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INTRODUCTION

Contributions of landscape genetics – approaches, insights, and future potential

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Introduction

Landscape genetics is an emerging field that seeks to understand how specific landscape features and microevolutionary processes such as gene flow, genetic drift, and selection interact to shape the amount and spatial distribution of genetic variation (Manel *et al.* 2010). Its conceptual basis is founded in landscape ecology, population genetics, and spatial statistics, which are integrated to address landscape-scale research questions and hypotheses (Manel *et al.* 2003; Storfer *et al.* 2007; Storfer *et al.* 2010). When the term 'landscape genetics' was first proposed (Manel *et al.* 2003), it was not clear how it differed from established disciplines such as population and geographical genetics. However, the focus of landscape genetics was refined to include spatially explicit research that specifically 'quantifies the effects of landscape composition, configuration and matrix quality on gene flow and spatial genetic variation' (Storfer *et al.* 2007). Early research models in this discipline focused on the terrestrial landscape, but the field has expanded to include 'riverscape' and 'seascape' systems (Fausch *et al.* 2002; Galindo *et al.* 2006, 2010; Selkoe *et al.* 2008, 2010). Across all ecosystems, a common emphasis is unravelling the influence of landscape and environmental features on the distribution of genetic variation.

Three main forces have driven the current rapid growth of landscape genetics. First, managers and conservation biologists have shifted to landscape and ecosystem level planning to address the challenge of maintaining viable populations within an increasingly human-impacted world (Agee & Johnson 1987; Leitão *et al.* 2006; Trombulak & Baldwin 2010). This paradigm shift is linked to the important development of metapopulation theory (Hanski & Gilpin 1991; Harrison & Hastings 1996; Hanski & Simberloff 1997) and the emergence of the discipline of landscape ecology (Urban *et al.* 1987; Turner 1989; Hansson *et al.* 1995; Pickett & Cadenasso 1995). Second, technological improvements in molecular methods and corresponding decreases in cost per sample have made it physically and financially feasible to collect large amounts of genetic data from hundreds of individuals at a landscape scale (Storz 2005). Third, improvements in geographic information systems and remote sensing tools have greatly increased our ability to quantify landscape and environmental variables at biologically meaningful scales (McGarigal & Marks 1995; Wulder *et al.* 2004; Thomassen *et al.* 2010). The field of landscape genetics draws from all three of these conceptual and technical advances to explicitly evaluate hypotheses that examine how landscape and environmental features shape gene flow among populations, the spatial patterning of genetic variation, and local adaptation.

The overwhelming majority of landscape genetic studies have addressed the question of how landscape features affect connectivity or create barriers to gene movement. Animal studies, in particular, are likely to focus on how natural and anthropogenic landscape features affect animal-mediated gene movement. In fact, 62% of landscape genetic studies examine vertebrates (Storfer *et al.* 2010). These studies have effectively documented patterns of connectivity on landscapes and identified barriers to movement. Plant studies have been less likely to utilize a landscape genetic approach, comprising only 14.5% of the current studies (Storfer *et al.* 2010). However, this discrepancy is not because plant researchers are not concerned with the genetic consequences of landscapes. Indeed, numerous plant studies have documented the impact of landscape factors such as fragmentation and isolation on genetic processes such as inbreeding and inbreeding depression, loss of genetic diversity, and gene flow (Holsinger 1993; Young *et al.* 1996; Sork *et al.* 1999; Sork & Smouse 2006; Aguilar *et al.* 2008). As plant biologists increase their attention on connectivity, we should also see an increase in spatially explicit analyses that utilize the spatially explicit tools of landscape genetics (for an example see Dyer *et al.* 2010).

Understanding the spatial pattern of genetic variation is an important contribution of landscape genetics. Landscape effects on the distribution of neutral genetic variation can help identify corridors and barriers to gene flow, but the association between environmental and genetic gradients can provide initial evidence of the impact of natural selec-

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tion (Endler 1986; Holderegger *et al.* 2006; Manel *et al.* 2010a). Environmental correlations with neutral genetic markers can help identify opportunities for natural selection (e.g. Sork *et al.* 2010), but the mapping of adaptive genetic variation that underlies the phenotypes under selection provides even stronger evidence (Storz 2005; Balding 2006; Hancock & Di Rienzo 2008; Stinchcombe & Hoekstra 2008). Recently, researchers have begun to contrast neutral and adaptive variation using AFLP's (Bonin *et al.* 2006; Joost *et al.* 2007; Freedman *et al.* 2010) in order to identify adaptive genetic variation. However, as next-generation genomic tools become more accessible (Beaumont & Balding 2004; Storz 2005), we will see the surfacing of landscape genomic studies that examine genetic variation associated with functional genes (Hancock *et al.* 2008; Eckert *et al.* 2010). It appears that the study of spatial patterns of adaptive variation will become a strong tool for incorporating the process of selection into landscape genetics.

Through the development of new approaches and new questions arising out of research that explicitly links genetic data with landscape and environmental variables, the field of landscape genetics can provide valuable insights into how the evolutionary processes of gene flow, genetic drift, and natural selection have been influenced by landscape-scale processes to shape current patterns of genetic variation. Understanding these processes will allow us to predict the response of current populations to anthropogenic forces, such as climate change, human population growth, habitat destruction, and fragmentation.

Contributions and overview of the special issue on landscape genetics

This special issue was designed to highlight the diversity of questions that can be investigated through an interdisciplinary landscape genetics framework and furthermore introduce new analytical approaches and update the current status of the field and its future potential. The issue includes 22 contributions that span a diversity of terrestrial, marine, and freshwater landscapes and range from topical reviews to new methods with empirical application. For this special issue, we have five major goals. First, we provide broad reviews of landscape genetics (Storfer *et al.* 2010) and landscape genetics applications for infectious disease emergence and spread (Biek & Real 2010). Second, we include methodological commentaries that identify unique issues and challenges in landscape genetics (Anderson *et al.* 2010; Epperson *et al.* 2010; Storfer *et al.* 2010; Thomassen *et al.* 2010). Third, we point out topics where landscape genetics has a specific contribution to molecular ecology and evolution. The most obvious areas are as follows: (i) functional connectivity and landscape resistance to gene flow (Braunisch *et al.* 2010; Cushman & Landguth 2010; Goldberg & Waits 2010; Meeuwig *et al.* 2010; Murphy *et al.* 2010; Shirk *et al.* 2010; Spear *et al.* 2010) and (ii) the linkages between genetic patterns and ecological process (Bruggeman *et al.* 2010; Galindo *et al.* 2010; Selkoe *et al.* 2010). Fourth, we illustrate the connection with phylogeography including studies that uncover historical and current landscape processes in landscape genetics (Dyer *et al.* 2010; Knowles & Alvarado-Serrano 2010). Fifth, we explore adaptive landscape genetics by including studies examining the impact of landscape environmental factors on adaptive genetic variation (Eckert *et al.* 2010; Freedman *et al.* 2010; Manel *et al.* 2010a,b; Sork *et al.* 2010).

Methodological reviews and commentaries

The interdisciplinary nature of landscape genetics creates a number of unique methodological challenges centred on integrating and analysing spatially explicit environmental variables and genetic data at a landscape scale. A recent review of research needs in landscape genetics highlighted analytical limitations as one of four major challenges in the field (Balkenhol *et al.* 2009). Empirical analysis articles in this special issue address these challenges using a diversity of novel and creative approaches, and this section of methodological reviews and commentaries highlights some of the key methodological approaches, considerations, and challenges in landscape genetics. Thomassen *et al.* (2010) review current methods and data sources for making continuous spatial predictions from biological variation using spatial and environmental predictor variables. This review article overviews a diversity of regression methods, decision tree approaches, and generalized dissimilarity modelling techniques summarizing the advantages and limitations of each method and ending with a section on key challenges and opportunities for future research. Epperson *et al.* (2010) examine the current and future role of computer simulation approaches in the development of landscape genetic theory and methods. This article reviews the development of stochastic space–time simulation approaches and the roles of simulations in testing model assumptions, characterizing the properties of statistical estimators, and testing alternative hypotheses in empirical data sets. One major methodological challenge in landscape genetics is interpreting spatial genetic patterns that are the outcome of multiple biotic and abiotic processes operating at different spatial and temporal scales. Anderson *et al.* (2010) review these challenges and discuss approaches for addressing the challenges by providing guidance to researchers on appropriate analysis methods and sampling and study designs.

Functional connectivity and landscape resistance to gene flow

The most common objective of landscape genetic studies is to identify the landscape or environmental features that facilitate or constrain genetic connectivity (Storfer *et al.* 2010). The ability of researchers to evaluate functional connectivity and landscape resistance to dispersal and gene flow has greatly improved with the introduction of high-resolution GIS data (Thomassen *et al.* 2010) and methods for estimating cost surfaces based on hypotheses about movement probabilities in different land cover types (Adriaensen *et al.* 2003; McRae 2006) and methods for modelling ocean currents (Galindo *et al.* 2010; Selkoe *et al.* 2010). Unravelling these relationships can increase our basic understanding of how landscape and environmental features influence the movement and distribution of organisms and genes while also making important applied contributions to corridor and reserve design, invasive species management, and predictions of impacts of future environmental change on connectivity. The first three articles in this section address important methodological challenges in evaluating functional connectivity, while the last four articles evaluate landscape resistance and functional connectivity for a diversity of taxonomic groups in terrestrial and aquatic systems.

One of the most common approaches for evaluating functional connectivity is to develop resistance surfaces that represent hypothesized relationships between landscape features and gene flow. Spear *et al.* (2010) critically review the approaches that have been used to parameterize resistance surfaces, discuss the biological assumptions and considerations that influence analyses using resistance surfaces, and provide guidelines for researchers using resistance surfaces in landscape genetics. They also include a valuable discussion of novel approaches for creating resistance surfaces and alternative methods for evaluating functional connectivity and landscape resistance. Accurately differentiating alternative models of landscape resistance to gene flow is particularly challenging, and the next two articles greatly enhance the future of landscape genetics by introducing and validating possible approaches. Using an individual-based, spatially explicit simulation model, Cushman & Landguth (2010) evaluate the ability of a causal-modelling hypothesis testing approach to discriminate between the landscape genetic hypotheses of isolation by distance (Wright 1943), isolation by barrier (Ricketts 2001) and isolation by landscape resistance (Cushman *et al.* 2006; McRae 2006). The authors also assess how rapidly new landscape genetic processes can be detected using this statistical approach and demonstrate the value of incorporating a hypothesis testing framework when using mantel and partial mantel tests in landscape genetic analyses. Shirk *et al.* (2010) apply a causal-modelling hypothesis testing framework in their evaluation of landscape resistance models for mountain goats (*Oreamnos americanus*) in a fragmented region of the state of Washington. They introduce a novel model selection framework for evaluating alternative landscape resistance models using expert opinion as a starting point and reveal that elevation, water bodies, human development, and roads have important impacts on functional connectivity.

The next two articles are unique among landscape genetic studies because they evaluate the effect of both within- and between-patch variables on functional landscape connectivity. Meeuwig *et al.* (2010) assess the influence of natural waterfall barriers, waterway distance, habitat patch size, and the spatial distribution of populations on connectivity of migratory bull trout (*Salvelinus confluentus*) populations in stream–lake network in northwest Montana, USA. They evaluate 18 competing landscape genetic models using linear statistical models and an information-theoretic approach and find the best support for multivariate models that include both within- (patch size) and between-patch variables. When evaluating barriers between sampling areas, incorporating asymmetric (i.e. one-way) and symmetric (i.e. two-way) barriers to gene flow was particularly important. Murphy *et al.* (2010) introduce gravity models as a new landscape genetic method for evaluating hypotheses of functional connectivity that includes both between-site and at-site landscape processes. They apply this graph theory approach to a large metapopulation complex of Columbia spotted frogs (*Rana luteiventris*) in central Idaho and identify the presence of predatory fish, site productivity and growing season, topographical complexity, and distance between sites as important landscape variables influencing functional connectivity in this system.

The final two articles in this section introduce novel approaches for evaluating functional connectivity of terrestrial animals and highlight the implications of their results for conservation planning. Goldberg & Waits (2010) examine the influence of different landscape variables on landscape resistance to gene flow in two pond breeding amphibians, Columbia spotted frogs (*R. luteiventris*) and long-toed salamanders (*Ambystoma macrodactylum*), in northern Idaho, USA. They use a multivariate, multimodel information-theoretic approach to evaluate the support for competing models of landscape resistance that include physical variables (slope, soil type, solar insulation), land cover, and combinations of these variables. The resulting model parameters are used to detect similarities and differences in landscape resistance between codistributed species and to predict species-specific responses to future landscape change. Braunisch *et al.* (2010) present a new approach to investigate the relative effect of different landscape features on gene flow for a fragmented population of capercaillie (*Tetrao urogallus*) in the Black Forest, Germany, and to parameterize a spatially explicit corridor model. Using pair-wise individual relatedness as a response variable, they present an alternative approach to traditional least-cost path modelling that is adjustable to the species- and sex-specific dispersal patterns and incorporates stochasticity in path selection. The spatially explicit results of the analyses are then used to identify priority areas for the preservation or restoration of metapopulation connectivity.

Linking genetic patterns and ecological process

Another key contribution of landscape genetics is unravelling the ecological processes that shape observed patterns of genetic variation (Storfer *et al.* 2007; Holderegger & Wagner 2008). Patterns at selectively neutral loci will reflect various ecological processes that are influenced by the landscape and environment including individual movement, dispersal, behaviour, survival, and reproduction. These latter two processes will reflect the outcome of natural selection, and any loci linked to genes associated with survival and reproduction will reflect the impact of selection. Articles in this section increase our understanding of both within- and among-site processes that drive patterns of genetic diversity and structure in terrestrial and marine systems. Bruggeman *et al.* (2010) elucidate the linkages between ecological processes and genetic patterns using an individual-based, spatially explicit red-cockaded woodpecker population model to evaluate the influence of both landscape composition (patch size) and configuration (patch isolation) on abundance, effective population size (N_e), and F_{ST}. This innovative study introduces the use of o-ring statistics to quantify variation in landscape patterns at different spatial scales and quantifies how processes both within- and among-populations shape genetic variation and structure. Selkoe *et al.* (2010) improve our mechanistic understanding of the links between oceanographic and ecological processes and genetic variation by evaluating patterns of genetic variation and structure among three species: kelp bass *Paralabrax clathratus*, Kellet's whelk *Kelletia kelletii* and California spiny lobster *Panulirus interruptus* in southern California, USA. The authors use information-theoretic model selection and linear modelling to evaluate the role that kelp bed size, sea surface temperature, ocean particle flow models play in shaping genetic diversity and structure in this marine system. Galindo *et al.* (2010) provide a seascape genetics framework for testing coupled biological–physical oceanographic models by using them to generate simulated spatial genetic patterns and then testing these predictions with empirical genetic data. In applying this approach to the acorn barnacle, *Balanus glandula*, in northern California, the authors discover a mismatch between predicted data and empirical data and refine the biological–physical oceanographic model based on their results demonstrating an important role for seascape genetics in elucidating the factors influencing larval dispersal and improving oceanographic models. This approach suggests that selection on alleles may be an important feature of gene flow and lays the groundwork for complex seascape models to be used to evaluate alternative hypotheses.

Uncovering historical and current landscape processes

Phylogeographic studies combine information about the geographic distribution of individuals with their gene genealogies to make inferences about the effects of migration, population expansion, genetic bottlenecks, and vicariance on the evolutionary history of species (Avise 2000). Phylogeography has always taken into account the effect of physical characteristics of the landscape to study gene movement. However, because it studies gene movement over long time intervals, the influence of climate fluctuations on demographic and distributional changes has been important component of phylogeographic investigations. As these studies have incorporated spatially explicit approaches into their analysis, the primary distinction between phylogeography and landscape genetics is focusing on historical vs. contemporary time scales. In this section, we include two studies that illustrate the similarity of the two disciplines and their use of spatially explicit tools. These studies illustrate that phylogeographic history shapes contemporary spatial patterns and highlight the importance of incorporating population history into landscape genetic studies.

Dyer *et al.* (2010) address a traditional landscape genetic question of population connectivity through a study of the endemic plant, *Euphorbia lomelii*, of the Baja California desert. They point out that the phylogeographic background of those populations hampers our ability to identify how spatial and ecological factors impact gene movement and tackle this challenge by extending a graphical population network approach (Dyer & Nason 2004) to a model that conditions their analysis of bioclimatic factors by incorporating the confounding influence of phylogeographic relationships. Their model identified specific bioclimatic variables that gene exchange among populations, but importantly they also showed the conditioning their models of least-cost path analysis on phylogeographic history changed which variables were most critical. Knowles & Alvarado-Serrano (2010) provide a converse example by utilizing the spatially explicit landscape context of their populations to address phylogeographic questions of range expansions and colonizations in flightless grasshoppers (genus *Melanoplus*) currently found on the Sky Islands of the Rocky Mountains. In their study, they utilize spatially explicit climate variables to build ecological niche models (ENM) that they combine with phylogeographic information to understand the genetic consequences of distributional shifts. This integration of niche shifts and landscape heterogeneity allows them to create a more accurate picture of the history of colonization since the Last Glacial Maximum, 21 000 years ago. By coupling ENMs, landscape features, and colonization events, they were better able to dissect the contribution of historical events in shaping the genetic patterns of contemporary populations.

Impact of landscape environmental factors on adaptive genetic variation

The latest expansion of landscape genetics is the analysis of adaptive genetic variation (Manel *et al.* 2003; Holderegger *et al.* 2006). Neutral genetic markers can be used to identify geographic patterns of neutral genetic variation that can be correlated with environmental gradients as preliminary evidence of natural selection (Endler 1986; Westfall & Conkle 1992). While they can help identify regions that may experience similar selective pressures, they also have the confounding effects of population history. New statistical analyses of large numbers of AFLP loci have started the trend to identify outlier loci among numerous neutral loci (Beaumont & Nichols 1996; Bonin *et al.* 2006; Joost *et al.* 2007), especially when combined with association of these outlier loci with environmental gradients (Balding 2006). On the other hand, the rapid rise of next-generation technologies has created access to genomic tools for identifying adaptive genetic variation that will be better evidence of local adaptation, if the loci are tied to functional genes (Storz 2005; Hancock & Di Rienzo 2008;

Stinchcombe & Hoekstra 2008; Coop *et al.* 2010). Here, we include four studies that demonstrate the insight we gain from these three approaches.

To test for genetic and climate associations in valley oak (*Quercus lobata*), Sork *et al.* (2010) transform single-locus nuclear microsatellite markers into multivariate genotypes. These multivariate genotypes are sensitive measures of differentiation because they include interallelic associations that accumulate small effects across loci. Thus, these variables include the effects of selection and genetic drift. Using genotypes from trees sampled throughout the species' range in California, their correlation analysis indicates a strong relationship of genetic variation and climate variables, such as temperature seasonality and maximum temperature, even when controlling for geography. They use this information about climatically associated genetic structure to identify regions where oak populations may be most vulnerable to climate change. This study demonstrates how the spatial distribution of multivariate genotypes markers can provide a sensitive indicator of genetic differentiation associated with geographic and environmental variables.

One vertebrate study (Freedman *et al.* 2010) and one plant study (Manel *et al.* 2010b) illustrate the application of AFLP loci for identifying patterns of adaptive variation. Freedman *et al.* (2010) conduct a genome scan of AFLP loci in an African rainforest lizard occurring along a forest–savanna ecotone. By comparing loci that behave neutrally with those that appear to be under selection, their findings illustrate genetic gradients indicating adaptive diversification along this cline. They integrate information from niche models and mitochondrial sequence data to propose that this diversification took place during periods of expansion and refugial isolation played a lesser role. Manel *et al.* (2010b) analyse geographic patterns in AFLP loci in *Arabis alpina* sampled from numerous sites across the European sites and on a smaller scale within three mountain massifs of the French Alps. Using an approach that takes into account spatial autocorrelation, they are able to identify climate variables creating the genetic gradients and identify the spatial scale for the analysis of selection. Both studies demonstrate a sophisticated examination of environmental associations of genotypic variation.

Eckert *et al.* (2010) provide an excellent example of a landscape genomics approach to analyse geographic patterns of single nucleotide polymorphism (SNP) variation in 1730 loci in 682 individuals of loblolly pine (*Pinus taeda* L.) sampled from the entire range. They utilize a Bayesian model, which controls for population history to examine the association of genetic gradients with multivariate climate variables. They found that numerous loci with significant genetic differentiation across the geographic sites. Because of their knowledge of sequences of functional genes, they found that many of the significant loci were functional genes for drought stress. Their study illustrates the advantages of annotated genomes when looking for adaptive genetic variation. However, even without those related data, their study demonstrates the feasibility of using SNPs to identify candidate genes under selection.

The study of adaptive variation is becoming an important area of landscape genetics. We see that neutral markers such as microsatellites and AFLP's can identify spatial patterns that suggest a role of natural selection in landscape genetic processes, especially when accounting for population history and spatial autocorrelation. Nonetheless, we anticipate that the trend will shift increasingly towards candidate genes with known functional roles.

Conclusions

Landscape genetics has made its strongest contribution in evaluating the impact of landscape features on gene movement to understand the role of landscape features, physical barriers, and anthropogenic landscape changes on connectivity and isolation of populations. Most studies have been concerned with regional movement and a contemporary time scale, although historical migration and colonization are shaped by the landscape as well. The analysis of gene movement has utilized methods introduced by landscape ecology, geography, spatial statistics, and population genetics, but increasingly, we see new methods specifically developed for landscape genetics. These methods provide rigorous mechanisms for testing hypotheses about how landscape and environmental features influence effective population size, genetic diversity, and gene flow when studies are designed properly and at the appropriate spatial scale.

Landscape genetics offers a framework for testing the influence of site-specific environmental factors on geographical patterns of adaptive variation. This line of questioning will be enhanced by the advancement of genomic tools and methods that can separate population history from natural selection. For studies that use this approach to assess the potential of populations to respond to climate change, it would be valuable to also model the potential of populations to track climate change through gene movement. In some cases, suitable habitats may shift to areas where proximity and landscape features allow such movement and in other cases not. Plant studies that document patterns of genetic variation in candidate loci under selection should also be paired with common garden experiments to associate those patterns with phenotypic traits and their fitness consequences. Animal studies will also need to associate genotypes with phenotype.

Ultimately, the future development of the field of landscape genetics will depend on the integration of knowledge and research methods across the disciplines of population genetics, landscape ecology, geography, spatial statistics, ecology, evolution, and phylogeography. The adoption of methodological approaches from other disciplines and the introduction of new landscape genetic tools are generating new insight into the impact of ecological and evolutionary processes that maintain populations across landscapes. This discipline has tremendous potential for generating new hypotheses about the role of landscape context at a time when environmental change through landscape transformation and climate shifts is presenting new challenges for the survival of species. The goal of this special issue is to bridge the gap among disciplines and inspire discussion and future research in landscape genetics.

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