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Considering spatial and temporal scale in landscape-genetic studies of gene flow

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Abstract

Landscape features exist at multiple spatial and temporal scales, and these naturally affect spatial genetic structure and our ability to make inferences about gene flow. This article discusses how decisions about sampling of genotypes (including choices about analytical methods and genetic markers) should be driven by the scale of spatial genetic structure, the time frame that landscape features have existed in their current state, and all aspects of a species' life history. Researchers should use caution when making inferences about gene flow, especially when the spatial extent of the study area is limited. The scale of sampling of the landscape introduces different features that may affect gene flow. Sampling grain should be smaller than the average home-range size or dispersal distance of the study organism and, for raster data, existing research suggests that simplifying the thematic resolution into discrete classes may result in low power to detect effects on gene flow. Therefore, the methods used to characterize the landscape between sampling sites may be a primary determinant for the spatial scale at which analytical results are applicable, and the use of only one sampling scale for a particular statistical method may lead researchers to overlook important factors affecting gene flow. The particular analytical technique used to correlate landscape data and genetic data may also influence results; common landscape-genetic methods may not be suitable for all study systems, particularly when the rate of landscape change is faster than can be resolved by common molecular markers.

Keywords: autocorrelation, dispersal, gene flow, sampling, space-time processes, spatial genetic structure

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Introduction

The field of landscape genetics has emerged as a synthetic discipline that combines concepts and tools from population genetics, landscape ecology, geography, and spatial statistics (Manel *et al.* 2003; Holderegger & Wagner 2008). Landscape genetics examines how landscape features affect recurrent microevolutionary processes (including gene flow and drift) in a spatially explicit manner at multiple spatial and temporal scales (Manel *et al.* 2003; Storfer *et al.* 2007; Holderegger & Wagner 2008; Balkenhol *et al.* 2009). Spatial and temporal considerations figure prominently in sample design, the efficacy of choices of molecular marker types, and selection of appropriate analytical tools (Storfer

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et al. 2007). While some studies have examined landscape effects on patterns of genetic variation at different spatial and temporal scales, researchers have only recently begun to formally consider scale effects on landscape-genetic inference (e.g., Cushman & Landguth 2010). Issues related to scale are believed to be a critical but largely unexplored subject in landscape genetics (Balkenhol *et al.* 2009).

The lack of a formal discussion of scale issues in landscape genetics could be due in part to confusion surrounding the many meanings and uses of the term 'scale' in the contributing fields of geography, spatial statistics, landscape ecology, and population genetics (Dungan *et al.* 2002). For example, 'scale' has been used variably to refer to map scale, grain, extent, lag, resolution, or support (Box 1). Dungan *et al.* (2002) suggested that researchers avoid vague usage of the term 'scale' and should discriminate between scales of phenomena, scales of sampling, and scales of analysis. Practically, this means that the spatial scale of sampling and analysis should be dictated by the ecological attributes of the study organisms and should coincide with the spatial distribution and time frame over which hypothesized phenomena have influenced spatial genetic structure.

This article reviews multiple considerations of spatial and temporal scale associated with the collection and analysis of landscape-genetic data for studies of gene flow. It is focused primarily on sampling and analysis of genetic and landscape data at different spatial scales, but also discusses connected issues of temporal scale. We start with issues of scale related the spatial sampling of genotypes, including questions about whether to sample individuals, groups, or populations. Next, we discuss how to characterize the landscape of interest with particular focus on how the resolution, grain, and extent of spatial data might influence study results. We then address the more complex question of how to relate measures of population-genetic structure to ecological or landscape heterogeneity in a statistical framework (Balkenhol *et al.* 2009). Finally, we discuss how recent landscape change and historical landscape states can be accounted for in landscape-genetic studies by careful choice of markers and analytical methods.

Spatial scale of sampling and analysis

Scale considerations for genetic sampling: individuals, groups, or populations?

Complex scale considerations come to bear when choosing how to sample and analyse genetic information at the level of individuals, groups, or populations. Population-based sampling in landscape-genetic studies is often chosen for species with discontinuous distributions or occupying clearly defined and separated habitats, especially over large geographic scales. Recently, however, landscape genetics has shifted towards individual-based sampling and analysis, especially when organisms are

Box 1 Scale synonyms and common usage within allied disciplines of landscape ecology

Scale synonyms:	*Grain*: the size of the elementary sample unit for analysis or of a phenomenon. Grain is expressed as the surface, area, or volume over which sampling is conducted. Grain is particularly relevant in the context of sampling of landscape data in genetic analysis (i.e., the pixel size of a raster map) *Extent*: the total area sampled or analysed. The spatial extent of sampling is important as it ensures that a sufficient number of populations or individuals are included and to ascertain that various landscape elements are included in statistical analysis *Lag*: refers to the spacing or interval between units of sampling, analysis, or phenomena. Lag distances should be dictated by species vagility and based on the degree of heterogeneity in composition and connectivity of landscape features. Genetic sampling at distances beyond functional dispersal distances will negatively affect the ability to detect effects of landscape features on spatial genetic structure (Box 3) *Thematic resolution*: the detail of data classes used to model landscape features
Common usage:	*Spatial statisticians* use scale in a variety of contexts associated with sampling, analysis, and the phenomena being studied. Terms such as grain, extent, lag, and resolution are commonly used *Geographers* often use scale in a cartographic context, as in map scale, map extent (or area), and map resolution. Scale terms and synonyms from spatial statistics are often used when analysing data *Ecologists* often use scale in the context of grain to describe the size of the elementary sample unit, or the scale of the process being studied (or the observed pattern). Scale is also commonly used to describe the spatial extent of the sample area. For example, the term 'landscape scale' is sometimes used as an antonym of 'local scale' to describe studies occurring over larger geographic extents *Population geneticists* often use scale to describe the spatial extent of the sample population or the scale of observed genetic differentiation. For example, the terms 'fine-scale' (Dick 2008) and 'microgeographic' (Selander & Kaufman 1975) have both been used to describe genetic differentiation over short geographic distances

continuously distributed (Segelbacher *et al.* 2010; Cushman & Landguth 2010; Freedman *et al.* 2010; Sork *et al.* 2010). Ideally, the choice should be made so that the data are best suited to the spatial and temporal scale of the ecological and evolutionary processes under consideration. For example, Bayesian *K*-means clustering algorithms (Pritchard *et al.* 2000; Corander & Marttinen 2006) have become popular tools for characterizing population-genetic structure based on individual genotypes in landscape-genetic studies. However, these methods are not suitable for the analysis of continuously distributed organisms exhibiting genetic isolation by distance (Box 2 and 3; Schwartz & McKelvey 2009) because differentiating between a pattern of isolation by distance and discrete population structure is impossible if sampling is not regular. For example, *Arabidopsis thaliana* exhibits isolation by distance at all geographic scales in its native Eurasian range, without any natural breaks in habitat features or distribution that could be used to delineate population boundaries (Platt *et al.* 2010). Hence for species like *A. thaliana*, Bayesian *K*-means clustering algorithms that assume discrete population structure may be of little utility, or even misleading, when used to infer landscape effects on gene flow. In such situations, genetic sampling points should be positioned such that large gaps relative to potential barriers to gene flow are avoided; otherwise, genetic discontinuities could be inferred simply because of unsampled individuals or populations.

Potential problems also arise in landscape-genetic studies when traditional methods of analysis intended for genetic 'demes' (e.g., F_{ST}; Wright 1951), within which restricted gene flow leads to coancestry, are applied to groups of individuals that locally co-occur, but where the spatial scale of mating exceeds the spatial boundaries of groups (Wilson 1977; Waples & Gaggiotti 2006). For example, using behavioural and genetic evidence for the timber rattlesnake (*Crotalus horridus*), Anderson (2010) found a high frequency of mating bouts between males and females from different overwintering hibernacula. This result suggested that patterns of genetic structure among hibernacula were best explained by behavioural and demographic factors resulting in natal philopatry, sex-biased dispersal, and/or a limited number of breeding adults, rather than by gene flow and drift *per se* (Bushar *et al.* 1998; Clark *et al.* 2008). These findings are especially pertinent to landscape-genetic studies conducted over relatively limited spatial scales, because other behavioural and demographic factors beyond gene flow may substantially affect observed patterns of genetic variation at this level (Storz 1999; Balloux 2004); in such cases, measures applicable to individuals or groups of individuals (e.g., shared allele distance) may be used in landscape-genetic framework to make inferences about dispersal, but not necessarily gene flow, *per se*. Such findings also suggest that researchers should be cautious when using landscape-genetic methods to make inferences about dispersal and gene flow for difficult to observe species. Furthermore, this underscores the importance of preliminary behavioural and/or ecological information in the design of landscape-genetic studies, so that individuals are sampled in locations and at times that are actually relevant to gene flow (i.e., population units associated with mating behaviours; Latch & Rhodes 2006).

However, researchers in landscape genetics often do not have relevant a priori behavioural and ecological information about the study species to sample appropriately. This can be especially problematic when organisms have different life stages that respond to landscape features and environmental variables at different spatial

Box 2 Sampling considerations from isolation by distance theory

Recommendations regarding the spatial scale of sampling for landscape genetics can be drawn from studies of isolation by distance (IBD) in two-dimensional systems (Epperson 2005a). Both theoretical considerations in IBD models and results of practical applications suggest that sample sizes of 50–100 individuals are minimal, and studies should try to have a few hundred individuals in many cases. The signal of spatial genetic structure may be particularly weak for high gene flow species (Waples 1998). However, appropriate sample size also depends on how many loci will be assayed. Under the null hypothesis of a random distribution, for pairwise spatial measures, the number of pairs of distinct genotypes that are used largely determines the variance of the estimator (Cliff & Ord 1973). Hence for summary spatial measures, the variance can be reduced either by increasing numbers of loci (or alleles) or sample size; usually, several loci should be used because of the high level of stochasticity typical of spatial-temporal genetic processes (Epperson 2003). There are instances where it has been shown that accuracy of estimated spatial measures can be more readily achieved by increases in sample size relative to increases in number of loci (Murphy *et al.* 2008; Epperson 2010). Finally, there is evidence that in IBD processes, the signal to noise ratio decreases with increasing spatial scale (Epperson 2010), suggesting that the ability to detect significant spatial genetic structure at larger spatial scales features may require larger sample sizes or greater numbers of markers. However, further research is needed to determine how useful such guidelines might be in more complex landscapes where geographic distance is a poor predictor of landscape resistance

Box 3 A cautionary note about scale and genetic isolation by distance

Past confusion over issues of scale is exemplified by interpretations of the spatial scale and magnitude of spatial autocorrelation produced in isolation by distance (IBD) processes in two-dimensional space (Guillot *et al.* 2005). Frequently, the area over which there is positive spatial autocorrelation of genetic variation has been mistakenly equated with Wright's neighbourhood size ($4\pi D\sigma^2$; Wright 1943) where D is the population density and σ^2 is the axial variance of dispersal distances; the σ^2 term can also be considered as the rate of spatial divergence of two lineages from a common ancestral lineage (Rousset 1997). The spatial scale of autocorrelation is usually much larger than, and nonlinearly related to, neighbourhood size. Therefore, while the former can be a measure of the spatial scale of spatial genetic structure, the latter cannot. To make correct inferences using the relationship between dispersal and spatial autocorrelation under IBD, measures of dispersal distance must be scaled by density. Then the predicted autocorrelation values can be obtained as a function of distance (Epperson 2005a)

In addition, the scale at which individuals are sampled (extent and lag, Box 1) must be considered to determine the predicted values of autocorrelation among sampled genotypes. Epperson (2003) discussed considerations of dispersal scale and scale of sampling in empirical studies. Much of the confusion may be because of an assumption that gene movement during a single generation equates to spatial autocorrelation, when typically spatial autocorrelation of genetic variation accrues over time. Under more complex (i.e., multivariate; Spear *et al.* 2010) landscape processes, we may expect similar dangers in ignoring the temporal scale over which phenomena have existed and influenced spatial genetic structure

and temporal scales. For example, Chaput-Bardy *et al.* (2008) sampled populations of damselflies (*Calopteryx splendens*) within and among stream networks, in which larvae are aquatic but adults are terrestrial. The authors found evidence of isolation by distance both along stream networks and with Euclidean distance, suggesting that both life stages contribute to population structure. Thus, understanding landscape effects on gene flow for this species necessitates incorporating both terrestrial and aquatic features. Stream-breeding amphibians also exhibit dispersal patterns in which larvae are restricted to aquatic corridors while adults are terrestrial. For example, gene flow in Idaho giant salamanders (*Dicamptodon aterrimus*) follows stream corridors with little evidence for overland connectivity (Mullen *et al.* 2010), whereas coastal tailed frogs (*Ascaphus truei*) demonstrated no evidence of restriction to stream connectivity (despite obligate stream use by larvae), and only terrestrial landscape variables were important in explaining genetic structure (Spear & Storfer 2008). In plant species, pollen and seed often disperse at different scales. For example, pollen dispersal is extensive in eastern white pine (*Pinus strobus*), but seed dispersal is more limited (Epperson & Chung 2001). Such case studies demonstrate that many relevant ecological and landscape processes occur at multiple spatial and temporal scales, which indicates that all aspects of a species biology or life history should be carefully considered in landscape-genetic studies.

Spatial scale considerations for sampling landscape data: grain, extent, and resolution

Multiple factors that act at various spatial scales affect spatial connectivity and rates of gene flow across a landscape. These factors can include abiotic (e.g., rivers, topography, environmental conditions), biotic (e.g., forest structure, vegetation composition, and presence of prey, predators, or competitors), and anthropogenic features (e.g., roads, dams, urban areas, pipelines). Emergent patterns of gene flow are the result of the interactions between structural landscape connectivity and how organisms respond to landscape structure (Manel *et al.* 2003). Terrestrial organisms respond to complex landscape structure at their own unique set of spatial and temporal scales, based on their inherent dispersal abilities and sensitivity to environmental change (D'Eon *et al.* 2002).

Spatial and environmental features that contribute to either facilitating (i.e., connectivity) or reducing (i.e., resistance) rates of movement can be of various sizes and can also vary temporally (e.g., seasonally or over longer time frames because of climatic or successional changes). Such landscape spatial heterogeneity not only influences, directly or indirectly, landscape connectivity, but also the probability of site occupancy (Spear *et al.* 2010) in potentially complex ways that are scale dependent.

For computational analysis of landscape-genetic data, landscape features have most frequently been modelled as continuous surfaces with raster data and less frequently as discrete objects in vector format. The grain of landscape data determines pixel size in a raster surface or minimal polygon size of homogenous landscape features for vector data (Fig. 1a) and should be smaller than the average home-range size or dispersal distance of the study organism (Fortin & Dale 2005). For raster-based analysis, it is important to select an appropriate sampling grain carefully. If too small, information is likely to be redundant; if too large, relevant information on landscape features may be overly smooth, potentially obscuring inferences about the effects of particular

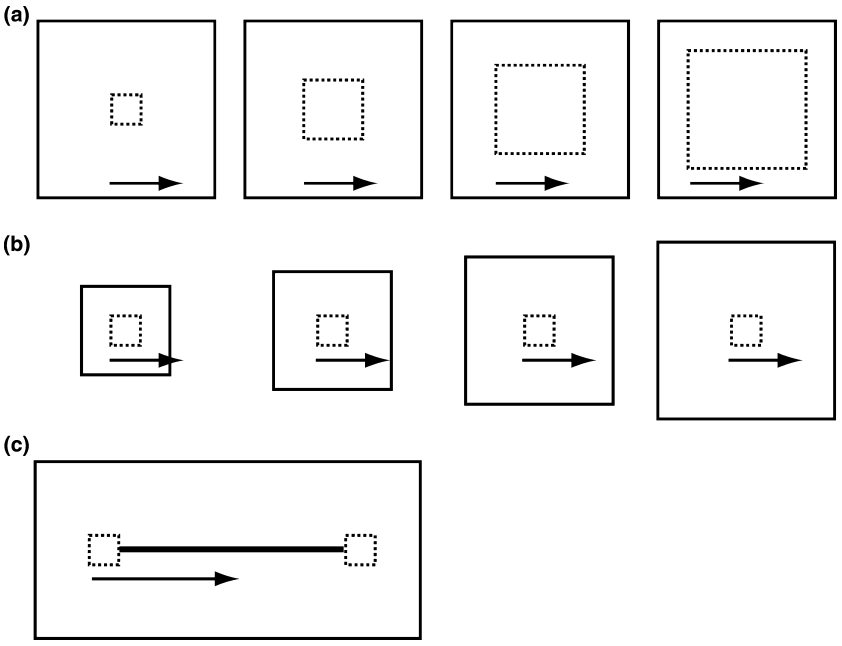

Fig. 1 Important aspects of landscape data sampling: (a) grain size, (b) extent size, and (c) spatial distance between sampling units. The dotted line is used for the grain, the solid line for the extent, the bold line for the distance between sampling units, and the arrow line indicates the dispersal distance of an organism.

landscape features on gene flow. When possible, the smallest possible initial grain of data collection is preferred because data can be merged to a coarser resolution as needed (Wu 2004; Fortin & Dale 2005). However, Cushman & Landguth (2010) found that the thematic resolution (Box 1; Buyantuyev & Wu 2007) influenced the results of partial Mantel tests more than sampling grain, which suggests that simplifying continuous landscape variables into discrete classes may result in low power to detect landscape effects on gene flow.

The position of the study area and the determination of its extent are also critical decisions (Plante *et al.* 2004). The study area size or extent (Fig. 1b; O'Neill *et al.* 1996, 1999) should be larger than the area occupied by the population of interest and larger than expected dispersal distances (Fig. 1c). If the study area extent is too small relative to the scale of gene flow, the influence of gene flow from populations or individuals outside the study area may overwhelm any signature of landscape effects in the sampled study area (Cushman & Landguth 2010). Hence, the construction of a buffer zone surrounding the study area (ideally proportional to species dispersal ability) should be considered in future landscape-genetic analysis (Fortin & Dale 2005). However, sampling at distances beyond functional dispersal or migration distances can also decrease the signature of landscapes effects on gene flow (Murphy *et al.* 2008).

Scale considerations for statistical analysis of landscape-genetic data

Determining how landscape features affect gene flow requires appropriate sampling of individual genotypes and landscape variables, as well as a suitable approach to integrate genotype data and landscape data (Manel *et al.* 2003; Holderegger & Wagner 2008). It is primarily the resistance, or conversely the permeability (McRae 2006; Spear *et al.* 2010) of landscape features between sampling locations that determines genetic distance or differentiation among individuals or populations at neutral molecular markers. Nevertheless, correlating genetic and landscape distances is not always straightforward because many analytical options exist, including: Mantel tests, constrained ordination, and multiple regression on distance matrices (Balkenhol *et al.* 2009; Legendre & Fortin 2010). To complicate matters further, it has also been demonstrated that the specific analytical technique used to correlate landscape data and genetic data may influence landscape-genetic results (Raufaste & Rousset 2001; Storfer *et al.* 2007; Balkenhol *et al.* 2009). Furthermore, the scale of sampling of the landscape (i.e., the grain, extent, and resolution) introduces different landscape features that may affect gene flow. Therefore, the methods used to characterize the landscape between sampling sites may be a primary determinant for the spatial scale at which analytical results are applicable. For example, a straight-line network connection (Garroway *et al.* 2008) is one method used to measure and correlate landscape features with gene flow among sites without a priori hypotheses of landscape permeability or resistance; significant landscape associations detected along networks are often dependent on the corridor width used to assess landscape structure between sampling locations. Murphy *et al.* (2010) tested landscape associations of western toads (*Anaxyrus boreas*) with different corridor widths. They

found that using different widths was informative for understanding the scale at which landscape variables affect connectivity. For example, land cover variables were only correlated with genetic distances at finer scales, and ridgelines were significant only at broader scales, while some variables, such as precipitation (having an indirect effect on gene flow through habitat humidity), were included in models at all scales. Emaresi *et al.* (2010) also found that landscape-genetic models differed by straight-line corridor widths in an investigation of the alpine newt (*Mesotriton alpestris*). Such studies demonstrate that the use of only one scale may lead researchers to overlook important factors affecting gene flow and support assertions from the landscape-ecology literature that landscape variables can influence ecological processes differently at multiple scales (Keitt & Urban 2005).

While it is relatively easy to account for scale by adjusting corridor widths or lengths in straight-line networks, it is less clear how to readily incorporate landscape variables at different scales in least-cost distance modelling, one of the most popular approaches in landscape genetics (Storfer *et al.* 2007, 2010). One potential idea analogous to varying corridor width would be to construct resistance surfaces at different pixel sizes and use the different surfaces to run separate least-cost or circuit theory analyses (Cushman & Landguth 2010).

Another popular landscape-genetic approach is to simply overlay the results of a clustering analysis (i.e., cluster membership) with a perceived barrier to gene flow and then to qualitatively compare the spatial coincidences of cluster boundaries or barriers with particular landscape features (Manni *et al.* 2004; Guillot *et al.* 2005; Balkenhol & Waits 2009; Clark *et al.* 2010). Overlay methods are a good exploratory tool, but even this relatively simple approach strongly depends on scale. At fine spatial scales, there may be noise in the genetic data set associated with intrademic structure, and at large spatial scales, it may be difficult to distinguish between landscape effects on migration and genetic drift from other microevolutionary forces (e.g., mutation). Moreover, simple overlay methods are not statistical in nature because they do not assess the possibility that genetic boundaries and landscape data are associated because of random chance. This is why spatial overlap statistics should be used to test for significant overlap of boundaries with landscape data (Fortin & Dale 2005).

A major, ongoing challenge in landscape-genetic studies of gene flow is accounting for heterogeneity in the landscape at different spatial scales. Global statistical analyses may be inappropriate as they assume that the underlying process is stationary (i.e., its properties are independent of the absolute location and direction in space; Fortin & Dale 2005). If the process is nonstationary, one should consider statistics that can measure the degree of spatial structure at local scales, such as local indicators of spatial association (LISA; Anselin 1995) and geographically weighted regression (GWR; Fotheringham *et al.* 2002). Such statistical analyses have not yet been commonly used in landscape genetics, but a recent example used GWR to demonstrate that different models of genetic connectivity for Rocky Mountain tailed frogs (*Ascaphus montanus*) were supported in privately and publicly managed forests despite close spatial proximity of the two land ownerships (Spear & Storfer 2010). Further evaluation of how nonstationarity at different spatial scales affects landscape-genetic inferences about gene flow is likely a fruitful avenue for future research in this field.

Replication across scales and landscapes

Because each landscape has its own series of historical events and set of landscape features, unique conditions raise critical issues of replication. How can researchers replicate uncontrolled landscape structure (such as spatial configuration of land cover) and other environmental features (such as elevation) at different scales? The choice of landscape features to study as well as the methods used to parameterize measures of landscape permeability or resistance (Spear *et al.* 2010) have to be evaluated for each study region independently. A priori identification of suspected variables of importance would allow researchers to attempt to choose replicate landscapes that are most similar in amount and configuration of particular landscape features. However, the sampling of many landscape-genetic studies is opportunistic (i.e., where genetic sampling is feasible), and in some cases it may be impossible to evaluate specific hypotheses that relate landscape resistance to gene flow across study landscapes (Spear *et al.* 2010).

Temporal scale of sampling and analysis

Landscape change as reflected by loss of habitat quantity and quality, as well as fragmentation, has greatly accelerated during the last 50 years (Lindenmayer & Fischer 2006). Ecologists have long realized that landscape changes may occur so rapidly that there is a time lag between causal events or processes (e.g., forest clearing or agricultural intensification) and biological response (e.g., species extinction). For instance, the past and not the present landscape explains current plant diversity in Swedish grasslands (Lindborg & Eriksson 2004). Researchers studying metapopulation processes also recognize the importance of legacy effects from previous conditions

(Harding *et al.* 1998; Kuussaari *et al.* 2009), especially for past extinction and recolonization events (Wade & McCauley 1988). In genetic terms, the strength and duration of such legacies largely determine whether genetic markers and statistical analyses can quantify relationships between current landscape features and gene flow.

Scale considerations in choice of genetic markers

The choice of molecular markers used in landscape-genetic studies has a strong influence on both the spatial and temporal scales over which inference about gene flow are possible. Accordingly, researchers need to consider whether the genetic markers used vary at the temporal and spatial scales at which genetic change is expected or hypothesized to occur. Such considerations related to temporal scale have been extensively reviewed (Holderegger & Wagner 2008; Balkenhol *et al.* 2009) and are only briefly discussed here with respect to neutral loci.

Until recently, three types of DNA-based markers have commonly been used for landscape-genetic studies: microsatellites, amplified fragment length polymorphisms (AFLPs), and organellar (mitochondrial [mtDNA] or chloroplast [cpDNA]) DNA sequences, although the vast majority of studies have used microsatellites (Storfer *et al.* 2010). Choice of marker type should be dictated by rates of mutation and consideration of the time scale over which measures of variation among individuals and populations (e.g., genetic distances or differentiation) have accrued. Importantly, it has been shown that under isolation by distance (Box 2 and 3), most spatial autocorrelation is created over 20–50 generations (Epperson 2005b) and that earlier coalescent events are almost spatially independent (Barton & Wilson 1995). Twenty to 50 generations is usually not enough time for more than one mutation to accumulate on a genealogy even for microsatellite loci. Hence, nearly all current spatial genetic information on identity by descent is contained in extant allelic states (Epperson 2005b). Furthermore, isolation by distance theory shows that for loci with more than about five alleles, the spatial distributions of individual alleles are nearly independent (Epperson 2004). This suggests that highly variable loci such as microsatellites (typically scored by allelic state/size) are efficient for studies of fine-scale genetic structure (Cavers *et al.* 2005). Hence, in most cases, among these three types of markers, microsatellites are best for investigations regarding the consequences of contemporary landscape-level habitat loss and fragmentation.

Amplified fragment length polymorphisms are usually coded in a binary way by fragment presence or absence (Bonin *et al.* 2007). Although little is known about mutation processes and despite the problem of fragment homoplasy in AFLPs (Meudt & Clarke 2007), this marker type has often been used to infer genetic distances and differentiation in a way similar to microsatellites, especially in plants (Storfer *et al.* 2010). However, AFLPs have also been applied in landscape-genetic studies to make inferences about gene flow at larger spatial scales and longer temporal scales (Sander *et al.* 2006; Chaput-Bardy *et al.* 2008; Thiel-Egenter *et al.* 2009).

Mitochondrial and chloroplast DNA evolve at comparatively slower rates and thus are best suited for questions of historical change over large spatial scales. Because of their low mutation rate, homoplasy over long time periods (or among geographically distant populations) is less of a problem than for microsatellites and, probably, for AFLPs (Takazaki & Nei 2008). It is worth noting that gene flow of organellar genomes is often mediated entirely by one sex (Scribner *et al.* 2001), and hence spatial patterns of genetic variation may occur at different spatial scales. By using multiple markers with different modes of inheritance (e.g., maternally inherited mtDNA or cpDNA vs. biparentally inherited microsatellites), one can reveal differences in the long-term accumulated effects of sex-bias in dispersal in animals or distinguish between pollen and seed dispersal in plants (Trapnell & Hamrick 2005). For example, measures of population differentiation (F_{ST}) for markers with different inheritance patterns have been used to estimate pollen to seed ratios of movement for a large variety of plant species (Ennos 1994; Petit *et al.* 2005). In many cases, however, pollen and seed dispersal may interact and it may be useful to measure their separate and combined influence on spatial genetic structure. For example, Grivet *et al.* (2009) proposed a novel indirect assessment of the separate male and female gametic contributions to total effective parental size (N_e), based on parental correlations estimated via kinship coefficients, which can be applied to microsatellite DNA data sets that include unambiguous genotypes for male and female gametic contributions. Such methods requiring only one marker type may be particularly useful for landscape-genetic studies of gene flow in plant populations (i.e., when compared to studies based on several marker types) because they allow the effects of pollen and seed dispersal to be assessed at the same spatial and temporal scales.

Many issues of scale will be affected by advances in high-throughput sequencing that are now making it possible to easily obtain large numbers of markers such as microsatellites (Abdelkrim *et al.* 2009) or single nucleotide polymorphisms (SNPs) for nonmodel organisms (Manel *et al.* 2010). Single nucleotide polymorphisms

technology allows the genotyping of large numbers of loci and individuals for a moderate cost. SNPs therefore should be of great value to landscape-genetic studies. About 50 bi-alleleic SNP loci should provide the same genetic resolution as 20 highly polymorphic microsatellites (Smouse 2010). However, as population processes of mating and dispersal are highly stochastic (Epperson *et al.* 2010), the characterization of landscape-genetic processes generally requires extensive replication over loci.

Larger microsatellite data sets as well as large SNP data sets will permit inferences about gene flow in species that exhibit high levels of dispersal, have large neighbourhood sizes and thus exhibit weak genetic structure at small spatial scales. In addition, large genetic data sets will permit landscape geneticists to detect weak genetic structure caused by ecological and evolutionary processes that have only acted over short time periods.

Temporal lags in effects of landscape features

It is important to consider the duration over which landscape features have existed in current states (Harding *et al.* 1998) when making inferences about landscape effects on gene flow. Relatively few studies have attempted to disentangle the effects of historic vs. current landscapes, but those that have demonstrate different processes operating at different temporal scales. A recent approach involves reconstructing historic landscapes and using the residuals from the historic analyses to quantify the additional effects of contemporary landscapes (Vandergast *et al.* 2007; Dyer *et al.* 2010). Such analyses thus attempt to describe the influence of contemporary landscape features after accounting for historic landscape effects. For instance, the contemporary landscape explained only slightly more genetic differentiation than did the reconstructed historical landscape in the rain forest bird *Orthonyx temmii* (Pavlacky *et al.* 2010).

Consequently, there is a time lag to consider between the processes that caused the formation of spatial genetic structure and the observed spatial genetic structure itself (Box 3), in particular when effective population sizes are large (Excoffier 2004). In one simulation study, Murphy *et al.* (2008) found that landscape effects on spatial genetic structure become detectable when about five generations have passed since the causal event or process occurred; Cushman & Landguth (2010) found a similar result. In other words, even in rapidly changing landscapes, genetic effects might appear within a relatively short time, especially for short-lived species, many of which have generation times <1 year. In long-lived species (e.g., trees), five generations might account for several hundred years and time lags can thus be assumed to be particularly long. However, it should be noted that some landscape-genetic studies have detected rapid genetic responses to landscape change. For example, Zellmer & Knowles (2009), using partial Mantel correlations of genetic distance matrices with geographic distance and landscape resistance matrices, found that patterns of genetic population divergence in wood frog (*Rana sylvatica*) reflected the recent (>1978) rather than the historical landscape (≈1800). Similarly, studies on the genetic effects of roads have often found marked decreases in genetic diversity and substantial increases in genetic differentiation of populations affected by roads in a variety of species ranging from short-lived insects to long-lived mammals and reptiles, even though many roads have only recently been constructed (Balkenhol & Waits 2009; Corlatti *et al.* 2009; Clark *et al.* 2010). However, there are also examples of temporal lags in genetic response (Holzhauer *et al.* 2006; Spear & Storfer 2008).

Issues with temporal lags also raise concern about the use of traditional methods of population-genetic analysis to estimate gene flow in landscape-genetic studies. For example, methods based on differentiation among population-genetic demes (i.e., F_{ST}) or genetic distance among individuals (D_c) assumes migration-drift equilibrium, which may be violated when landscapes change rapidly (Sork *et al.* 1999). For the investigation of the genetic effects of contemporary landscapes on current gene flow patterns, alternative approaches such as assignment tests (Cornuet *et al.* 1999; Manel *et al.* 2005) and parentage analysis (Jones *et al.* 2009) should be considered.

Conclusions

Issues of scale permeate all spatial and landscape analyses (Dungan *et al.* 2002). The nature of the data and questions in landscape genetics adds layers of additional scale complexity that is not always taken into consideration. Future studies need to consider scale issues prior to sampling and experimental design, otherwise they risk collecting data that is inadequate for the questions they wish to address. This involves three stages: determining the appropriate scale of genetic data collection, collecting appropriate landscape data at corresponding spatial scales, and proper statistical analysis of the genetic and landscape data. Nevertheless, we have only just begun to understand how spatial variability in landscape models (including thematic resolution for raster data) influences our ability to make meaningful inferences about gene flow from observed spatial genetic structure. As additional genetic

and spatial data become available in greater volume and quality, scale-related considerations will become increasingly relevant to studies trying to disentangle the complex relationships between spatial heterogeneity and gene flow. Meaningful inference of such relationships will require continued explicit consideration of the role of spatial and temporal scale.

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