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PERSPECTIVE

# Landscape genetics since 2003: status, challenges and future directions

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**Abstract** A scientific symposium on landscape genetics, held at the 2013 IALE Europe Conference in Manchester UK (September 2–8, 2013), highlighted status, challenges and future avenues in the field. Key topics included analytical aspects in landscape genetics, conceptual progress and application of landscape genetics for conservation management. First, analytical aspects referred to statistical relationships between genetic and landscape data. It was suggested that linear mixed models or Bayesian approaches are particularly promising due to more appropriate and powerful ways for analyzing landscape effects on genetic variation. Second, supplementing neutral genetic variation with adaptive genetic variation is very promising. However, research needs to go beyond the identification of genomic regions under selection and provide information on the ecological function of adaptive genetic regions. Conceptually, endogenous processes (e.g., life-history attributes such as dispersal) require consideration as supplementary factors in shaping the genetic variation in addition to landscapes. Also, the temporal dimension in landscapes for both the past and the future should be given increased attention as the genetic responses to landscape change may be non-simultaneous, resulting in time lags. As for applied conservation management, landscape genetics can provide important baseline information such as basic data on species movement in a spatial context, assessments of the spatial need for management efforts, or evaluations of the effectiveness of already existing management measures.

**Keywords:** IALE Europe congress 2013 · Symposium review · Quantitative assessments · Genetic data · Landscape data · New developments · Research needs

## Introduction

Ten years ago, the seminal paper of Manel et al. (2003) coined the term landscape genetics to understand how landscape features and adaptive processes such as gene flow, genetic drift and selection drive the degree and the spatial distribution of genetic variation (Manel et al. 2003, 2010). The field has experienced an almost exponential increase in published papers (Storfer et al. 2010). Fast advancing molecular technologies, increasing availability of high-resolution environmental data,

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and ever-growing computer power for conducting complex spatial analyses allow us to quantitatively link landscape features to the spatial distribution of neutral and adaptive genetic variation (Balkenhol et al. 2009a; Epperson et al. 2010).

Latest trends in landscape genetics were discussed at a symposium, recently held at the 2013 IALE Europe Conference in Manchester UK (September 2–8, 2013), to highlight future avenues and challenges in the field. An international set of scientists fostered the exchange of expertise and contributed 14 papers dealing with a broad range of topics (http://www.iale2013.eu/landscape-genetics). Foci included (i) landscape genomics: a step forward, (ii) overrated landscape effects: which multiple processes may shape genetic variation? (iii) landscape legacies: how does the past shape current genetic variation? (iv) stop the confusion: which statistical methods to use for explaining landscape effects on genetic variation? (v) useful information: the role of landscape genetics for management and conservation.

The production of genetic data is currently soaring for both neutral and adaptive genetic diversity. Whereas adaptive genetic diversity is subject to natural selection, neutral genetic diversity is neutral with regard to selection, i.e., the fitness of individuals is not directly affected by alleles or gene variants (Reed and Frankham 2001). The overall genetic variation and genetic differentiation of individuals and populations is caused by both local adaptation and population processes. The latter include migration, dispersal and gene flow, etc. (Frankham et al. 2002), processes which are traditionally assessed using neutral genetic markers (Holderegger et al. 2006). To date, most landscape genetic studies rely on neutral genetic markers such as microsatellites to derive Fst and related genetic distance measures. Whereas such population-based measures are well established and broadly accessible, more powerful ways for detecting landscape effects on genetic variation are provided by individual-based approaches, including clustering methods, parentage analyses, and genetic distances calculated among individuals. These individual-based methods provide much higher temporal resolution for detecting landscape genetic relationships (Landguth et al. 2010; Blair et al. 2012), and do not require the a priori definition of discrete populations. This makes individual-based approaches particularly valuable for analyses within continuously distributed populations, or in gradient landscapes. However, the various individual-based approaches have different advantages and limitations, and future studies should ideally try to combine multiple options and identify the circumstances under which each approach is most suitable (Balkenhol et al. in press). For example, parentage analysis provides real-time estimates of actual dispersal and has already been used to infer landscape effects on functional connectivity (Clark et al. 2008; Andreasen et al. 2012). However, the spatial pattern of dispersal found via parentage analysis usually relates to only a few individuals and a single point in time. Thus, landscape genetic relationships found via parentage analysis may be too temporally fine-scaled to provide a good representation of the overall influence of landscape on population genetic structure, so that additional approaches should be used in addition to parentage analysis. Another application of contemporary gene flow may refer to the evaluation of process-based models. Process-based models simulate the movement of biota as a function of a broad range of specific model parameters which often lack empirical data for evaluation (Bolliger et al. 2003). Estimates of current gene flow may provide valuable data to evaluate the spatial dispersal kernels in such process-based models (Jones and Muller-Landau 2008; Klein et al. 2011), also calling for assessments of the directionality of gene flow to identify source-sink dynamics across heterogeneous landscapes (Bolliger et al. 2011).

## Landscape genomics: a step forward

Despite the intense use of neutral markers of the past 10 years, future landscape genetic studies will increasingly assess adaptive genetic variation, as it gives clues to the biological function and local adaptations of entire genomic regions. A major research task for the future is a comprehensive comparison of different methods for identifying adaptive genetic variation in whole-genome sequencing data (Jones et al. 2013) because conflicting results can occur among different methods for detecting outliers, i.e., genomic regions which are likely under selection (K. Leempoel, EPFL, Lausanne, Switzerland). Efforts to apply statistical methods relying on significance tests (e.g., logistic regression) are currently in progress and considered a potential solution for analyzing next generation sequencing data (S. Stucky, EPFL Lausanne, Switzerland: Samβada, successor of MatSam (Joost et al. 2007, 2012)).

Once adaptive genetic data is reliably identified, environment effects on it can be quantified. This is the focus of landscape genomics, which has already led to an improved understanding of the nature of genes involved in local adaptation (Manel and Holderegger 2013). At the same time, landscape genomics needs to go beyond the identification of genomic regions under selection and provide information on the ecological function of adaptive genetic regions. A key step forward would merge the information from both, the adaptive and neutral genetic variation, which would then allow assessments on how genes under selection disperse across landscapes, or how gene flow counterbalances local adaptation (Manel and Holderegger 2013).

## Overrated landscapes: which multiple processes may shape genetic variation?

Simultaneous to the rapid rise of genetic data, increasing availability of spatial environmental data allows for evermore detailed landscape representations (Porter et al. 2012). It has been shown that the ability to detect the drivers of genetic variation are highly sensitive to both the composition and the configuration of landscapes (Jaquiery et al. 2011). Whereas landscape composition characterizes the mixture of landscape elements (e.g., forest, settlement), landscape configuration refers to the spatial arrangement of the landscape elements. It could well be that several smaller forest patches adjacent to each other are a much more decisive for spatial genetic structure than the total area of forest in a landscape. To date, however, landscape genetic studies have primarily looked at effects of landscape composition and matrix quality (Angelone et al. 2011; Keller et al. 2013), whereas the spatial arrangement of landscapes has been largely neglected (M. van Strien, PLUS ETHZ, Switzerland). Indeed, the general role of landscape characteristics in shaping genetic variation needs to be addressed in more detail in future studies. While efforts to represent landscapes organism-specifically and functionally (e.g., as resource models) may result in better explanatory power, T. Lander, National History Museum London, UK, also showed that least-cost paths and circuit-theoretic approaches performed worse than simple straight-line distances for explaining pollen movements among populations of a plant species (*Prunus avium*) pollinated by generalist insects (Lander et al. 2011). Thus, given a sampling strategy which ensures that populations or individuals are sampled densely enough to avoid omissions, landscapes may be generally more permeable for species movement and gene flow (Bolliger et al. 2011; Reding et al. 2013). Are landscape features overrated in driving genetic variation? Indeed, contributors at IALE highlighted that general population characteristics (e.g., population density, local carrying capacity) or endogenous processes such as species-specific life-history attributes (e.g., mating systems, behavior) should receive more attention in landscape genetics (Clark et al. 2008; Andreasen et al. 2012; Reding et al. 2013). Notably, V. Helfer, University of Salzburg, Austria, found that the reproduction mode (i.e., monogamy, polygamy, or promiscuity) strongly determines genetic effects of landscape barriers to gene flow. V. Helfer also suggested to assess overlapping and non-overlapping generation systems in landscape genetic simulation studies, as current studies usually focus only on the latter (Blair et al. 2012). In addition, species-specific behavioral aspects (Cushman and Lewis 2010) or individual variation could be a decisive endogenous factor shaping genetic variation across landscapes (F. Pflüger, University of Göttingen, Germany; T. Lander, National History Museum London, UK). Thus, are there principles that will allow the development of general models for landscape genetics, or does the future lie in increasingly complex species- and landscape-specific models based on more and better field data?

## Landscape legacies: how does the past shape current genetic variation?

The rapid production of landscape data refers not only to the level of detail, but also to the spatial extent and the temporal resolution which can be accounted for. Similar to Krauss et al. (2010) and Helm et al. (2006), C. Folly (WSL, Birmensdorf, Switzerland) highlighted that historical habitat properties (here: historical wetland size) explained today's allelic richness in the plant *Succisa pratensis* better than recent habitats. Thus, landscape legacies affect current genetic variation (Epps et al. 2013), particularly when populations may not have yet come to equilibrium with current conditions. This is certainly important to consider when projecting gene flow into the future as a result of changing landscapes (Van Strien et al. in press).

## Stop the confusion: which statistical methods to use for explaining landscape effects on genetic variation?

While the increasing amount of genetic and landscape data allows for exploring new conceptual avenues, progress is still hampered by methodological challenges on how to link genetic variation with the environment in a statistically valid way. This is a particular challenge for analyses of neutral genetic structure, which often require pairwise comparisons (e.g., distances) between populations or individuals. The response and explanatory variables are in the form of (dis)similarity or distance matrices, in which values are not independent of other values in the same row/column. Therefore, (partial) Mantel tests have been frequently applied in landscape genetics to test for statistical significance (Cushman and Landguth 2010; Landguth et al. 2010; Storfer et al. 2010). However, it has been shown that Mantel and partial Mantel tests may exhibit higher type-1 error rates than multivariate regression approaches (Balkenhol et al. 2009b). Similarly, Legendre and Fortin (2010) suggest that the power of linear correlation, regression and canonical analysis is far greater than that of the (partial) Mantel tests. This indicates that multivariate, non-linear methods are likely better suited for to detect a relationship in genetic data when one is present (Balkenhol et al. 2009b; Legendre and Fortin 2010; Van Strien et al. 2012). To supplement the current controversy on Mantel tests, T. Graves (Colorado State University, USA) gave an overview of do's and don'ts related to this method and concluded that they should not be used as the Mantel r appears to be a poor and biased criterion for inferring landscape effects on gene flow (Graves et al. 2013). As pointed out by M. van Strien (PLUS, ETH Zürich, Switzerland), linear mixed effect models which account for dependency between pairwise observations in a distance matrix are a more appropriate way to go (Yang 2004; Van Strien et al. 2012). Similarly, Bayesian approaches may provide more appropriate and powerful ways for analyzing landscape effects on genetic variation (Kuroe et al. 2011; Hanks and Hooten 2013).

## Useful information: the role of landscape genetics for management and conservation

Landscape genetics has great potential to provide baseline information for applied sciences and conservation (Segelbacher et al. 2010). As outlined by J. Bolliger, WSL, Switzerland, there are three important contributions to be made: first, landscape genetics may provide baseline information on dispersal and movement of threatened species (Keller et al. 2010), second, it may contribute to optimizing management measures such as wildlife corridors (Sawyer et al. 2011; Epps et al. 2013), and third, it may help evaluate the effectiveness of conservation measures (Aavik et al. 2012, 2013). For example, if management measures (e.g., corridors) are too similar to the breeding habitat of a species, the genetic exchange via the corridor may be reduced as individuals choose to settle within corridors, thus severely jeopardizing the functional role of management measures (F. Pflüger, University of Göttingen, Germany).

Among baseline information of species movement, hypotheses on which landscape elements foster or hinder species movement are probably most important. T. Flavenot (National Museum of Natural History, Paris, France) showed that quarrying in landscapes is likely hindering genetic exchange between amphibian species (*Bufo calamita, Bufo bufo*), whereas the multispecies assessment presented by C. Vernesi (Centro Ricerca e Innovazione, Fondazione Edmund Mach, Italy) showed that the genetic pattern of four out of five mammals follow the same biogeographical barrier. M. Mateo-Sanchez (Technical University of Madrid, Spain) presented how to parse out local resource use and resistance to movement. Conclusions were that movement preferences and habitat selection are not driven by the same environmental factors and should be considered separately when studying the resistance of a landscape. Finally, J. Guerrero (University of Glasgow, UK) assessed the role of dams as barriers for the movement of otters in Mexico.

## Conclusions for future avenues in landscape genetics

(1) As landscape data are increasingly available at finer resolutions across large spatial scales, landscape geneticists enthusiastically relate

landscape features to explain observed genetic variation. While this allows new hypotheses to be tested, endogenous processes shaping the genetic structure such as population density, life-history attributes referring to dispersal and migration, or mating systems with overlapping generations require consideration as additional factors in shaping the genetic variation in natural populations. Additionally, the temporal dimension in landscapes for both the past and the future should be given increased attention as the genetic responses to landscape change may be non-simultaneous, resulting in time lags.

(2) While quantitative assessments of landscape complexity often relate to landscape composition, increasing attention should be given to the spatial configuration (i.e., spatial arrangement of landscape patterns).

(3) Inferring genetic connectivity based on dispersal using assignment methods or parentage analysis is of increasing importance for projecting gene flow as a result of future changing landscapes, or for assessing the directionality of gene flow to reliably identify source-sink dynamics on the landscape.

(4) When explaining pairwise genetic data with landscape features, linear mixed models or Bayesian approaches may provide more appropriate and powerful ways for analyzing landscape effects on genetic variation compared to (partial) Mantel tests.

(5) Adaptive genetic variation will play a key role in shaping landscape genetics and genomics. However, links between landscapes and adaptive genetic variation need to go beyond purely associative studies, ultimately combining information on adaptive and neutral genetic variation.

(6) Landscape genetics can provide important baseline information for applied conservation management such as basic information on species movement in a spatial context, assessments of the spatial need for management measures, or evaluate the effectiveness of already existing management measures.

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