

Ten years of landscape genetics

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Landscape genetics is now ten years old. It has stimulated research into the effect of landscapes on evolutionary processes. This review describes the main topics that have contributed most significantly to the progress of landscape genetics, such as conceptual and methodological developments in spatial and temporal patterns of gene flow, seascape genetics, and landscape genomics. We then suggest perspectives for the future, investigating what the field will contribute to the assessment of global change and conservation in general and to the management of tropical and urban areas in particular. To address these urgent topics, future work in landscape genetics should focus on a better integration of neutral and adaptive genetic variation and their interplay with species distribution and the environment.

Global change and genetic variation

The key drivers causing loss of biodiversity (i.e., the diversity of genes, species, and ecosystems) are overexploitation, invasive alien species, pollution, climate change, and, especially, the degradation, fragmentation, and destruction of habitats [1–3]. The complete extinction of an entire species is the most conspicuous result of this biodiversity loss. However, long before an entire species is finally lost, genetic diversity will already be substantially affected: it has been estimated that distinct populations are going extinct about three orders of magnitude faster than entire species [4]. The vanishing of populations is a process directly linked to the loss of intraspecific genetic diversity. It is therefore of great importance that we understand how the loss of genetic diversity caused by the aforementioned factors influences evolutionary processes [5–7]. In this respect, key questions are: (i) how has recent global change (i.e., land use and land cover as well as climate change) affected patterns of neutral and adaptive genetic variation; and (ii) are species likely to adapt to ongoing global change on an ecological time scale?

The main objective of modern landscape genetics is to improve our understanding of the effect of global change on genetic patterns to address these two key questions. After ten years of landscape genetic research, where are we in understanding the interaction between the landscape and evolutionary processes? Here we review the past ten years of landscape genetics, including recent methodological and conceptual advances, and then discuss the future of this

discipline with a particular focus on potential applications in terms of adaptation to global change and the conservation of natural resources.

Glossary

Adaptation: the process by which a population or a species globally or locally adapts to its environment. Adaptation refers to both the current state of being adapted and the dynamic evolutionary process that leads to adaptation.

Adaptive genetic variation: variation at loci that are under selection.

Covariance structure: incorporating a matrix of pairwise covariances of data into a model allows researchers to statistically account for the autocorrelation of data.

Cross-validation approaches: partition of a sample of data into complementary subsets, performing analysis on one subset (training set) and validating the analysis on another subset (validation or testing set). Used to validate regression models using an independent dataset.

Environmental association: landscape-genomic approach to detect loci at which allele frequencies are significantly correlated with environmental factors.

Gene flow: in its widest sense, the transfer of alleles or genes from one entity to another (e.g., between populations).

Genome scan: genotyping of many samples at a large number of loci across a genome to see whether any variant is associated with a phenotypic trait or environmental factor.

Isolation by distance: decrease in genetic similarity among samples with increasing geographical distance.

Landscape genetics: aims to inform on the interactions between landscape features and evolutionary processes, mainly gene flow and selection.

Landscape genomics: a subfield of landscape genetics investigating how environmental factors affect patterns of adaptive genetic variation.

Least-cost path: a path that minimizes the costs of movement through a landscape. Different resistance values to movement are assigned to several landscape elements in a cost surface.

Genetic clustering: grouping a set of individuals based on their genotype.

Genome-wide association study (GWAS): a genomic method searching for loci in a genome scan that are significantly associated with phenotypic traits. Conceptually similar to environmental association studies in landscape genomics.

Mantel test: a statistical test to detect correlation between two (or three in partial Mantel tests) distance matrices. In landscape genetics, this is usually a correlation between a matrix of pairwise genetic distances and matrices of pairwise geographic or landscape distances.

Migration-drift equilibrium: state in which the loss of alleles through genetic drift is compensated by the gain of alleles via gene flow.

Mixed linear models: a statistical model (linear regression) containing both fixed (i.e., known) and random (i.e., unknown) effects.

Model species: a species for which the full genome and significant amounts of genomic information are available.

Moran's eigenvector maps (MEM): MEM analysis produces uncorrelated spatial eigenfunctions used to dissect spatial patterns of a studied variation (e.g., allele frequencies) across a range of spatial scales.

Multiple regression on distance matrices: a multivariate expansion of the Mantel test.

Neutral genetic variation: variation at loci that are not under selection. Neutral loci can show the signals of adaptation if they are strongly linked to loci under selection.

Outlier loci: loci identified as showing signs of selection using population-genomic methods and genome scans.

Overlay: a purely visual inspection of spatial coincidences between the location of genetic group or genetic boundaries and any landscape element in GISs.

Population genomics: captures signals of selection by searching for loci in a genome scan that show higher or lower differentiation among populations (i.e., outlier loci) than expected under neutral evolution.

Seascape genetics: landscape genetics in marine ecosystems.

Single nucleotide polymorphism (SNP): genetic variation at a single position in a genome (usually for only two alleles).

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Ten years of landscape genetics

For a long time, researchers aimed to combine ecology and population genetics. However, this was a complicated task because of the disparities between the two scientific communities. The introduction of landscape genetics in this journal ten years ago [8] helped to stimulate a decade of research by facilitating the integration of researchers in the fields of population genetics, landscape ecology, and spatial statistics.

Over the past ten years, landscape genetics has increased our understanding of two main evolutionary processes: gene flow and adaptation. First, landscape genetics has helped a move from the study of gene flow in a purely theoretical space characterized by geographical distances only, to the study of gene flow in heterogeneous and fragmented landscapes providing estimates of functional connectivity (Box 1). Second, and in parallel with technical progress made in sequencing methods, landscape genetics has offered an empirical approach to investigate patterns

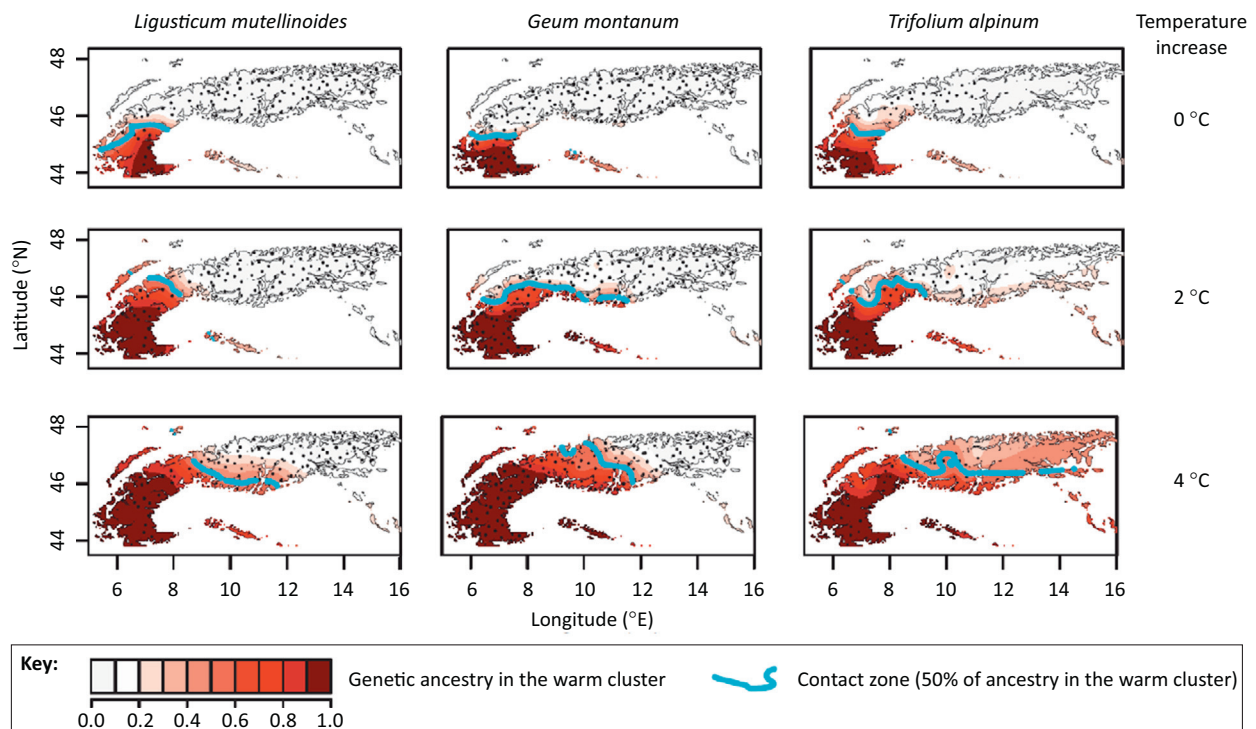
Box 1. Functional connectivity, genetic structure, and climate change

Dispersal is the process by which individuals are driven out of their birth habitat (or population) to reproduce in another habitat (or population). This process is a key factor for population persistence, especially in fragmented landscapes [76]. Dispersal in heterogeneous landscapes leads to the notion of functional connectivity. Functional connectivity has been defined by Taylor *et al.* [77] as ‘the degree to which the landscape facilitates or impedes movement among resource patches’. It describes the response of individuals to landscape features (in terms of dispersal behavior, mortality risks, and inferred costs to movement) as well as the resulting dispersal rates. Functional connectivity is one component of connectivity, the other being structural connectivity. Structural connectivity simply states that habitat patches (and the populations living therein) are linked by spatial structures in a landscape (e.g., hedgerows, field edges, stepping stones), irrespective of whether they provide functional connectivity. Other terms are used to describe connectivity, such as population, habitat, or landscape connectivity [78], but they often do not discriminate between structural and functional connectivity.

Functional connectivity can be estimated in various ways [79]. In the context of landscape genetics, measuring genetic connectivity by gene

flow [70] is one method of interest. Historical and contemporary gene flow can be estimated from genetic distances or assignment and parentage tests [71].

Functional connectivity is of crucial importance for tracking shifting niches under climate change [7]. Hitherto, studies of the impact of climate change on connectivity are scarce. For example, Wasserman *et al.* [80] combined landscape-resistance estimations of current functional connectivity and simulations of future landscapes under climate change to investigate the effect of climate change on the connectivity of the American marten in the northern Rocky Mountains. These authors found that even moderate warming scenarios will result in large reductions in functional connectivity. In another approach studying the effect of climate change on genetic structure, Jay *et al.* [81] predicted how the genetic structure of multiple alpine plants will change under diverse climate-change scenarios (Figure 1). They found that cold-adapted population clusters mainly found at the northern fringe of the Alps will be replaced by more warmth-adapted clusters immigrating from the south-western border of the Alps. Such studies can also be used to estimate the migration rates required for pre-adapted genotypes to keep up with ongoing climate change.



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Figure 1. Predictions of genetic structure displacement in three alpine plant species (*Ligusticum mutellinoides*, *Geum montanum*, and *Trifolium alpinum*) under different temperature scenarios. Predictions are for mean annual temperature increases of 0, 2, and 4 °C. For each location on the maps, the color intensity represents the amount of genetic ancestry (or individual admixture coefficients) for clusters adapted to warm temperatures. The blue lines represent the contact zone between ‘warm’- and ‘cold’-adapted populations [80]. Reproduced, with permission, from [81].

of adaptive genetic variation in wild and domestic [9] species in real landscapes, making it possible to detect environmental factors driving the process of adaptation [10]. Below, we describe the main topics that have contributed most significantly to the progress of landscape genetics during the past ten years.

A toolbox for studying genetic connectivity

Landscape genetics provides a set of tools to correlate the spatial heterogeneity of landscapes with estimates of gene flow and has inspired numerous methodological and conceptual developments. Landscape-genetic studies have mostly used simple (or partial) Mantel tests, which relate a matrix of genetic distances between individuals or populations to matrices of geographical (Euclidian) or landscape distances – for example, based on single [11] or multiple least-cost paths (i.e., circuit theory; [12]) – to investigate landscape effects on gene flow [13]. Such studies, known as causal modeling [11], usually test several hypotheses of landscape permeability, estimated by least-cost paths derived from different cost surfaces, and then evaluate which one best explains the matrix of pairwise genetic distances.

However, Mantel tests and related methods such as multiple regression on distance matrices have been strongly criticized [14]. Because of non-independence in the response and predictor variables, the actual degrees of freedom are unknown and common methods to select the best model from a set of alternative models such as R^2 or the Akaike information criterion (AIC) are invalid [15]. One alternative to deal with the problem of non-independence is the use of mixed effect models incorporating the covariance structure of allele frequencies [16].

Unless hypotheses are strictly formulated in terms of distances, future analyses in landscape genetics should not

use Mantel tests or related methods [17]. In the long term, landscape genetics needs to find ways to measure gene flow directly from raw data (e.g., allele frequencies) and then use diverse types of multiple regression (in the case of a single response variable) or canonical redundancy analysis (for multiple response variables) when investigating gene flow in response to landscape configuration and composition [17].

Genetic patterns depend on temporal and spatial scale

Landscape genetics stresses the importance of temporal-scale effects [18]. One prominent feature is lag times. Hitherto, most landscape-genetic studies used genetic distances among populations to estimate gene flow. However, genetic distances (mainly) reflect historical patterns of gene flow and might not be indicative of gene-flow patterns in contemporary landscapes. However, empirical studies have found that genetic distances reflect contemporary landscapes better than historical landscapes (e.g., [19]), and Landguth *et al.* [20] showed, in a simulation study, that implementing a barrier will rapidly result in a detectable genetic response, whereas the removal of a barrier will become measurable only with a time lag of many generations. Accordingly, the question of the relevance of time lags in landscape genetics remains to be settled.

The effects of spatial scale on genetic patterns have only recently been tackled in landscape genetics by restricting analyses to those populations within certain distance classes; for example, maximal migration distance or neighboring populations. By doing so, researchers have found that distinct landscape effects are often detected only up to certain distances. For instance, a damselfly stuck to streams during short-distance dispersal but used open agricultural land during long-distance dispersal [21]. A

Box 2. Spatial graphs

A graph is a mathematical object comprising nodes (dimensionless points represented by dots) and edges (lines). Spatial graphs are used in evolution or ecology to quantify and understand the interactions among individuals, populations and habitats (i.e., nodes) and processes among nodes such as movement or dispersal behavior (i.e., edges) [82]. Nodes can have attributes; for instance, they can be characterized by census population size or genetic diversity. Edges can be weighted by nearest neighbor, maximal dispersal distance or estimates of gene flow, for example.

Graph theory was first used in biology to model organisms and their interactions in aspatial graphs and networks (e.g., [83]). Algorithms were then developed to integrate spatial information into graphs [84,85]. In a spatial graph, nodes have explicit locations and edges link locations (Figure 1). Specific hypotheses can be tested by comparing an observed graph with a theoretical random graph. A random graph starts with only the nodes; edges are added to randomly chosen pairs of nodes.

Several of the local and global properties of graphs can be used to test specific hypotheses about the structure of ecological systems and to compare observed and theoretical graphs. The degree of a node is simply the number of other nodes linked to it. Clustering is the proportion of edges there are among the neighboring nodes of a specific node in comparison to a fully connected neighborhood. The centrality of a node counts as the fraction of shortest paths between pairs of nodes that pass through this node. Centrality metrics evaluate the paths between all possible pairwise combinations of sites across a landscape to rank each site's contribution to facilitating interactions (e.g., gene flow) across the whole network [86]. A network is said to

be modular if it is arranged in groups of nodes that interact frequently among themselves but show little interaction with nodes from other modules.

Spatial graphs have rarely been used in landscape genetics to investigate hypotheses regarding the connectivity of a set of populations (but see [22,87,88]). The potential of spatial graphs in the field of landscape genetics is based on the possibility of comparing spatial graphs drawn up with different links between patches, such as: (i) edges representing topological connectivity in a planar graph; (ii) functional links of shortest and least-resistant corridors for dispersal; and (iii) edges showing smallest genetic distances.

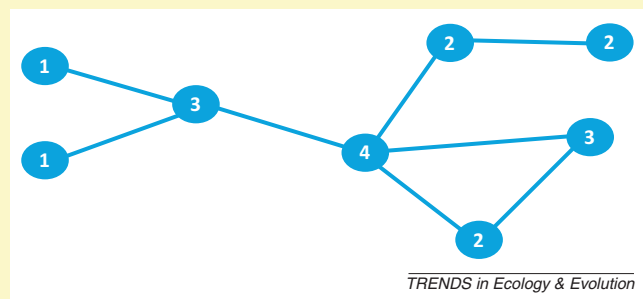


Figure 1. Example of a spatial graph. The degree of the nodes (i.e., the number of nodes to which a particular node is linked) is shown in white.

topic related to scale effects is population arrangement, which also influences landscape genetic patterns and has not yet been investigated in depth [16]. Graph theory can help in understanding how scale and population topology influence spatially explicit patterns of gene flow [22] (Box 2).

Geographic information systems (GISs) facilitate the interpretation of results and communication with practitioners

The use of geo-referenced genetic data within a GIS is a prerequisite for spatial-based analysis of spatial ecological processes [23]. One important application of GISs in landscape genetics is the overlay of land use, land cover, or topographical maps with genetic groups or genetic boundaries [24]. The resulting maps are intuitively appealing, easy to understand, and can be used for illustration when communicating landscape genetic findings to practitioners or the public. For instance, the spatial separation of genetic clusters obtained using Bayesian clustering of roe deer genotypes coincided with the position of motorways in Switzerland [25], indicating fragmentation due to this infrastructure. Overlays should also enable the elaboration of maps of (adaptive) genetic diversity to prioritize conservation areas [26], or genetic maps could be combined with phenotypic maps in microevolutionary studies. There is also a potential application of overlays in the identification of current and future hotspots of disease outbreaks. However, overlays have not been used for these purposes and their potential therefore remains to be fully assessed.

Seascape genetics

Marine ecosystems have been largely understudied in landscape genetics [27], because of their distinct environmental differences with terrestrial ecosystems [28]. In marine ecosystem, seawater currents, water temperatures, or resource gradients are of particular importance. Consequently, seascape genetics has emerged as an independent but expanding branch of landscape genetics [29,30].

Marine ecosystems largely preclude direct observation [30]. Therefore, genetic methods are powerful tools to characterize connectivity among marine populations or to determine the relevant spatial scale of population structure. Recently, several in-depth studies have investigated larval dispersal by combining biophysical oceanographic models and seascape genetics. For example, Selkoe *et al.* [31] found significant and consistent correlations between kelp beds and both genetic differentiation and diversity in three temperate reef species at a small spatial scale of the Southern California Bight. These shared patterns suggested that a single spatial marine-management strategy should effectively protect multiple species. Selkoe *et al.* [31] also found significant correlations between migration probabilities estimated from an ocean circulation model and genetic differentiation, indicating that ocean currents drive gene flow for some species.

Seascape genetics, however, would gain from using more large-scale sampling to capture wide-ranging patterns of connectivity and from being more aware of the progress being made in terrestrial landscape genetics,

because the statistical approaches and methodological concepts applied in the two fields are broadly the same.

Landscape genomics, a powerful tool for studying adaptive genetic variation

Landscape genomics (a branch of landscape genetics) aims to identify environmental or landscape factors that influence adaptive genetic diversity in wild species using genome scans with a large number of molecular markers genotyped per individual. The development of landscape genomics was greatly aided by the emergence of large genomic and environmental datasets in population genomics [32].

So far, most landscape-genomic studies have used population genomic tools such as outlier locus detection (e.g., [33]) (Table S1 in the supplementary material online). In these studies, the allelic distribution at identified outlier loci is *a posteriori* correlated with the distribution of environmental factors. However, specific landscape genomic approaches have also been developed that directly correlate allele frequencies with environment factors (e.g., [34,35]) (Table S1 in the supplementary material online). One important point in landscape-genomic studies is the need to account for genetic structure and/or demographic effects during analysis. This can be done using linear mixed models or Moran's eigenvector maps [36].

Recently, the availability of large single nucleotide polymorphism (SNP) datasets (with millions of molecular markers genotyped per individual) based on next-generation sequencing techniques has encouraged the development of new techniques for genome-wide association studies (GWASs) [37,38]. GWASs search for associations of SNPs with particular phenotypic traits that are stronger than would be expected under neutral evolution. Such SNPs indicate genomic areas that are potentially under selection for a given trait. The GWAS approach is conceptually close to landscape genomic approaches that evaluate the association of SNPs with environmental factors instead of phenotypic traits.

Although landscape genomics is currently establishing a flexible framework for linking patterns of adaptive genetic variation to environmental heterogeneity, evolutionary biology issues are also enjoying a revival. Questions such as 'what is the relationship between global and local patterns of adaptation?' and 'how important are spatial scale and habitat heterogeneity in maintaining adaptive genetic variation?' are highly relevant for the management of biodiversity under global change.

The future of landscape genetics

Although landscape genetics has evolved considerably over the past 10 years, there remains room for future development. In this section, we develop some areas in which landscape genetics could contribute significantly to future scientific progress.

Prediction and conservation management

Great hopes have been placed in landscape genetics' ability to inform conservation management by providing fundamental knowledge on dispersal ecology, fragmentation, functional connectivity, and the effectiveness of connectivity measures [39–41]. Similarly, landscape genomics can

determine which populations should be given priority when conserving adaptive genetic variation [42]. Consequently, it is time for landscape genetics to evolve from a descriptive to a more predictive science to have more impact on conservation management. This requires, first, an understanding of the behavior of multiple species in the same or multiple landscapes [43] and, second, extrapolation from one species to other species and from one landscape to other landscapes.

Multispecies landscape-genetic or -genomic studies are a promising approach to achieve successful conservation strategies [26], because it is almost impossible to deduce general landscape effects on gene flow or local adaptation from single-species studies. For example, Amos *et al.* [44] used genetic data to rank various alternative models, from high-resistance models for sedentary species (i.e., species that barely move through the landscape) to a 'no isolation by distance' model for the most mobile species (i.e., the landscape has no effect on movement), in ten woodland birds. Landscape-genetic or -genomic studies could also compare species from diverse taxonomic groups or different habitat types in the same landscape [45]. Recently, Manel *et al.* [46] showed that, for 13 wide-ranging alpine plants, the same environmental variables drive adaptive genetic variation at the whole biome scale of the European Alps. This example shows that carefully selecting a representative set of ecologically relevant species (e.g., common or dominant species) makes it possible to identify general patterns that go far beyond single-species studies. High-throughput next-generation sequencing and the reduction in processing costs per sample open perspectives for deriving large genomic datasets for a large number of organisms. Comparing the genetic patterns of many species will make it possible to test hypotheses on the processes that cause variation among species in the same or different ecosystems [47]. Investigating several species also makes it possible to determine whether there is selection at the community level [48] and whether parallel evolution has occurred [49]; questions of importance not only for science but also for conservation biology [50]. Regarding prediction, cross-validation of landscape genetic models is an important step in the elaboration of successful conservation strategies. Once a landscape genetic model for a species of conservation concern has been developed for one particular landscape, this model's predictive power can be assessed using various cross-validation approaches, such as leave-one-out or *k*-fold [51]. If the model's predictive power is sufficient, landscapes could now be changed *in silico* according to a specific change scenario. For instance, does the construction of a residential area dramatically influence functional connectivity? Do ecological compensation areas significantly increase gene flow? However, few corresponding studies have so far been conducted.

Spatial graph theory and simulations can be helpful in addressing questions relevant to predictive conservation [52] (Box 2). They resolve gene-flow patterns at multiple spatial scales [53] and can identify populations of particular relevance to the integrity of habitat networks or the maintenance of metapopulations [54], allowing the testing of various scenarios of landscape change.

Landscape genetics in tropical regions

About two-thirds of all known species occur in the tropics [55], but before 2010 only 10% of landscape-genetic studies focused on tropical regions [27] and only one further study was published up to 2013. This is illustrated by tree species. Despite the existence of about 100,000 tree species worldwide, mostly in the tropics, genetic and genomic research has focused on a few temperate species. Tropical trees have barely been studied, with the exception of a few economically important species such as coffee [56], cocoa, and papaya.

Deforestation is of particular concern in the tropics [57]. It has accelerated alarmingly during recent decades as a result of increasing demands for fuel, timber, and agricultural land associated with human population growth [58]. This unprecedentedly rapid disruption of tropical forests is a greater threat to global biodiversity than any other contemporary phenomenon [57]. It requires the urgent development of appropriate conservation strategies considering both species and evolutionary processes. In an example from Ecuador, a tropical area recognized as a hotspot of biodiversity, Thomassen *et al.* [26] combined species-distribution models, landscape genetics, and reserve-design algorithms to prioritize seven amphibian, bird, and mammal species. They concluded that priority areas for intraspecific variation, located mainly on the slopes of the Andes, were largely congruent among species, but clearly underrepresented in existing reserves.

The landscape-genetic toolbox offers many possible applications for the preservation of endangered species in tropical regions, especially regarding decreases in functional connectivity [59] (Box 1) as well as understanding centers of adaptation [26].

Landscape genetics in urban areas

Urban areas covered 0.5% of the planet's land area in 2000 and are predicted to expand 12-fold between 2000 and 2050 [60]. Until 2010, only 7% of landscape-genetic studies had been conducted in urban areas [27] and only one further study has been published since.

Urban areas (and cities) are highly fragmented landscapes. Landscape genetics can be extremely useful in assessing connectivity in urban species. However, many of the analytical approaches commonly used in landscape genetics assume equilibrium conditions such as migration-drift equilibrium [61]. Given the highly dynamic nature of urban systems [62], where fast landscape changes can cause high population extinction and recolonization rates, equilibrium conditions will often not be satisfied. Therefore, focusing on developing landscape-genetic tools that are less dependent on equilibrium conditions would be beneficial for landscape genetics, not only with respect to urban landscapes but in general, because most ecosystems will change in faster and more dynamic ways under global change. For example, Unfried *et al.* [63] studied the relationship between land cover and genetic differentiation in song sparrows (*Melospiza melodia*) in the Seattle metropolitan region. Their results suggested that urban development reduced song sparrow population connectivity. Because population dynamic equilibrium will not be reached, this loss of connectivity is set to increase in the future.

How global change affected, affects, and will affect patterns of neutral and adaptive genetic variation

Although essential for species persistence in the longer term, the consequences of global change on genetic diversity have so far been understudied [7]. Landscape genetics can play an important role in filling this gap by improving our understanding of the effects of global change on genetic diversity, both neutral and adaptive. Increased understanding requires improved knowledge of the molecular basis behind adaptively relevant traits and phenotypic variation (via adaptive diversity) and of the distribution of genetic variation concomitant to populations and species shifts (via neutral diversity).

The first step is to conduct surveys of the current distribution of environmental factors within landscapes and to determine how they influence the distribution of adaptive genetic variants. Several studies have recently found that annual temperature regimes influence the distribution of adaptive genetic variation in model [64,65] and non-model [46,66] organisms. Recent innovative research has applied niche modeling to *Arabidopsis thaliana* genotypes sampled across the species' ecological niche based on the analysis of candidate SNPs for flowering time [67]. Banta *et al.* [67] showed that later-flowering genotypes have a more restricted range potential and narrower niche breadths than earlier-flowering genotypes. This indicates that some geographical regions contain habitats suitable for some genotypes but not for others. This study neatly illustrates how it is essential to consider the intraspecific (i.e., genetic) diversity level when studying the impact of global change on species responses.

In a second step, studying contemporary gene flow using neutral genetic variation should make it possible to investigate the potential for adaptive genes to spread across landscapes. If this potential is high, gene flow will enable populations and species to adapt to changing environmental conditions not only due to standing genetic variation, but also owing to gene migration. For instance, Shimizu *et al.* [66] developed a mechanistic model of how genetic variation at the self-incompatibility locus in *Arabidopsis halleri* reacts and changes under specific temperature scenarios. Obviously, changes in allele frequencies at the self-incompatibility locus will have a substantial influence on gene flow patterns. Similar hypotheses could be developed for many species, once loci that are relevant under global change have been identified.

The third step combines spatial patterns of adaptive genetic variation with information on the pace of gene flow and makes it possible to forecast the future spatial distribution of adaptively relevant genetic variation in a whole species range under diverse global-change scenarios. Although such applications have not yet been conducted at ecological time scales, they now appear feasible [68] thanks to the ever-increasing sophistication of landscape-genetic and -genomic tools.

Concluding remarks

After 10 years of landscape-genetic research, it is fundamental to go beyond the mere description of patterns. Progress has been made toward a more theoretical

interpretation of the processes (gene flow versus selection versus drift versus recombination) behind observed patterns of genetic variation [69]. Landscape genetics now offers promising tools to better understand genetic patterns–process relationships. For example, landscape genomics already contributes to our understanding of the nature of genes involved in local adaptation to environmental heterogeneity. However, landscape genomics also has to proceed from identifying the loci or genomic regions under selection to dissecting and characterizing the underlying genes, genome architecture, molecular mechanisms, and ecological functions as well as their interactions.

Pattern–process analysis also needs to go beyond the separation of neutral and adaptive genetic variation. Currently, landscape genetics uses neutral genetic variation to estimate gene flow, but it would benefit immensely from improved integration of estimates of contemporary gene flow; for example, as measured with assignment methods [70,71]. At the same time, landscape genomics uses sophisticated methods to identify loci under adaptation. It is clear that these two branches of landscape genetics have not yet come together (but see [72]). This would represent a major step forward in evolutionary biology and molecular ecology. It would lead to the detailed analysis of how gene flow spreads alleles of adaptive relevance across landscapes, of how strong gene flow counteracts local adaptation, and of how strong selection advantages of immigrating alleles have to be to become established in resident gene pools [40]. For instance, Andrew *et al.* [73] studied adaptation under a regime of substantial gene flow in a sand dune species of sunflower. These authors found that isolation by adaptation also increases divergence at neutral loci when natural selection against immigrants reduces the rate of gene flow between different *Helianthus petiolaris* ecotypes in different dune habitats. Similar approaches could be used to monitor gene escape from genetically modified organisms (GMOs) [74,75] in situations where protective measures, such as isolating crop strips, have been implemented to reduce gene flow from GMO fields. They could also be used to optimize reserve design by integrating the evolutionary potential or adaptability of species [26] (Box 1).

Finally, the virtue of landscape genetics is that it has increased general awareness of the important effects that spatial patterns of landscape elements and environmental factors exert on neutral and adaptive genetic variation. In other words, landscape genetics has brought population genetics and evolutionary research closer to the empirical world as seen and experienced by organisms. This endeavor should continue.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tree.2013.05.012>.

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