 2008) approaches to evaluate genetic structure and source-sink dynamics of cougars (*Puma concolor*) in the Great Basin Desert. They detected five populations (south, west, north, east, and central) with asymmetric levels of gene flow, which indicated that the south population was a source while the east, west, and north populations were sinks. The east, west, and north populations had higher levels of hunting and human disturbance while the source area of the south had multiple wildlife refuges and low hunting pressure (Andreasen et al. 2012).

Graph theoretic approaches (Chapter 10) also show great potential for evaluating the importance of individual core areas or nodes to the population viability and connectivity of populations. Using this network-based approach, Garroway et al. (2008) evaluated the influence of landscape characteristics on genetic connectivity and subpopulation level productivity among fisher (*Martes pennantii*) subpopulations sampled from 34 habitat patches in Canada. Fishers in this region were characterized by a higher level of clustering than expected by
chance and a short mean path length connecting all pairs of nodes. Nodes with high value for maintaining connectedness in the system were identified and nodes with the greatest snow depth (and thus lower quality habitat) showed less connectedness in the network. These results supported previous work showing that fishers exhibit short dispersal distances, are territorial, and relatively philopatric (Kyle et al. 2001; Koen et al. 2007). From a conservation perspective, this research demonstrated that there was much resiliency to the loss of nodes in the network and suggested that current harvest regimes are unlikely to affect genetic connectivity or induce genetic differentiation.

12.5 DETECTING AND PREDICTING THE RESPONSE TO LANDSCAPE CHANGE

Landscape genetics approaches are useful for examining how landscape change has influenced genetic connectivity and how connectivity might change in response to future landscape change (Table 12.3). Long-term viability of populations can be investigated by assessing temporal changes in population genetic structure and genetic diversity that reflect the ability of populations to persist and evolve in response to future changing environments (Frankham et al. 2010; Allendorf et al. 2012). Furthermore, genetic structure is influenced by processes that occur over multiple generations and thus can be used to understand the importance of both historic and contemporary conditions, especially if genetic markers are used that mutate at different rates (see Chapter 3). The other requirements for such an analysis are representations of landscapes from at least two different time points, either a past landscape or a future predicted condition. Thus, there have been two different types of studies investigating landscape change with genetic markers: a retrospective approach in which genetic structure is correlated with both present and past landscape representations and a future predictive approach in which simulations are used to extrapolate current correlations to future landscape change. A third possibility is a “space for time approach” in which

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<tr>
<td>Holzhauer et al. (2006)</td>
<td>Metrioptera roeseli</td>
<td>individual</td>
<td>Landscape patterns from 50 years ago explained genetic structure better than current patterns</td>
</tr>
<tr>
<td>Keyghobadi et al. (2005a, 2005b)</td>
<td>Parnassius smintheus</td>
<td>population</td>
<td>Genetic differentiation correlated with contemporary landscape, but genetic diversity correlated with past landscape</td>
</tr>
<tr>
<td>Murphy et al. (2010a)</td>
<td>Anaxyrus boreas</td>
<td>population</td>
<td>Genetic connectivity partially associated with recent fires</td>
</tr>
<tr>
<td>Pavlacky et al. (2009)</td>
<td>Orthonyx temmincki</td>
<td>population</td>
<td>A slightly stronger relationship with contemporary rather than historic landscape; results differed when using different metrics of genetic differentiation</td>
</tr>
<tr>
<td>Spear &amp; Storfer (2008)</td>
<td>Ascaphus trupei</td>
<td>population</td>
<td>Timber harvest patterns from 20–40 years were correlated with current estimates of genetic distance</td>
</tr>
<tr>
<td>Spear et al. (2005)</td>
<td>Ambystoma tigrinum</td>
<td>population</td>
<td>Significant correlation of increased gene flow with recently burned forest; suggest fires facilitate connectivity</td>
</tr>
<tr>
<td>Spear et al. (2012)</td>
<td>Ascaphus trupei</td>
<td>population</td>
<td>Gene flow among populations in portions of the volcanic zone subject to logging and reforestation more constrained by climatic factors than those in unmanaged area</td>
</tr>
<tr>
<td>Wasserman et al. (2012, 2013)</td>
<td>Martes americana</td>
<td>individual</td>
<td>Climate change scenarios predicted a loss of habitat correlated with genetic connectivity</td>
</tr>
</tbody>
</table>
detecting and predicting the response to landscape change

landscapes reflecting different conditions at the same time point are compared, but these scenarios are less ideal due to confounding differences between landscapes (McGarigal & Cushman 2002; Short Bull et al. 2011).

It has long been recognized that different aspects of genetic structure can change at different temporal rates (Crow & Aoki 1984), but Keyghobadi et al. (2005b) was one of the first to explicitly address this using landscape genetic methodology. This study used seven microsatellite loci developed for an alpine butterfly (Parnassius mintheus) to compare landscape correlations with genetic differentiation and genetic diversity in the Rocky Mountains of Alberta, Canada. The authors used aerial photography to assess landscape conditions in 1952 and 1993 to examine historic and contemporary configurations of meadow and forest. They applied a metric of patch connectivity of both meadows and forests (accounting for dispersal through these two habitat types) as the landscape measure to correlate with aspects of genetic structure. They represented genetic diversity through expected heterozygosity \( H_e \) and genetic differentiation with \( G_{ST} \) (see Chapter 3 for detailed descriptions of these measures). Heterozygosity had a stronger correlation with the historic landscape, whereas \( G_{ST} \) had a greater correlation with the contemporary landscape, suggesting that measures of genetic differentiation may be more appropriate tests of contemporary landscape change. Similarly, Zellmer and Knowles (2009) detected a significant association of \( F_{ST} \) with contemporary landscape resistance in a wood frog metapopulation after controlling for historic landscapes, but found no association with historic landscapes after controlling for contemporary resistance. However, other studies have demonstrated that patterns of genetic differentiation can have a temporal lag effect. For instance, Holzhauer et al. (2006) studied bush-crickets (Metrioptera roeseli) in a rural grassland district of Germany and found that genetic similarity was correlated best with landscape configurations 30–50 years before the study, and that the strength of correlation steadily decreased with more recent landscape configurations. Similarly, Spear and Storfer (2008) found a 20–40 year time lag with a timber harvest date on the Olympic Peninsula of Washington and coastal tailed frog (Asaphus truei) genetic differentiation based on 13 microsatellite loci.

An alternative approach for incorporating landscape change through time is to represent genetic connectivity as different metrics that change at different temporal scales. The advantage of this approach is that it allows the researcher to test the relative influence of historic and recent genetic connectivity. For instance, Pavlacky et al. (2009) studied logrunner (Orthonyx temminckii) connectivity in an Australian subtropical rainforest that had become fragmented due to European colonization. The authors used two types of genetic analysis based on 10 microsatellite loci: a traditional measure of \( F_{ST} \) and an estimate of migration using the coalescent approach. Based on \( F_{ST} \) analyses, there was similar support for historic and recent landscape composition, although the historic landscape had a slightly higher correlation with forest cover and patch density. In contrast, coalescent estimates of migration had a stronger correlation with the contemporary, fragmented landscape, suggesting it is more reflective of the recent landscape changes that have constrained gene flow. Asymmetric migration observed in logrunners was later associated with the degree of isolation of patches (Pavlacky et al. 2012).

Despite these examples, there are few studies for which researchers have been able to reconstruct past landscapes. Instead, most studies interested in landscape change rely on the assumption that recent, as opposed to historic, landscape changes have caused observed changes in genetic structure. For instance, both Murphy et al. (2010a) and Spear et al. (2005) found that increased gene flow in amphibians was associated with the broad-scale fires in Yellowstone National Park and interpreted this to mean that the recent disturbance had shifted genetic structure. However, recent disturbances may simply be correlated with a spatially associated historic process, resulting in incorrect inferences regarding the process influencing gene flow. One way to address this issue is to study landscapes that have identical or very similar histories but that have had recent landscape changes not dependent on the historic condition. For instance, after the Mount St. Helens eruption, areas in the blast zone that had the same degree of volcanic disturbance were subject to different management regimes. Spear et al. (2012) found that variables associated with gene flow in coastal tailed frogs were different depending on post-eruption management, as populations occurring in areas managed for post-eruption timber were limited by multiple climatic variables and populations in the unmanaged landscape were largely influenced by topography. Since the landscapes before management were highly similar, this study was able to make a stronger inference that the management regime led to differences in genetic structure.

The previous examples all focused on understanding the effect of past landscape change on genetic
connectivity. Nonetheless, the current rate of global change demonstrates the need to predict future anthropogenic impacts on genetic connectivity. A series of recent papers have provided examples of predictive landscape genetics. Wasserman et al. (2010) applied an individual-based causal modeling approach to infer relationships between landscape patterns and gene flow processes in a study of the American marten (Martes americana) in the United States northern Rocky Mountains. They found that gene flow was a function of elevation, with minimum resistance to gene flow at 1500 m. Alternative hypotheses involving isolation-by-distance, geographical barriers, effects of canopy closure, roads, tree size class, and an empirical habitat model were not supported. Simulation modeling (Chapter 7) was then used to predict the effects of potential climate change on population connectivity and genetic diversity of the American marten population (Wasserman et al. 2012). They then evaluated the influence of five potential future temperature scenarios involving different degrees of warming on population connectivity and genetic diversity (Wasserman et al. 2013). Resistant kernel dispersal models (Compton et al. 2007) were used to assess population connectivity and the CDPOP model (Landguth & Cushman 2010) was used to simulate gene exchange among individual martens under each climate change scenario. Even moderate warming scenarios were shown to result in very large reductions in population connectivity and the size of genetic neighborhoods, with consequent declines in allelic richness and expected heterozygosity. Such predictions can then guide the development of genetic monitoring protocols (Schwartz et al. 2007) that can determine if predictions are accurate and, if not, develop alternative models that better explain the observed genetic changes. However, testing predictions will be difficult for organisms with long generation times and therefore studies on organisms with rapid generations would be most valuable for understanding the potential reliability of predictive landscape genetics.

12.6 COMMON LIMITATIONS OF LANDSCAPE GENETIC STUDIES INVOLVING TERRESTRIAL ANIMALS

The preceding overview of landscape genetic studies of terrestrial animals demonstrates how the field of landscape genetics has created a better understanding of the variables that influence connectivity in terrestrial animal systems and contributed to the conservation and management of many species. However, there are also some important limitations common to many terrestrial landscape studies. The top seven limitations that we identified based on our knowledge of the field and other previous reviews include the following. (1) Few or no hypotheses are explicitly stated and tested in many landscape genetic studies (Storfer et al. 2010; Segelbacher et al. 2010). (2) Most studies evaluate landscape genetic questions and hypotheses in a single landscape and thus provide no replication (Segelbacher et al. 2010). (3) The majority (90%) of studies focus on a single species and thus do not provide insight into the response of multiple species to the same landscape variables (Storfer et al. 2010). (4) Landscape genetic analyses are rarely combined with other data types like field data collected from radiotelemetry or mark-recapture (Spear et al. 2010). (5) Most studies do not evaluate the genetic response to landscape genetic variables at multiple spatial scales (Manel & Holderegger 2013). (6) Landscape genetic researchers rarely conduct uncertainty analyses (i.e., using simulation) (Epperson et al. 2010; Jaquiéry et al. 2011). (7) There can be marked differences in movement behavior (McDevitt et al. 2013; Elliot et al. 2014a) and landscape connectivity (Amos et al. 2014; Elliot et al. 2014b; Paquette et al. 2014) between sexes, size classes, and age classes of the same species, which are highly relevant to ecological understanding and conservation applications, but which have been rarely addressed in landscape genetics research. Below, we highlight groups of terrestrial animal case studies that address many of these limitations while testing ecological hypotheses about gene flow in heterogeneous terrestrial landscapes.

12.7 TESTING ECOLOGICAL HYPOTHESES ABOUT GENE FLOW IN HETEROGENEOUS LANDSCAPES

12.7.1 Testing landscape resistance hypotheses in black bears

One of the first studies to formally evaluate the support for multiple landscape resistance hypotheses in comparison to null models of isolation-by-distance (IBD) and isolation-by-barriers (IBB) was conducted on the American black bear (Ursus americanus). The relative support of more than 100 alternative hypotheses about the effects of landscape features such as roads, elevation
gradients, forest cover, and topographical slope on genetic differentiation was tested in an American black bear population in northern Idaho, USA (Cushman et al. 2006). Follow-up papers evaluated the methods employed (Landguth & Cushman 2010; Cushman & Landguth 2010a, 2010b), tested the results with independent radiotelemetry data (Cushman & Lewis 2010), and spatially replicated the study to evaluate whether generalities in relationships between bear genetic differentiation and landscape features held across a number of study areas (Short Bull et al. 2011). Testing multiple competing resistance hypotheses (Cushman et al. 2006), verifying the high performance of the analytical methods employed (Cushman & Landguth 2010a), evaluating the predicted resistance maps using independent movement data (Cushman & Lewis 2010), and confirming these relationships across a large replicated study gave the researchers high confidence that forest cover, human development, roads, and elevation drive landscape resistance for black bears in the northern Rocky Mountains.

**12.7.2 Comparative landscape genetics studies**

One promising and relatively unexplored area of research is comparative landscape genetics of multiple species in a shared landscape (Table 12.4). Evaluating genetic diversity and population structure of multiple species in the same landscape can increase our ability to identify similarities and differences among species in response to a common set of landscape features. In one of the first and most comprehensive comparative landscape genetic studies, Manier and Arnold (2006) evaluated potential barriers and ecological correlates of several population genetic parameters for three interacting species, the western toad (*Anaxyrus boreas*), a terrestrial garter snake (*Thamnophis elegans*), and a common garter snake (*Thamnophis sirtalis*), in a 1000 km² landscape of northern California, US. They found the same landscape barrier in snakes, a 300 m escarpment formed by a series of block faults, but no evidence of this barrier in the western toad. They identified different variables, as well as some commonalities, that influenced migration of the three species including the presence of conspecifics (*T. elegans, T. sirtalis*), the presence of competing species (*T. elegans*), the presence of predators (*A. boreas*), geographic distance (*T. elegans, A. boreas*), elevation (*T. elegans, A. boreas*), and pond depth (*T. elegans, A. boreas*). When evaluating landscape variables that explained genetic distance (*Fst*), geographic distance was significant for all species while elevation also was significant for *T. elegans* and the presence of *T. elegans* and differences in pond perimeter were important for *T. sirtalis*. This study provides important insight into the microevolutionary processes that influence the population genetic structure for a group of interacting species and is one of the only studies to demonstrate the impacts of interspecific competition and predation on migration or gene flow.

Goldberg and Waits (2010) also conducted a comparative landscape genetics study by evaluating landscape genetic patterns of the co-distributed Columbia spotted frog (*Rana luteiventris*) and long-toed salamander (*Ambystoma macrodactylum*) in a 213 km² study area in northern Idaho. These species are phylogenetically, physiologically, and behaviorally distinct, but share many of the same breeding ponds in this region (Goldberg & Waits 2009). The authors evaluated (i) whether genetic patterns in this area were structured by distances along drainages at a broad scale or by watershed at a fine scale and (ii) what combinations of landscape features were most likely to predict variation in genetic distances between breeding locations for each species. Forested land cover was hypothesized to be associated with lower landscape resistance values for both species to minimize water loss. The riparian watershed network in this landscape was not found to be associated with gene flow for either species, and thus terrestrial movements across the landscape were likely to be driving gene flow patterns. For both species, urban and rurally developed land cover types provided the highest landscape resistances but the species differed in their response to other landscape variables. Resistance values for long-toed salamanders followed a moisture gradient where forest provided the least resistance, whereas agriculture and shrub/clearcut provided the least resistance for Columbia spotted frogs.

In a comparative landscape genetic study of woodland-dependent birds, Harrisson et al. (2012) evaluated the impacts of habitat loss and fragmentation on four bird species sampled at over 55 sites across 12 replicated landscape blocks (100 km² each) in southern Australia. They sampled a gradient of woodland tree cover ranging from 11% to 78% and conducted analyses at multiple spatial scales including within landscape, between landscapes, and with all landscapes combined. They collected nuclear DNA data from 6–16 neutral loci for three species known to decline
with loss of forest habitat (decliners), the eastern yellow robin (Eopsaltria australis), weebill (Smicornis brevirostris), and spotted pardalote (Pardalotus punctatus), and one tolerant species, the striated pardalote (Pardalotus striatus). The authors found that genetic diversity and effective population size decreased with decreasing forest cover for the decliner species but not the tolerant species. Also for two decliner species, the robin and weebill, the relatedness of individuals increased in more fragmented habitats and an isolation-by-distance effect of increased relatedness at smaller spatial scales was detected for the robin species, the least mobile decliner. However, no significant genetic differentiation was detected for any species despite simulation analyses that indicated sufficient time had passed since fragmentation to create detectable genetic structure under scenarios with moderate restrictions of gene flow. In the same study system, Amos et al. (2014) expanded analyses to 10 bird species and demonstrated sex-specific responses to habitat fragmentation for four species with the philopatric sex more affected by fragmentation in three of the four species. Overall, these studies provide a good example of how species and sexes may respond differently to habitat loss and fragmentation and provides evidence that some species of birds can maintain gene flow and connectivity in the face of major habitat alteration.

Other comparative landscape genetic studies have examined the effects of roadways and urbanization on the genetic structure of multiple terrestrial animals. For example, Riley et al. (2006) used radiotelemetry data and nuclear DNA microsatellite data to demonstrate that a freeway in southern California, US, was a partial barrier to both bobcats (Lynx rufus) and coyotes (Canis latrans). Delaney et al. (2010) investigated the genetic effects of urban fragmentation on three lizards, the side-blotched lizard (Uta stansburiana), western skink (Plestiodon skiltonianus), and western fence lizard (Sceloporus occidentalis), and one bird, the wren tit (Chamaea fasciata) in southern California, and found that the greatest restriction to gene flow occurred across the widest and oldest expanses of urban area, which included a major highway. Also, Frantz et al. (2012) found that a motorway in Belgium created a barrier for red deer (Cervus elaphus) but not wild boars (Sus scrofa). In a study of sympatric newt species in Greece, gene flow of the species with a terrestrial form of dispersal (Lissotriton vulgaris) was restricted by roadways while roads had no effect on genetic structure of the newt species (Triturus macedonicus) with an aquatic mode of dispersal (Sotiropoulos et al. 2013).

12.7.3 Scale dependence and threshold effects in landscape genetics

The effect of scale on ecological processes is a centrally important question (Wiens 1989; Levin 1992) because of the fundamental dependencies between scale and pattern and between pattern and process (Wu & Loucks 1995; Chapter 2). Landscape genetics explicitly focuses on how relationships between genetic processes and landscape patterns vary in heterogeneous environments in relation to spatial and temporal scales. Extensive work has focused on how apparent relationships between landscape patterns and species occurrence change with scale of observation (e.g., Tischendorf 2001; Thompson & McGarigal 2002; Cushman 2006; Corry & Nassauer 2005; Cushman et al. 2008). These studies have clearly shown that the drivers of an ecological process may each act at unique scales in space and time (Wiens 1989). It is critically important to correctly match the scale of each driving variable to the response process.

Despite the central importance of scale dependence in landscape genetics very few studies have explicitly focused on scale issues in landscape genetics (Anderson et al. 2010; Table 12.4). One of the earliest examples of a study that assessed scale dependence in landscape genetics was conducted by Cushman and Landguth (2010b), who showed using simulations that the strength of landscape-genetic relationships was highly dependent on matching the grain, extent, and thematic resolution of the analysis with that of the underlying biological process. An empirical analysis that provided a similar insight was conducted by Angelone et al. (2011). They examined the effects of landscape elements on genetic differentiation at three distance classes reflecting varying frequencies of European tree frog (Hyla arborea) movement, and found that different variables (rivers, geographic distance, roads, and forest cover) were associated with gene flow at different distance classes ranging from 0 to 8 km, indicating scale dependence of the relationship between frog dispersal and landscape structure. Similarly, in a landscape genetics study of boreal toads (Bufo boreas) in Yellowstone National Park, Murphy et al. (2010a) found that landscape variables were significantly associated with genetic differentiation at different spatial
### Table 12.4 Examples of landscape genetic studies that tested ecological hypotheses for terrestrial animals by (a) applying a comparative landscape genetics framework and (b) assessing scale dependence and threshold effects.

#### (a) Comparative landscape genetic studies

<table>
<thead>
<tr>
<th>Citation</th>
<th>Species</th>
<th>Unit of analysis</th>
<th>Inference or conclusions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amos et al. (2014)</td>
<td>10 woodland dependent birds</td>
<td>population</td>
<td>Four of the least mobile species impacted by forest loss and fragmentation and philopatric sexes more affected</td>
</tr>
<tr>
<td>Delaney et al. (2010)</td>
<td><em>Uta stansburiana,</em> <em>Plethodon skiltonianus,</em> <em>Scelopus occidentalis,</em> <em>Chamaea fasciata</em></td>
<td>individual, population</td>
<td>For all species, gene flow most restricted across the widest and oldest expanses of urban area, which included a major highway</td>
</tr>
<tr>
<td>Frantz et al. (2012)</td>
<td><em>Cervus elaphus,</em> <em>Sus scrofa</em></td>
<td>individual</td>
<td>Motorway created barrier for <em>C. elaphus</em> but not <em>S. scrofa</em></td>
</tr>
<tr>
<td>Goldberg &amp; Waits (2010)</td>
<td><em>Ambystoma macrodactylyum,</em> <em>Rana luteiventris</em></td>
<td>population</td>
<td>Development was least permeable land cover for both species and movement was not restricted to riparian corridors. Agriculture, shrub, and forest cover had different levels of permeability for each species</td>
</tr>
<tr>
<td>Harrison et al. (2012)</td>
<td><em>Eopsaltria australis,</em> <em>Smicronis brevirrostris,</em> <em>Pardalotus punctatus,</em> <em>Pardalotus striatus</em></td>
<td>population</td>
<td>Genetic diversity and effective population size decreased with decreasing forest cover for all species except <em>P. striatus</em></td>
</tr>
<tr>
<td>Manier &amp; Arnold (2006)</td>
<td><em>Anaxyrus boreas,</em> <em>Thamnophis elegans,</em> <em>Thamnophis sirtalis</em></td>
<td>population</td>
<td>Landscape variables that restricted gene flow varied across species; <em>T. elegans</em> and <em>T. sirtalis</em> had the same natural landscape barrier</td>
</tr>
<tr>
<td>Riley et al. (2006)</td>
<td><em>Lynx rufus,</em> <em>Canis latrans</em></td>
<td>individual</td>
<td>Highway partial barrier to gene flow in both species, stronger effect for bobcats</td>
</tr>
<tr>
<td>Sotiropoulos et al. (2013)</td>
<td><em>Lissotriton vulgaris,</em> <em>Triturus macedonicus</em></td>
<td>individual, population</td>
<td><em>L. vulgaris</em> showed more differentiation than <em>T. macedonicus</em>; roads restricted gene flow in <em>L. vulgaris</em> but not <em>T. macedonicus</em></td>
</tr>
</tbody>
</table>

#### (b) Assessing scale dependence and threshold effects

<table>
<thead>
<tr>
<th>Citation</th>
<th>Species</th>
<th>Unit of analysis</th>
<th>Inference or conclusions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Angelone et al. (2011)</td>
<td><em>Hyla arborea</em></td>
<td>population</td>
<td>Different landscape variables (rivers, forest cover, geographic distance, and roads) were associated with gene flow at different distance classes ranging from 0 to 8 km</td>
</tr>
<tr>
<td>Balkenhol et al. (2013)</td>
<td><em>Marmosops incanus</em></td>
<td>population</td>
<td>Genetic diversity was significantly lower in landscape with 31% forest cover compared to landscapes with 49% and 86%; genetic structure was significantly lower in the landscape with 86% forest cover</td>
</tr>
</tbody>
</table>

(continued)
scales ranging from 60 m to 960 m. The optimal cross-scale model included metrics measured at fine scales (canopy, elevation relief ratio), mid-scale (impervious surfaces), broad scale (ridges), and across multiple scales (growing-season precipitation and slope temperature–moisture). However, cross-scale models only improved the percentage of variation explained by 3–5%.

Other recent studies have also demonstrated the importance of considering spatial scale and network topology when conducting landscape genetic analyses. For example, Galpern et al. (2012) used a novel approach based on patch-based landscape graphs to develop resistance surfaces with multiple spatial grains to evaluate landscape-genetic relationships among woodland caribou (Rangifer tarandus caribou). Their results showed that using multiple spatial grains can reveal landscape influences on genetic structure that may be overlooked with a single grain, and that coarsening the grain of landcover data may improve landscape genetic inferences for highly mobile species. In a similar study, Keller et al. (2013) studied landscape-genetic relationships among wetland grasshopper (Stethophyma grossum) populations in a fragmented agricultural landscape and evaluated results across multiple spatial scales and network topologies. They found that the highest model fits were obtained when restricting landscape genetic analysis to smaller scales (0–3 km) and neighboring populations (Keller et al. 2013).

One key question in landscape and conservation genetics is whether there are landscape-scale threshold effects of habitat loss or fragmentation that lead to major increases in genetic structure and losses of genetic variation. So far, only a few studies have attempted to address this research question (Table 12.4). Lange et al. (2010) evaluated threshold effects of habitat fragmentation for a grassland species of bush cricket, Metrioptera roeselii, and a forest-edge species, Pholidoptera griseoaptera. No threshold effects were detected for the grassland species, but for the forest-edge species genetic differentiation ($G_{ST}$, Jost’s $D$) increased substantially and genetic
diversity was significantly lower when the amount of suitable habitat dropped below 20% in the very high fragmentation class. In a similar study, Balkenhol et al. (2013) evaluated the effects of varying levels of forest fragmentation on genetic diversity and structure in a marsupial forest-specialist species (Marmosops incanus) of the Brazilian Atlantic forest and detected threshold effects. For example, genetic diversity was significantly lower in the landscape with 31% forest cover compared to landscapes with 49% and 86% forest cover and genetic structure was significantly lower in the landscape with 86% forest cover compared to the more fragmented landscapes.

12.8 KNOWLEDGE GAPS AND FUTURE DIRECTIONS

Landscape genetic studies published to date have been primarily descriptive and few have been hypothesis-driven (Segelbacher et al. 2010; Storfer et al. 2010). This limits the ability of landscape genetics to provide broader insights into important ecological and evolutionary questions and makes these studies highly vulnerable to inferential errors when only one or a few models are tested (Cushman & Landguth 2010a). Thus, it is important to develop explicit hypotheses in the early stages of a landscape genetics study so that the sampling design can be optimized to improve the inferential power and to also consider the use of controlled experiments for testing hypotheses. Another important challenge in testing landscape genetic hypotheses is differentiating the impacts of historic and recent landscape change on genetic diversity and structure.

One of the factors currently limiting our understanding of landscape-genetic relationships in terrestrial animals is the relatively limited taxonomic and geographic scope of current research. Several reviews of the effects of habitat heterogeneity and fragmentation over the past 10–15 years have demonstrated a bias toward temperate forest ecosystems in developed countries and vertebrates, especially birds and mammals, as focal species (McGarigal & Cushman 2002; Storfer et al. 2010; Zeller et al. 2012; Manel & Holderegger 2013). However, these chosen study systems may not be the most tractable to landscape genetic questions. For example, more studies could focus on small mammals, like rodents, given the relative sensitivity of these species to recent landscape change because of relatively short generation times and limited dispersal distances (e.g. Landguth et al. 2010). Additionally, invertebrate taxa provide a good study system because they are more sensitive to climate change and other environmental perturbations and tend to be easily manipulated in controlled experimental studies (e.g. McGarigal & Cushman 2002; Prather et al. 2013). While applied studies of single species of conservation interest are important and will continue and be useful to those focal systems, more research is needed on model organisms and multispecies systems to address central questions in landscape genetics.

There has been extensive debate and considerable disagreement about the best analytical methods for evaluating relationships between landscape structure and gene flow processes. Naturally, the choice of method will depend on the nature of the question and will differ for studies aiming at identifying the drivers of long-term patterns in gene flow than those focused on measuring current gene flow, and likewise will differ between these and studies addressing the effects of landscape factors on adaptive genetic variation. Some generalities, however, have emerged, such as the importance of verifying the performance of statistical methods using simulation modeling (e.g., Cushman & Landguth 2010a; Jacquiéry et al. 2011; Shirk et al. 2012; Graves et al. 2013), developing generalized frameworks to compete multiple alternative hypotheses in a unified framework (e.g., Cushman et al. 2006; Wasserman et al. 2010), and the importance of employing analytical and statistical approaches that enable effective optimization of predictions of pattern–process relationships (e.g., Wang et al. 2009; Shirk et al. 2010; Cushman et al. 2014). These are large and abiding challenges that will remain the focus of research in landscape genetics for years to come. Chapter 5 of this book presents a comprehensive framework that enables delineation of different approaches of landscape genetic analysis based on the scope and objectives of analysis.

Another key for landscape genetics to successfully address many ecological hypotheses is to move to a more process-based approach when designing studies. One of the major criticisms of current correlative analytical approaches is that they do not directly model key factors driving gene flow, such as inter- and intra-specific competition, mating system, or dispersal patterns (Graves et al. 2013). To date, a vast majority of studies have used unvalidated expert opinion in the absence of empirical data on movement or gene flow to parameterize resistance surfaces (Spear et al. 2010;
Zeller et al. 2012), leading to a high degree of uncertainty in predictions. While there are a number of formal methods to assess variability of expert opinion and combine and weight expert rankings, which improve its implementation (e.g., Burgman 2004; Okoli & Pawlowski 2004), it is desirable to utilize empirical data wherever possible. In some instances where it would be excessively expensive or time consuming to gather empirical data to parameterize resistance surfaces and when there is considerable urgency, such as when dealing with endangered species in a rapidly changing landscape, careful utilization of methods to integrate expert knowledge may be appropriate.

Dispersal can be incorporated by linking individual behavior and fine-scale movement data to gene flow (e.g., Cushman & Lewis 2010). With the increasing availability of GPS telemetry for small organisms, a more nuanced understanding of how individual movement changes genetic patterns is possible and can serve as model inputs (e.g., Elliot et al. 2014b). The availability of fine-scale movement data can also allow for a better classification of different types of movement (Zeller et al. 2014), which can be used to focus on the movements relevant to gene flow. Further discussion of these issues is presented in Chapter 8.

While modeling dispersal is becoming more feasible, processes such as inheritance and mating are still difficult to study in nature, particularly in vertebrates. A solution to this is the linkage of empirical landscape genetics modeling with individual-based simulation of gene flow in complex landscapes (e.g., Landguth & Cushman 2010; Shirk et al. 2012; see Chapter 6). Simulation modeling can easily incorporate a number of processes and the mechanisms by which a landscape resists gene flow can be inferred by evaluating the relationship between landscape models and an observed pattern of genetic isolation. Furthermore, simulation modeling allows for more robust sensitivity analyses that can elucidate which factors are likely to most influence genetic structure, and important processes can then be focal points for future empirical studies. If applied to a variety of organisms and study systems, the simulation approach can also identify general patterns that will be relevant across landscape genetic studies. For example, simulations could assess how different mating systems affect landscape genetic results if organisms with similar dispersal tendencies are modeled.

Ultimately, responses to global change are one of the most important avenues for research for landscape genetics and many biological disciplines (Manel & Holderegger 2013). Thus, simulation modeling along with empirical genetic work across a variety of current landscape conditions using both neutral and adaptive markers (see Chapter 9) is critical to predict how species will respond to climate change. Such studies are in their infancy, but a more rigorous framework is needed to advance predictive landscape genetics so that it can truly inform future actions to address global change.

In closing, we recommend a broadening of the scope of landscape genetics to address a wider taxonomic range across a more diverse set of ecological systems. Particular focus should be given to invertebrate taxa and rodents, which provide experimentally tractable study species, with short generation times and limited dispersal ability, making them ideal for landscape genetic studies. Also, there is great value in directly incorporating important processes into landscape genetic models and in synergistically combining empirical analysis and simulation modeling. We believe that these research areas will pay rapid dividends in increasing our knowledge of landscape genetic processes for terrestrial animal species and their influences on populations, species, and communities.

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Keyghobadi, N., Roland, J., & Strobeck, C. (2005a) Genetic differentiation and gene flow among populations of the


