

Landscape genetics: where are we now?

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Abstract

Landscape genetics has seen rapid growth in number of publications since the term was coined in 2003. An extensive literature search from 1998 to 2008 using keywords associated with landscape genetics yielded 655 articles encompassing a vast array of study organisms, study designs and methodology. These publications were screened to identify 174 studies that explicitly incorporated at least one landscape variable with genetic data. We systematically reviewed this set of papers to assess taxonomic and temporal trends in: (i) geographic regions studied; (ii) types of questions addressed; (iii) molecular markers used; (iv) statistical analyses used; and (v) types and nature of spatial data used. Overall, studies have occurred in geographic regions proximal to developed countries and more commonly in terrestrial vs. aquatic habitats. Questions most often focused on effects of barriers and/or landscape variables on gene flow. The most commonly used molecular markers were microsatellites and amplified fragment length polymorphism (AFLPs), with AFLPs used more frequently in plants than animals. Analysis methods were dominated by Mantel and assignment tests. We also assessed differences among journals to evaluate the uniformity of reporting and publication standards. Few studies presented an explicit study design or explicit descriptions of spatial extent. While some landscape variables such as topographic relief affected most species studied, effects were not universal, and some species appeared unaffected by the landscape. Effects of habitat fragmentation were mixed, with some species altering movement paths and others unaffected. Taken together, although some generalities emerged regarding effects of specific landscape variables, results varied, thereby reinforcing the need for species-specific work. We conclude by: highlighting gaps in knowledge and methodology, providing guidelines to authors and reviewers of landscape genetics studies, and suggesting promising future directions of inquiry.

Keywords: gene flow, genetic structure, genetic variation, landscape data, publication guidelines, spatial analysis, temporal trends

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Introduction

Landscape genetics is a rapidly growing field that integrates data and analysis methods from landscape ecology, spatial statistics, geography and population genetics to understand the spatial distribution of genetic

variation (Manel *et al.* 2003; Holderegger & Wagner 2006; Storfer *et al.* 2007). Rapid advances in our ability to obtain molecular genetic data and growth in availability of high resolution landscape data have led to dramatic increases in the number of landscape genetic publications in recent years (Fig. 1). The integrative approach of landscape genetics has addressed a broad array of questions, including: identifying specific barriers to dispersal (Manni *et al.* 2004; Latch *et al.* 2008;

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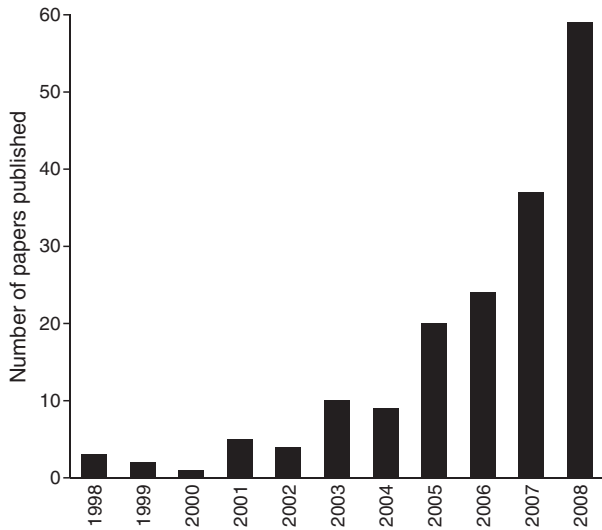


Fig. 1 Trend in number of landscape genetics publications per year published since 1998 (see Methods section for study inclusion criteria).

Guillot *et al.* 2008), quantifying diversity (Dominguez-Dominguez *et al.* 2007; Segelbacher *et al.* 2008), inferring the effect of landscape change (Wagner *et al.* 2006; Wang *et al.* 2008), identifying migrants in relation to landscape condition (Janssens *et al.* 2008; Wilmer *et al.* 2008), estimating source-sink dynamics (Lowe *et al.* 2006; Martinez-Solano & Gonzalez 2008), predicting spread of disease (Foley *et al.* 2005; Wood *et al.* 2007; Deter *et al.* 2008) or invasive species (Lecis *et al.* 2008), and comparing observed genetic patterns between contemporary and historic landscapes (Orsini *et al.* 2008; Spear & Storfer 2008).

The key distinction between landscape genetics and traditional population genetics studies is the incorporation of explicit tests of landscape heterogeneity on gene flow and genetic variation within and among populations (Holderegger & Wagner 2008). Recent studies have demonstrated that multivariate models that include landscape variables perform significantly better than simple isolation-by-distance tests in explaining variance in genetic distance among populations (Spear *et al.* 2005; Vignieri 2005; Foll & Gaggiotti 2006; McRae 2006; Spear & Storfer 2008; Murphy *et al.* 2010). As a result, analysis of landscape genetic structure is becoming increasingly spatial in nature, taking into account the relative influence of a variety of landscape characteristics on population connectivity (Holderegger & Wagner 2008; Balkenhol *et al.* 2009a; Spear *et al.* 2010). For many species, direct observation of dispersal and movement is difficult if not logistically infeasible, and as such, landscape genetics studies can reveal specific habitat variables that facilitate or impede dispersal and

consequent gene flow. Such insights can be valuable, for example, in constructing corridors to facilitate gene flow among habitat fragments or nature reserves (Zanese *et al.* 2006; Epps *et al.* 2007; Neel 2008). As landscapes around the globe are increasingly fragmented by humans, understanding matrix effects on functional connectivity among populations will become essential for conservation and management (Cushman *et al.* 2006; Murphy *et al.* 2010; Goldberg & Waits 2010).

Assessments of landscape effects on gene flow and dispersal can also yield ecological and evolutionary insights (Manel *et al.* 2003; Holderegger & Wagner 2006; Storfer *et al.* 2007). For example, we may predict local adaptation and evolutionary divergence among populations in different landscapes if gene flow is restricted by landscape features. Accordingly, landscape genetic studies are increasingly directed at understanding the spatial distribution of adaptive variation among populations (Manel & Segelbacher 2009; Manel *et al.* 2010), potentially aimed at conserving evolutionary potential of diverging populations (Grivet *et al.* 2008). As genetics studies incorporate increasing numbers of loci, genome scans will become more prevalent, leading to discovery of loci that contribute to local adaptation among populations.

Landscape genetic articles have appeared in diverse journals, on a wide variety of taxa, and have focused on diverse questions using numerous analysis methods. As with any rapidly growing field that brings together several previously distinct disciplines, challenges exist in terms of integrating theory, interdisciplinary communication, and combining and interpreting multiple data analysis methods in a single study (Storfer *et al.* 2007; Balkenhol *et al.* 2009a). Because of its interdisciplinary nature, there is no roadmap of how to conduct a landscape genetics study. As a result, researchers from several different backgrounds face many decisions regarding sampling design, choice of molecular markers, and data analysis methods.

Despite the variety of approaches used for landscape genetic studies, there are inherent characteristics that unite all such studies. Specifically, we defined landscape genetics in previous work as 'research that explicitly quantifies the effects of landscape composition, configuration and [or] matrix quality on gene flow and [or] spatial variation' (Storfer *et al.* 2007). Our goal with this current article is to review the current literature by using this definition to synthesize trends in: geographic areas, habitats and taxonomic groups studied, questions addressed, molecular markers used, genetic distance statistics employed, analysis methods employed and biological insights gained. We also evaluate whether articles report their spatial data sources, the use of baseline tests of genetic data (i.e. Hardy-Weinberg equilibrium (HWE))

and linkage disequilibrium) and the spatial extent of their study. Given the interdisciplinary nature of landscape genetics, we then assess whether there are differences among any of these trends between journal types (i.e. ecological vs. genetic) to evaluate the uniformity of publication standards. Finally, we present a qualitative summary of the biological insights in four broad categories of landscape genetics studies outlined in Storfer *et al.* (2007): effects of barriers, landscape variables that facilitate or impede gene flow, effects of temporal scales and species-specific hypothesis tests. We conclude with identification of knowledge gaps, recommendations for authors and reviewers of landscape genetics studies and highlight future directions for the field.

Methods

Literature search

We conducted a literature search for articles published between 1998 and 2008 using the 'Web of Science' (<http://www.isiknowledge.com>) with the following keywords (found in title, keywords, or abstract): 'landscape' and ('genetics' or 'genetic variation' or 'genetic structure'); 'GIS' and ('genetics' or 'gene flow' or 'genetic structure'); 'gene flow' and ('environmental factor' or 'environmental variable'); 'habitat fragmentation' and ('gene flow' or 'genetics'); 'connectivity' and ('gene flow' or 'genetics'), 'connectivity' and ('genetics' or 'gene flow'); 'spatial epidemiology' and ('genetics' or 'gene flow'), and 'geographical genetics.' Papers that self-identified as landscape genetics studies were also included. We recognize the limitations of this keyword-based search approach, but broader search terms such as 'spatial' and 'gene' yielded thousands of hits. Thus, we kept our search broad enough to obtain a large number of papers to summarize, but not so broad as to be logistically prohibitive. We realize that some papers may have been missed.

Data collection and validation

Our search retrieved 655 articles. After ensuring consistency of article assessment among co-authors by evaluating a pilot group of six papers entered by all co-authors, 20% of these 655 articles were randomly assigned to each of the co-authors for data collection. We first filtered the articles, removing literature reviews and purely theoretical papers. We retained only papers with empirical dataset(s) that included at least one landscape variable in addition to Euclidean distance. For example, if the authors compared spatial patterns of genetic variation between fragmented and unfragmented habitats, the paper was included. We also

retained all articles that self-identified as landscape genetics. After these criteria were applied, 174 papers remained for analysis and data entry into our database (see Table S1, Supporting Information).

For each publication, we collected basic information about the reference (title, year, journal), area where the study was conducted (habitat type, continent), species (taxonomic group, species name), research questions, genetic and statistical methods used, and basic data reporting (see Table S1a–c, Supporting Information for description of database fields).

Database entries were validated using the following process. First, five articles from each co-author (approximately 15%) were re-entered by an additional co-author and compared for consistency. When inconsistencies were detected between the re-entered records and the original records, all inconsistent fields were verified to detect and remove any data entry errors. Second, L.P.W. and M.A.M. validated the entire database by searching each record and then filling in missing data or double checking data that appeared suspicious or inconsistent.

Geographic and taxonomic trends

After determining the number of articles published per year (Fig. 1), we evaluated three general trends in landscape genetics studies: geographic distribution, type of habitat, and the taxonomic group(s) studied. First, to evaluate the geographic distribution of published landscape genetic studies, we calculated the percentage of time a continent was represented ($n = 184$; some studies included more than one continent). Second, we evaluated the proportion of studies in terrestrial vs. aquatic habitats. A study was classified as aquatic if the study species was restricted to the aquatic environment for all life stages; if the species was terrestrial during any life stage, then the study was classified as terrestrial. Third, we classified studies as either plant, animal, pathogen, or 'other' based on taxonomic groups studied. 'Animals' refers to both vertebrates and invertebrates, and 'other' encompasses non-pathogenic fungi and lichens because of the small number of studies for each of these groups. All species studied in a given article were counted individually, and some studies had multiple species. We then calculated the relative percentage of studies occurring within each taxonomic group separately.

Question types

We identified 12 major landscape genetics questions as identified by authors (see Table S1b, Supporting Information) and calculated the percentage of papers that addressed each of these questions. Studies that investigated multiple questions were represented multiple

times. We then calculated the percentage of studies within each taxonomic group that addressed specific landscape genetic questions. Percentages within each taxonomic group do not equal 100% because some studies had multiple questions, and we did not want to bias results by weighting studies that used multiple taxa more heavily than single taxon studies.

Molecular markers and genetic distance statistics

For each publication, we tabulated type of molecular markers used, mean number of loci and genetic distance statistic used. We then estimated the relative percentage (out of 100%) of uses of each molecular marker type or genetic distance statistic per year. The mean number of loci used was calculated separately for microsatellites and amplified fragment length polymorphisms (AFLPs). One study from 2007 was an outlier with a mean of 377 microsatellites (Cercueil *et al.* 2007), and was omitted from this analysis.

Analytical methods and landscape variables

We calculated the percentage of papers that used a particular analysis method (e.g. partial Mantel test) and percentage of papers using a method by year. Papers often used multiple methods, resulting in totals exceeding 100%. We also calculated the percentage of studies using a particular method out of the total number of studies in terrestrial vs. aquatic habitats, as well as among taxonomic groups.

Additionally, we calculated percentage of papers using binary (yes, no), categorical or continuous landscape variables by year for all papers that included at least one landscape variable. Some studies used multiple types of variables. Because of the small number of papers before 2004, all studies between 1998 and 2003 were combined for this analysis.

Trends among journal types

As landscape genetics has been identified as a field that integrates population genetics, landscape ecology and spatial statistics (Storfer *et al.* 2007), we assessed the extent to which such integration was reflected in consistency of study design, data reporting and analyses in ecology/conservation vs. genetics journals. Specifically, we evaluated whether there were differences between journal types in terms of: number of papers published, inclusion of an explicit sampling design, presentation of data to evaluate spatial data quality (X, Y coordinates for sample locations, study extent reported, source and nature of spatial data), and performance of tests to evaluate basic assumptions for analyses of genetic data (i.e. tests

for HWE and linkage disequilibrium). We also tabulated whether molecular marker type or data analysis methods differed among journal types (see Table S2, Supporting Information for categorization of journal types).

Synthesis of insights from landscape genetics literature

We surveyed the literature for generalities in ecological or evolutionary insights that emerged from multiple landscape genetics studies. We focused on four of the five the major question categories outlined in Storfer *et al.* (2007), including: influence of landscape variables and configuration on genetic variation, identifying barriers, effects of spatial and temporal scales, and species-specific hypothesis testing. Source–sink dynamics were not included due to the small number of studies.

Results

Geographic and taxonomic trends

The number of landscape genetics articles increased substantially during the last four years, reaching more than fifty published articles in 2008 (Fig. 1). In terms of geography, 169 (97%) papers focused on a single continent or island chain, three studies spanned two continents, one spanned four continents and one was across five continents. The majority of studies have been conducted in North America (39%) or Europe (35%) with only 4–8% representation from Africa, Asia, Australia or South America (Fig. 2a). Notably, 50% of the studies conducted in Africa and 25% in Asia were part of multi-continent projects.

Ninety percent of papers focused on a single species, 7% included two species and 4% studied three or more species. The highest percentage of papers focused on vertebrates (62%) followed by invertebrates (18%), plants (14.5%), bacteria (3%), viruses (3%), lichens (1%) and fungi (0.5%; Fig. 2b).

The majority of studies were conducted in terrestrial habitats (79%) compared with 15% in freshwater habitats and 6% in saltwater habitats (Table 1). Within terrestrial habitats, a large proportion of studies (40%) were conducted in a landscape with temperate forests, whereas only 10% included tropical forest habitats. Agricultural and urban landscapes were included in 11% and 7% of the studies, respectively.

Question types

Questions related to connectivity and barriers were addressed most frequently, comprising 30% and 50% of studies, respectively. Twenty percent of studies quantified landscape effects on diversity (Dominguez-

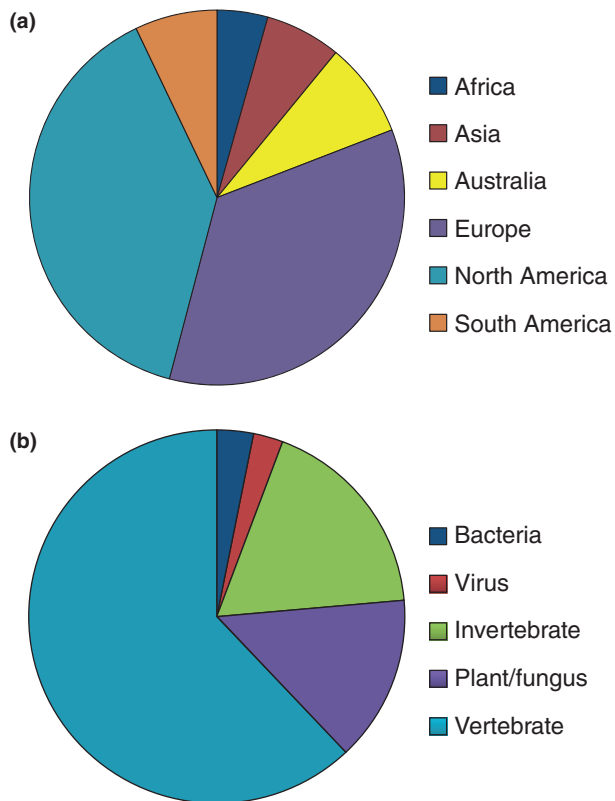


Fig. 2 (a) Proportion of landscape genetics studies per continent and (b) Proportion of landscape genetic studies for each taxonomic group.

Dominguez *et al.* 2007; Segelbacher *et al.* 2008). In contrast, questions related to corridors, source-sink and temporal lag of the genetic response to landscape change were rarely addressed (<5% in all cases). Fewer than 20% of studies addressed functional connectivity, which required a specific hypothesis of how the landscape would affect genetic structure. Questions addressed in the 'other' category included those related to adaptation of populations, kinship and parentage, and sex-biased dispersal.

Whereas in most cases the percentage of studies addressing a specific question did not vary by taxonomic group, there were a few notable trends (Fig. 3). Studies using animals (35%) were more likely to investigate barrier effects than in plants (16%) or pathogens (14%). Animal studies (21%) also more frequently had questions related to functional connectivity than plants (4%), a result likely because of interest in landscape structures that might restrict animal movement. Plants (8%) had a greater percentage of studies investigating temporal lag effects on genetic structure than other taxonomic groups (animals 2%, pathogens 0%), which might reflect the long persistence times of many plant populations and/or the ease of sampling multiple gen-

Table 1 Habitat types of landscape genetics studies

Habitat type	<i>n</i>	%
Agriculture	19	11
Alpine	15	9
Arctic	3	2
Desert	5	3
Freshwater	36	21
Meadow/shrub	47	28
Prairie	5	3
Saltwater	11	7
Temperate forest	68	40
Tropical forest	17	10
Urban	12	7
Other	8	5
Unclear/undefined	5	3
Terrestrial	137	79
Salt water	11	6
Freshwater	25	15
Total	173	

We used broad classifications of the type of habitat (Habitat Type) which were further generalized into terrestrial, salt water and fresh water (in grey). We present number of studies (number) and percent of studies (percent) with some portion of a given habitat classification in the study area. Note many papers had more than one habitat type and all were included so % is >100%. One paper was omitted as the organism was a disease with habitat that included both humans and water ($n = 173$).

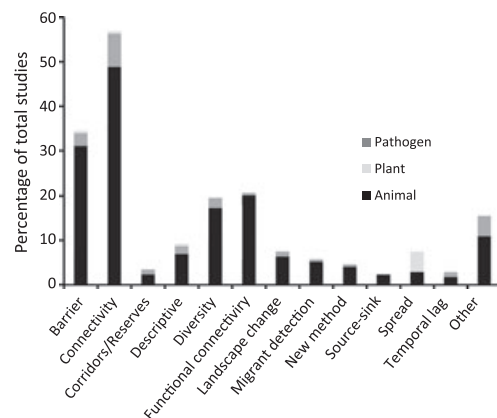


Fig. 3 Percentage of studies that addressed different landscape genetics research questions summarized by taxonomic group.

erations. Pathogen studies were primarily interested in disease spread (86% of studies), with little representation in other categories.

Molecular markers used

A total of 18 different types of genetic markers have been used in landscape genetic studies, including: microsatellites, allozymes, AFLPs, random amplified

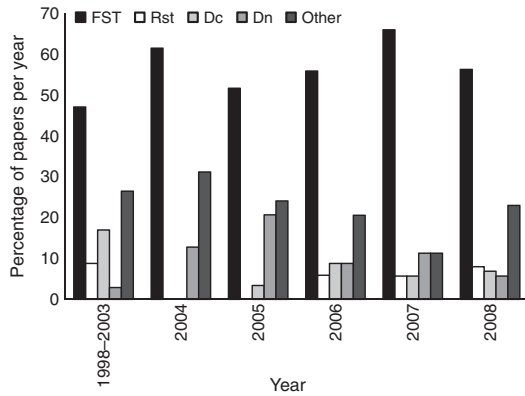


Fig. 4 Percentage of landscape genetic studies that used a particular genetic distance measure per year (F_{ST} includes G_{ST} and G'_{ST}), 'other' refers to all other distance measures than those given in the legend; D_c = chord distance; D_n = Nei's distance). Note that the years 1998–2003 ($n = 34$) have been merged due to small sample sizes within each year.

polymorphic DNAs (RAPDs) and mitochondrial DNA (mtDNA) or cpDNA sequences (Fig. 4). Genetic marker types used less often were combined into an 'other' category (e.g. RFLPs, nDNA sequences, SNPs, mtDNA microsatellites). Despite recent increases in technology to facilitate rapid SNP development and emphasis on their power for population genetics studies, only two studies used SNPs.

There were pronounced differences in the use of genetic marker types among taxonomic groups (Fig. 4). Microsatellites were used most often in animals (70%), whereas three marker types, microsatellites (31%), allozymes (31%), and AFLP (21%) were used commonly for plants. The mean number of microsatellite or AFLP loci did not show any clear trends over time (linear regression; microsatellites: $r^2 = 0.014$, $P = 0.176$; AFLPs: $r^2 = 0.131$, $P = 0.203$; Table S3, Supporting Information). The mean number of microsatellite loci used per year ranged from 7.6 (± 0.8 SE) to 15.2 (± 4.3), and the mean number of AFLP loci ranged from 71.8 (± 17.2) to 206 (± 91.1). All other marker types were rarely used. Studies on pathogens and other microorganisms (within the group 'other') often used highly specific molecular-genetic assays (75%).

Genetic distance statistics

Landscape genetic papers used a total of 19 different measurements of genetic distance, and articles often used more than a single genetic distance measure (Fig. 5). The most commonly used genetic distance measures were F_{ST} and its analogues (including G_{ST} , G'_{ST} , R_{ST}), genetic chord distance (D_c) and Nei's distance (D_n ; Fig. 5). Genetic distance measures used less

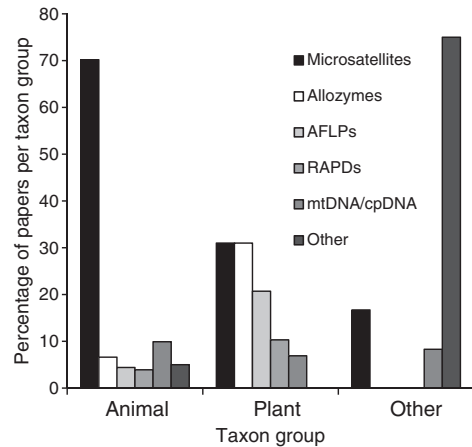


Fig. 5 Percentage of landscape genetic papers that used a particular genetic distance measure per year. Black: F_{ST} (including G_{ST}); white: R_{ST} ; light grey: Chord distance D_c ; grey: Nei's distance D_n ; dark grey: other distance measures; animals: $n = 181$; plants: $n = 29$; other (viruses, bacteria, fungi and lichens): $n = 12$).

often were combined into the 'other' category (e.g. D_{ps} , Rousset's a , allele and band sharing indices or CCA axis scores). Figure 5 also shows that there was no obvious trend in use of different genetic distance measures across years.

Analytical methods and landscape variables

The most commonly applied analytical approaches evaluated isolation-by-distance (Mantel tests, IBD) or Bayesian assignment tests to cluster individuals (Fig. 6). Ordination methods were the next most common (23% of studies overall), and it was preferentially used in animals (36%) vs. plants (18%; Fig. S2, Supporting

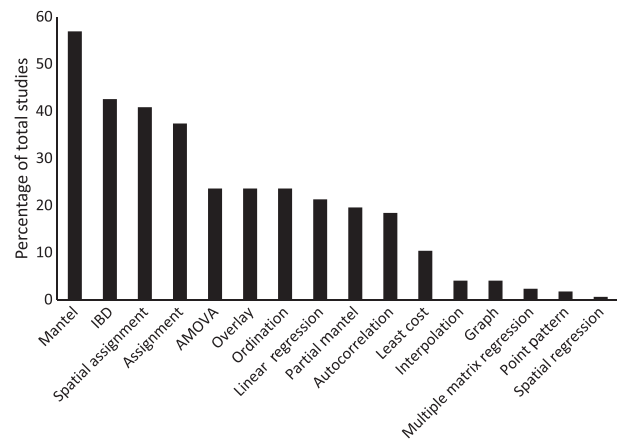


Fig. 6 Percentage of landscape genetic studies using a particular analytical method. Note that total percentage is greater than 100%, because some studies used multiple analytical methods.

Information). Global autocorrelation was more commonly used in terrestrial vs. aquatic studies (21% vs. 8%).

Across all years, 26% of papers did not *quantify* the impact of any type of landscape variable. When a relationship with landscape variables was quantified, linear regression or partial Mantel tests were most often applied (Fig. 6). In addition, when ordination was used, it was most often performed to cluster the genetic data without including landscape variables. There is a slight downward trend in use of categorical landscape variables over time, but binary and continuous variables showed no temporal trend (Fig. S3, Supporting Information).

The use of individual-based methods has increased over time although this may reflect increases in numbers of studies, as there was no temporal trend in the percentage of studies that used these methods (Fig. 6). Individual-based methods consider individual genotypes in estimations of genetic connectivity (e.g. Manel *et al.* 2007; Murphy *et al.* 2008), as opposed to clustering methods that calculate genetic distance among demes, such as F_{ST} or Nei's D_n . Plant studies tended to use individual based methods more often than animal studies (20% vs. 14%), likely because of the use of parentage analysis to investigate pollen flow in plants (Fig. S4, Supporting Information). All pathogen studies were individual-based, and because corresponding data were often point data (i.e. disease presence), linear regression, interpolation and point-pattern analyses were commonly applied.

Trends among journal types

Overall, the majority of landscape genetics papers were published in genetics journals (58%), with 32% in ecological/conservation journals and 10% in journals categorized as 'other' (including parasitology journals or broad general audience journals such as *Proceedings of the National Academy of Sciences, USA*). Although the difference is not statistically significant, papers published in genetic journals tended to have a larger sample size (mean = 624.51 individuals) than those published in ecological/conservation journals (mean = 505.98; *t*-test: $P = 0.24$). In both ecological and genetics journals, only

approximately one-third of studies had an explicitly stated sampling design (Table 2). There were differences in data reporting and tests of basic genetic assumptions between journal types as well (Table 1), most notably that a significantly higher proportion of studies published in ecology journals reported X , Y coordinates (30.9%, $\chi^2 = 10.25$, d.f. = 1, $P < 0.02$) than did genetics papers (15%).

Microsatellites were the most commonly used molecular marker (Fig. S5a, Supporting Information), regardless of journal type. RFLPs tended to be slightly more common in the 'other' journal category because of their widespread application in disease studies. RAPDs were used in 12% vs. 2% of studies published in ecology/conservation vs. genetics journals, respectively. Although non-significant, multiple molecular markers were used more often in genetics journals (Fig. S5b, Supporting Information).

Discussion

Interest in using landscape genetic approaches to understand how landscape process affect observed patterns of genetic variation has burgeoned in recent years, as evidenced by the dramatic increase in publications over time (Fig. 1). Consistent improvements in the ease of generating molecular data combined with the increased availability of high-resolution spatial data means that landscape genetics studies will continue to increase in number. As with any rapidly growing field, it is beneficial to reflect on current progress. In summarizing publications over the past 11 years, we found that landscape genetic studies still often lack: explicit hypotheses, detailed reporting of spatial data and analytical methods that are explicitly spatial. Below, we offer suggestions and guidelines for future studies.

Genetic markers and analytical methods used in landscape genetics

Recently, several authors have identified the need for a broader variety of both genetic and statistical analytical methods to be used in landscape genetics studies (Stor-

Table 2 Proportion of studies in ecology/conservation vs. genetics journals that reported: an explicit study design, how X , Y coordinates of samples were collected (XY), the spatial extent of the entire study (Extent), the source of the spatial data (spatial data), whether their genetic data were tested for Hardy-Weinberg equilibrium (HW), or linkage disequilibrium (LD)

	Study design	XY	Extent	Spatial data	HW	LD
Ecology/conservation	0.334	0.309*	0.362	0.819	0.642	0.619
Genetics	0.357	0.150	0.291	0.701	0.742	0.670

*Significant difference ($P < 0.05$) between ecology/conservation and genetics journals.

fer *et al.* 2007; Holderegger & Wagner 2008; Murphy *et al.* 2008; Balkenhol *et al.* 2009a; b; Guillot *et al.* 2009). Our review of the literature supports this recommendation.

Despite recent technological advances (e.g. next-generation sequencing) that have resulted in increased availability of microsatellites, SNPs, and AFLPs, the number of loci used in landscape genetics studies did not increase significantly over time. Nonetheless, recent reviews have shown the high statistical power to detect genetic differentiation using large numbers of SNP (Kohn *et al.* 2006) or AFLP loci (Meudt & Clarke 2007). Studies with hundreds to thousands of loci will be useful for genomic mapping, as well as identifying candidate loci for adaptation to different environmental conditions (Luikart *et al.* 2003; Stinchcombe & Hoekstra 2008; Holderegger & Wagner 2008; Manel *et al.* 2010). Using such population genomics approaches, loci that are statistical 'outliers' and show distinct patterns from the majority of loci studied across populations in different environments are assumed to be under selection or physically linked to those under selection (Luikart *et al.* 2003; Beaumont & Balding 2004; Stinchcombe & Hoekstra 2008). As an example, an assessment of 392 AFLPs in the common frog (*Rana temporaria*) among populations at varying altitudes in the Alps revealed eight candidate loci potentially involved in adaptation to altitude (Bonin *et al.* 2006). As concerns regarding anthropogenic global change continue to broaden, landscape genetics studies will increasingly focus on the spatial distribution of adaptive, as well as neutral, loci (Holderegger & Wagner 2008; Manel *et al.* 2010).

Second, our analysis showed that only a few traditional measures of genetic differentiation (mainly F_{ST} and analogues) or distance (e.g. D_n ; Fig. 5) were used across the majority of studies. Several of these metrics have equilibrium-based assumptions when assessing gene flow rates, despite studies in systems that are often not expected to be in equilibrium (e.g. anthropogenically altered habitats). As such, researchers should consider the use of other metrics that avoid equilibrium assumptions, such as D_{ps} (Bowcock 1995), when appropriate (see Murphy *et al.* 2010). Whereas genetic distance measures assume that populations sampled are distinct, Bayesian assignment methods do not. Bayesian assignment methods were also frequently used for genetic clustering purposes, and the use of spatial assignment tests, in particular, has increased over time, likely because of the increased availability of software (e.g. Geneland, Guillot *et al.* 2005; Spatial BAPS, Corander *et al.* 2007). Together, genetic distance measures and Bayesian clustering measures also assume that individuals are inherently clustered into groups, which can be problematic for species that are more uniformly dis-

tributed on the landscape, such as large mammals (Schwartz & McKelvey 2009).

Techniques such as a moving window approach using individual-based genetic distances (Manel *et al.* 2007) or creating a genetic surface using interpolation (Murphy *et al.* 2008) avoid assumptions of discrete genetic groups and may be particularly useful for animals or plants that have non-clumped or uniform distributions. If a gradient of genetic structure is represented as a genetic surface, then landscape pattern and genetic variation can be related using a variety of spatial statistical techniques circumventing the non-independent nature of pairwise data (Murphy *et al.* 2008). Genetic surfaces use spatial interpolation methods to identify connectivity among individual genotypes on the landscape (Murphy *et al.* 2008). Barriers can also be identified without a priori clustering of individuals using techniques such as wombling (Barbujani *et al.* 1989; Manel *et al.* 2007). Wombling identifies areas of abrupt genetic changes (in allele frequencies) by quantifying local variability in allele frequencies (Womble 1951; Barbujani *et al.* 1989). Recent methods that incorporate wombling have sought to weight the relative importance of barriers (e.g. Manel *et al.* 2007), whereas initial methods lacked the ability to discriminate the influence of different barriers.

Landscape genetic studies made substantial use of conventional population genetic analysis, mostly based on the above genetic distance measures. Specifically, more than half of the studies used Mantel or partial Mantel tests to analyse the correlation between a matrix of genetic distances and a matrix or matrices of geographic or landscape distances (Fig. 6). A recent simulation study that compared Mantel tests with several alternative methods showed that methods such as partial canonical correspondence analysis, multiple regression of distance matrices (Holzhauer *et al.* 2006), and Bayesian inference of immigration rates (Faubet & Gaggiotti 2008) had higher power and lower type I error than partial Mantel tests (Balkenhol *et al.* 2009b). In addition, there are concerns about the appropriateness of permutation procedures for significance testing among multiple matrices with non-independent or multicollinear variables in partial Mantel tests (Castellano & Balletto 2002; Rousset 2002). However, Cushman & Landguth (2010) simulated different patterns of isolation-by-distance, barriers and landscape resistance, and found the partial Mantel to be reliable for reaching the correct inference. As such, further investigation into the performance of partial Mantel tests under different scenarios is needed, and thus far, no generally accepted alternatives have been proposed. We found that the use of partial Mantel tests peaked in 2005 and has declined in recent years.

Linear regression or general linear models have also commonly been used in landscape genetics studies. However, these methods should be cautiously used because they are generally not appropriate for pairwise comparisons (in the case of genetic and landscape distances) or in situations where there is substantial autocorrelation (i.e. spatial non-independence of regression residuals of genetic and landscape data), unless significance testing relies on data permutation approaches (Fortin & Dale 2005). Potential alternatives that attempt to account for non-independence and/or spatial autocorrelation are classification and regression tree (CART) models (Murphy *et al.* 2010), spatial regression (Spear & Storfer 2008) and gravity models (Murphy *et al.* 2010).

Given the above mentioned limitations of landscape genetic applications with respect to laboratory methods and subsequent statistical analysis, alternative and innovative methods relating genetic data based on new types of molecular markers with various types of spatial, environmental and landscape data are needed for the further development of landscape genetics. Storfer *et al.* (2007), Balkenhol *et al.* (2009a) and Guillot *et al.* (2009) give overviews on a variety of alternative approaches for landscape genetic analysis and the availability of new landscape genetic simulations software will facilitate further comparisons of alternative methods (Landguth & Cushman 2010; Epperson *et al.* 2010).

Synthesis of insights from landscape genetics literature

Identifying barriers. Studies focused on understanding barriers to gene flow were among the first to incorporate landscape data in genetic analyses (Manel *et al.* 2003). Initial applications were directed toward identification of major breaks in genetic structure and visual association with landscape features (Monmonier 1973; Dupanloup *et al.* 2002). More recently, identification of barriers been extended to address more specific ecological and conservation questions, including: identifying linear features that act as barriers to gene flow, barriers in aquatic systems, cryptic barriers and barriers in relation to disease spread.

Linear features, such as rivers, mountain ridges, roads and anthropogenic habitat fragmentation, are the most obvious testable barriers to gene flow and frequently considered in landscape genetics studies. The effects of putative barriers on gene flow varies by species, ranging from no discernable effect on genetic structure (Gauffre *et al.* 2008), to extreme effects (Funk *et al.* 2005). Rivers have been identified as a barrier to gene flow in several taxonomic groups including small mammals, turtles and deer (Lugon-Moulin & Hausser

2002; Coulon *et al.* 2006; Mockford *et al.* 2007), but may actually facilitate gene flow in amphibians (Spear *et al.* 2005) and transgenic crops (Cureton *et al.* 2006). Major ridgelines are barriers to gene flow in amphibians (Funk *et al.* 1999, 2005) and meso-mammals (Zalewski *et al.* 2009), but may not be barriers to small mammals (Lugon-Moulin & Hausser 2002). Unlike these natural features which vary in effect by taxonomic group, roads and other human development have been identified as barriers across several taxonomic groups, including carnivores (Riley *et al.* 2006; Millions & Swanson 2007), ungulates (Epps *et al.* 2005; Kuehn *et al.* 2007; Perez-Espona *et al.* 2008) and amphibians (Manier & Arnold 2006; Murphy *et al.* 2010).

Clearly defined barriers are also present in aquatic systems. Dams are major barriers to gene flow in aquatic dependent species such as fish, even when passage systems are in place (Taylor *et al.* 2003; Wofford *et al.* 2005; Deiner *et al.* 2007; Raeymaekers *et al.* 2008; Skalski *et al.* 2008). In addition, natural physical barriers such as waterfalls were important for shaping genetic structure patterns in yellow perch (*Perca flavescens*; Leclerc *et al.* 2008), westslope cutthroat trout (Taylor *et al.* 2003), bull trout, (*Salvelinus confluentus*; Costello *et al.* 2003; Whiteley *et al.* 2006), coastal cutthroat trout (*Oncorhynchus clarki clarki*; Wofford *et al.* 2005), mountain whitefish (*Prosopium williamsoni*; Whiteley *et al.* 2006) and steelhead and rainbow trout (*Oncorhynchus mykiss*; Deiner *et al.* 2007). Interestingly, anthropogenic development along waterways can also be a barrier to gene flow, possibly because of changes in water temperature or chemistry (Wilcock *et al.* 2007). In addition, fragmentation of breeding habitat may have an additive effect with physical structures such as dams (Leclerc *et al.* 2008) and roads (Balkenhol & Waits 2009).

Barriers to gene flow can also be less obvious than distinct linear features or physical structures. Unsuitable natural habitat may be a significant barrier to gene flow (McRae & Beier 2007), as in the case of savanna habitats that fragment lemur populations (Radespiel *et al.* 2008) or dry grassland habitat fragmenting salamander populations (Rittenhouse & Semlitsch 2006). In addition, climate gradients have been shown to be cryptic barriers to gene flow, producing unexpected sharp breaks in genetic structure possibly because of species' environmental tolerance limits. This phenomenon has been observed in the apparently continuous habitat of Northern temperate regions (Geffen *et al.* 2004; Carmichael *et al.* 2007) and in salt-water habitat where cetaceans have abrupt discontinuities in genetic structure (Fontaine *et al.* 2007). In some cases, weakly genetically structured populations may be separated by the confluence of several features of low permeability, as in the combined effects of a river, highways and canals on

roe deer (*Capreolus capreolus*) gene flow in France (Coulon *et al.* 2006).

Identification of barriers to gene flow can also help predict the geographic nature of disease spread or assist with management. Barriers can quarantine disease within a limited geographic area (Rees *et al.* 2008). Rivers restrict spread of chronic wasting disease in deer (Blanchong *et al.* 2008) and control rabies outbreaks by acting as natural barriers to raccoon dispersal (Real & Biek 2007; Blanchong *et al.* 2008; Cullingham *et al.* 2009). In the example of rabies, understanding the spatio-temporal nature of disease occurrence combined with identification of barriers can result in effective vaccination strategies. That is, because rivers act as barriers, control strategies were focused on using vaccinated raccoon bait in areas where landscape variables facilitated dispersal and gene flow (Real & Biek 2007).

Although identifying barriers to gene flow provides insights into species' ecology, understanding complex relationships between gene flow and landscape condition requires more in-depth analyses (Cushman *et al.* 2006; Murphy *et al.* 2008; Cushman & Landguth 2010). For example, in grey wolves no statistical relationship was seen between genetic distance and hypothesized barriers, but a statistically significant relationship was observed between genetic distance and continuous landscape variables (Pilot *et al.* 2006). As many high-dispersing species may not have obvious barriers to gene flow over the spatial scale of typical landscape genetic studies, it is important to identify the relative influence of landscape variables on the spatial distribution of genetic variation.

Influence of landscape variables and configuration on genetic variation. In terrestrial systems, topographic relief was shown to negatively influence gene flow in many species, including most species of amphibians (Funk *et al.* 2005; Spear *et al.* 2005; Spear & Storfer 2008; Murphy *et al.* 2010), small mammals including voles (Berthier *et al.* 2004), red deer (*Cervus elaphus*; Pérez-Espona *et al.* 2008), wax palms (*Ceroxylon echinulatum*; Trénel *et al.* 2008) and golden-brown mouse lemurs (*Microcebus ravelobensis*; Radespiel *et al.* 2008). Elevational gradients resulted in reduced gene flow among high and low altitude populations of Columbia spotted frogs (*Rana luteiventris*; Funk *et al.* 2005) and long-toed salamanders (*Ambystoma macrodactylum*; Giordano *et al.* 2007). However, landscape features had little effect on gene flow and population genetic structure of several species of birds, including black-capped vireos (*Vireo atricapilla*; Barr *et al.* 2008) and Darwin's finches (Petren *et al.* 2005). In red-tailed hawks (*Buteo jamaicensis*), however, some populations appeared separated by mountain ranges such as the Sierra Nevada, while other mountain

ranges had little effect (Hull *et al.* 2008). Habitat preferences affected gene flow more appreciably, as evidenced by limited dispersal between Mediterranean central California habitats and more xeric inland west and southern habitats (Hull *et al.* 2008).

Seasonality can also affect gene flow. As an example, fisher (*Martes pennant*) population connectivity was inversely correlated with snow depth (Garroway *et al.* 2008). In the alpine snowbed herb, *Primula cunefolia*, flowering time at different altitudes was significantly affected by timing of snowmelt, and flowering segregation, in turn, led to fine-scale spatial genetic structuring (Hirao & Kudo 2008). Similar results were also seen in two of three snowbed herb species in a previous study (Hirao & Kudo 2004).

Effects of habitat fragmentation and land use change have been the focus of a large number of terrestrial landscape genetic studies, and fragmentation has reduced gene flow in many species, including: formica ants (Mäki-Petäys *et al.* 2005), common frogs (*Rana temporaria*; Johannson *et al.* 2005), alpine butterflies (*Parnassius smintheus*; Keyghobadi *et al.* 2005) and golden cheeked warblers (*Dendroica chrysoparia*), but not Amazon liverworts (*Radula flaccid*; Zartman *et al.* 2006), the tree species, *Sorbus aucuparia* (Bacles *et al.* 2004) or the yellow-footed antechinus (*Antechinus flavipes*; Lada *et al.* 2008). An example of one study suggesting negative effects of habitat fragmentation showed lower genetic variation in habitat patches less than 35 years old versus those greater than 35 years old in the forest herb, *Primula elatior* (Jacquemyn *et al.* 2004). A study in fragments vs. closed forest of Andean oak (*Quercus humboldtii*) showed detrimental effects of contemporary habitat on genetic variability (Fernandez & Sork 2007). Latitude and spatial other factors affected the distribution of genetic variation in the endangered California valley oak (*Quercus lobata* Née), leading to the recommendation of maintenance of corridors in reserve design and prioritization of genetically diverse populations to maintain evolutionary potential (Grivet *et al.* 2008).

Fragmented landscapes also affected dispersal movements of species. For example, gene flow among European roe deer populations more closely followed woodland corridors than disturbed habitat patches in a fragmented landscape (Coulon *et al.* 2004). Similarly, gene flow of Rocky Mountain tailed frogs (*Ascaphus montanus*) more closely followed riparian corridors in deforested landscapes than naturally regenerated post-fire landscapes (Spear & Storfer 2010). In addition, although habitat fragmentation did not appreciably alter gene flow in the yellow-footed antechinus, dispersal was reduced through agricultural landscapes (Lada *et al.* 2008). Habitat fragmentation also apparently did not affect gene flow in coyotes (*Canis latrans*)

which were not affected by obvious anthropogenic barriers such as roads; rather gene flow appeared restricted by habitat-specific breaks and natal site fidelity (Sacks *et al.* 2004). Results of habitat fragmentation for the forest herb, *Geum urbanum*, were mixed. Gene flow remained high between primary and secondary growth (i.e. post-harvest) forest fragments, but small populations were genetically more diverged than large populations (Venderpitte *et al.* 2007). Overall, given the variability in effects of habitat fragmentation on genetic variation and gene flow, studies that test the effects of fragmentation should be conducted before conservation and management decisions are implemented.

Landscape genetics studies have also been useful for revealing counterintuitive features that facilitate gene flow. For example, although rivers were thought as an a priori barrier to gene flow among populations of blotched tiger salamanders (*Ambystoma tigrinum melanostictum*) in Yellowstone National Park, they were actually found to facilitate gene flow (Spear *et al.* 2005). Upon further consideration, this result made sense because occasional flooding can allow enough dispersal across rivers to positively affect gene flow. Similarly, flooding apparently increased gene flow in the herb, *Primula sieboldii* (Kitamoto *et al.* 2005). In addition, counter intuitively, two studies in Yellowstone revealed that post 1988 fire-regenerated habitat facilitated gene flow among tiger salamanders (Spear *et al.* 2005) and boreal toads (*Bufo boreas*; Murphy *et al.* 2010). Although previously thought of as an impediment to gene flow, fire-regenerated shrub habitat probably provides shade closer to the ground than forested habitat, thereby facilitating amphibian dispersal.

In freshwater systems, landscape genetic studies revealed the importance of including both historic and contemporary landscape variables in explanatory models. For example, glacial history was important for explaining current levels of genetic diversity and structure in bull trout (*Salvelinus confluentus*; Costello *et al.* 2003), coastal cutthroat trout (Wofford *et al.* 2005), mountain whitefish (Whiteley *et al.* 2006), and brook charr (*Salvelinus fontinalis*; Angers *et al.* 1999). In brook charr, genetic structure was more consistent with historical hydrological structure predicted based on geomorphological and biogeographical models than current landscape structure (Poissant *et al.* 2005).

In river and spring systems, landscape genetic models that included the drainage pattern, direction and/or speed of water flow best explained genetic structure patterns in zooplankton (Michels *et al.* 2001), brook charr (Angers *et al.* 1999), and aquatic snails (Wilmer *et al.* 2008). In addition, dynamic and sporadic events such as flooding were critical for explaining genetic structure (Wilmer *et al.* 2008). The landscape variables

of slope, elevation and temperature were important predictor variables in multiple studies. For example, fish populations at higher elevations had lower levels of genetic diversity and lower levels of gene flow with other populations (Angers *et al.* 1999; Castric *et al.* 2001; Narum *et al.* 2008), and gene flow was negatively correlated with change in elevation between sampling sites for the stream salamander, (*Gyrinophilus porphyriticus*; Lowe *et al.* 2006). In addition, water temperature was the best predictor variable explaining genetic structure and variation among Atlantic salmon (*Salmo salar*) along the North American Atlantic coast (Dionne *et al.* 2008) and steelhead trout in the Pacific Northwest (Narum *et al.* 2008).

Anthropogenic impacts were associated with decreased gene flow and genetic diversity in multiple river systems. In particular, dams, tunnels and weirs were found to impede gene flow in yellow perch (Leclerc *et al.* 2008), westslope cutthroat trout (Taylor *et al.* 2003), three-spined stickleback (*Gasterosteus aculeatus*; Raeymaekers *et al.* 2008), bull trout (Costello *et al.* 2003) and coastal cutthroat trout (Wofford *et al.* 2005). Pulp mill impacts were also found to increase genetic structure in redbreast sunfish (*Lepomis auritus*; Theodorakis *et al.* 2006) and three-spined stickleback (Raeymaekers *et al.* 2008). A similar study focused in a coastal saltwater system showed that copper mine waste outputs restricted gene flow among populations of the kelp, *Lessonia nigrescens* in Chile (Faugeron *et al.* 2005).

In marine environments, landscape genetic studies have demonstrated that genetic diversity and structure are often best explained by analyses that include ocean currents (blue whiting, *Micromesistius poutassou*; Was *et al.* 2008; and kelp bass *Paralabrax clathratus*, Selkoe *et al.* 2010) and models of simulated transport of larvae (sea scallop, *Placopecten magellanicus*; Kenchington *et al.* 2006, and the intertidal barnacle, *Balanus glandula*; Galindo *et al.* 2010). In other studies, ocean temperatures were the most important predictor variable of genetic structure in the sea urchin, *Centrostephanus rodgersii* (Banks *et al.* 2007) while both temperature and salinity were key variables for explaining genetic structure patterns in Atlantic cod (*Gadus morhua*; Case *et al.* 2005). In a multi-species analysis along the California coast, cumulative kelp cover, a measure of habitat quality, was the most important variable for explaining genetic diversity and structure in kelp bass, Kellet's whelk (*Kelletia kelletii*) and California spiny lobster (*Panulirus interruptus*; Selkoe *et al.* 2010).

To summarize, the effects of a wide variety of landscape variables on population genetic structure have been considered. Several landscape variables such as elevation, ridgelines and topographic relief limited gene flow in several, but not all terrestrial species. In aquatic

species, drainage structure, slope, elevation and temperature were important explanatory variables. Anthropogenic features, such as deforestation, agricultural development, damming and other types of waterway manipulation decreased gene flow or affected movement pathways in some species, but had little to no effect on others. Some features, such as rivers and post-fire regenerated habitats facilitated gene flow, contrary to expectations. Taken together, this wide variety of studies suggest that, while there are some generalities, effects of landscape variables and habitat fragmentation vary among species, highlighting the need for species-specific studies.

Spatial and temporal scales. Determining the relative influence of contemporary vs. historic landscape features on gene flow is critical for understanding processes associated with anthropogenic landscape change (Keyghobadi *et al.* 2005; Storfer *et al.* 2007; Pavlacky *et al.* 2009). Yet, few landscape genetic studies have examined how landscape configuration at different time scales has influenced genetic structure, and therefore it is difficult to make broad conclusions. In addition, studies have defined the scale of 'historical' differently, from years (Orsini *et al.* 2008) to decades (Honnay *et al.* 2006; Spear & Storfer 2008) to prehistory (Vandergast *et al.* 2007). The need to account for historic effects in landscape genetic studies is likely highly dependent on both choice of molecular marker and the rate of landscape change, and thus is not necessarily generalizable across species and study areas. Two different methods have primarily been used to correlate current genetic data with reconstructed historic landscapes: correlating genetic data separately with landscape configurations from different time points (Orsini *et al.* 2008; Spear & Storfer 2008) or by creating regression models based on historic landscape, and then correlating the residuals from that model with the current landscape to account for previously unexplained variation (Vandergast *et al.* 2007; see also Dyer *et al.* 2010).

Vandergast *et al.* (2007) found evidence of both prehistoric and contemporary effects of landscape on Jerusalem cricket (*Stenopelmatus mahogani*) using mtDNA. Spear & Storfer (2008) examined correlation of current and historic patterns of timber harvest on Coastal tailed frog (*Ascaphus truei*) gene flow, which correlated strongly with harvest pattern from 20 years ago. This time lag may be due to the speed in which timber harvest can alter landscape structure, as well as the delay detection of a genetic signature of reduced dispersal because of a long generation time in Coastal tailed frogs. Similarly, Orsini *et al.* (2008) did not find a significant correlation of gene flow among populations

of the Glanville fritillary butterfly (*Melitaea cinxia*) current fragmented landscape fragments; rather, genetic structure was explained better by past events. In contrast, the contemporary landscape explained slightly more variation in genetic differentiation than a reconstructed historic landscape for the rainforest dwelling logrunner (*Orthonyx temminckii*; Pavlacky *et al.* 2009). Specifically, landscape heterogeneity facilitated gene flow before European settlement, but contemporary deforestation was shown to be the most important impediment to logrunner gene flow.

The effects of spatial scale have been investigated less frequently in landscape genetics studies. Yet, the spatial scale of variables used, the spatial scale of their influence on the species of interest, and functional scale of the species itself are all important considerations (Storfer *et al.* 2007). As an example, the relative influence of independent variables at different spatial scales can be tested to establish the most appropriate spatial scale to include in a model (Cushman *et al.* 2006; Murphy *et al.* 2010). Murphy *et al.* (2010) investigated scale of the landscape influencing connectivity for boreal toads (*Bufo boreas*) in Yellowstone by testing the influence of landscape variables at multiple bandwidths (from 30 to 960 m) connecting sites. They found habitat permeability and topographic roughness influenced population connectivity at fine scales, ridgelines were important at broad scales, and temperature and moisture had effects across spatial scales. In contrast, no effect of spatial scale was found in the spotted frog (*Rana luteiventris*; Murphy *et al.* 2010), possibly because of a smaller study area of that in boreal toads. Although small in size, genetic diversity of a beetle (*Carabus auratus*) was highly correlated with broad-scale availability of grasslands suggesting that functional connectivity does not necessarily operate at small spatial scales for small species (Sander *et al.* 2006).

In sum, few landscape genetics studies have been conducted across a variety of spatial scales or considered effects of temporal variation. Yet, with recent technological advances, we are increasingly able to collect large amounts of molecular data in short periods of time. Effects of spatial scale should be considered because the limited studies that do exist suggest different landscape features affect genetic variation at different spatial scales. As a result, studies that occur in a single area or in across a limited spatial scale may be limited in their inference regarding the effects of landscape variables on genetic connectivity. In addition, with increased global development, land use change and climate change, understanding effects of temporal scale variation will become increasingly important. As an example, knowledge of the effects of previous devel-

opment actions may allow simulation testing of landscape genetic effects of alternative proposed future development actions to facilitate management recommendations.

Species-specific hypothesis testing

A number of studies have used landscape genetic approaches to address a priori hypotheses regarding the species of interest. Often, the goals of such studies are to compare results with those of other work on the same system (Michels *et al.* 2001; Watts *et al.* 2004; Stevens *et al.* 2004). For example, Michels *et al.* (2001) measured flow rate of zooplankton (*Daphnia ambigua*), whereas Stevens *et al.* (2006a,b) experimentally measured both movement speed and permeability across different land covers in natterjack toads (*Bufo calamita*). In both studies, movement data were directly used to parameterize resistance surfaces in landscape genetic analyses. On the other hand, Watts *et al.* (2004) conducted mark–recapture and landscape genetic analyses separately for the damselfly (*Coenagrion mercurial*) and found the two approaches provided consistent results, supporting the hypothesis of a highly sedentary species. Another example was a study of the effects of successional stage on genetic structure in the lemon-yellow daylily (*Hemerocallis thunbergii*; Chung *et al.* 2007). As predicted, significant fine-scale genetic structure was found for three of four expanding, no mature, and only one senescing population of the daylily (Chung *et al.* 2007).

Landscape genetics has been used in several studies to distinguish between multiple alternative hypotheses, especially when other types of data have been inconclusive. Moore *et al.* (2008) was concerned with how recent land modification might influence current population structure of the tuatara (*Sphenodon punctatus*). Tuataras are long-lived, which would suggest a delayed response to recent change, but also sedentary, which would lead to faster effects of drift. Results suggested that the sedentary habits of this species led to a genetic response to current land use change. In another example, researchers were trying to reconcile results of fine-scale population structure in broadcast-spawning marine organisms that should have high gene flow (Banks *et al.* 2007). The authors used the sea urchin (*C. rodgersii*) to test whether broadcast spawners could lead to fine scale genetic structure. Although sea urchins have little genetic structure across most of their range, variation in sea surface temperature and geographic variables resulted in localized pockets of higher substructure (Banks *et al.* 2007). These results accounted for the discrepancies among other marine studies.

Recommendations for authors and reviewers

Because of the interdisciplinary, technical nature of landscape genetics, it may be unclear to both authors and reviewers what information should be reported in landscape genetics publications. We propose some guidelines regarding descriptions of which basic molecular and spatial components that should be included. We hope these guidelines will lead to improvements in consistency of data reporting among journals, as well as in interdisciplinary communication.

First, common tests to validate multi-locus genotypic data, such as tests of HWE and disequilibrium, should be presented. Genetic analyses using neutral markers, such as microsatellites, commonly assume HWE and linkage equilibrium. However, such tests were only reported in approximately 70% of studies. Although tests for deviation for Hardy–Weinberg or linkage equilibrium are not particularly statistically powerful, lack of HWE may indicate presence of null alleles, and positive linkage disequilibrium may indicate loci are non-independent. In either case, researchers should consider how such violations of assumptions affect results of data analyses, as well as possible exclusion of problematic loci altogether. In addition, authors should report data reproducibility, especially if using AFLPs, RAPDs or low quality DNA samples. Although some studies still use RAPDs, their use has subsided substantially due to concerns regarding repeatability.

The reporting of spatial data sources was inconsistent among both ecological and genetic journal types. Overall, few studies reported details of their spatial data sources, data resolution, how sample locations were recorded, spatial scale, and spatial data classification scheme. The source (e.g. LandSat), resolution (e.g. 30 m), and classification (e.g. NLCD2001) of each of these spatial data should be reported. As multiple metrics can be calculated from a single data layer, authors should clearly state which data sources were used to calculate which metrics (e.g. DEM used to calculate slope). Particularly for fine-scale studies, high accuracy of sampling locations may be essential. Once samples are collected, the source of sampling locations (GPS, quad-map, hunter reported, etc.) and some indication of error should be reported. Reporting the model of GPS unit is informative if formal error assessment is unavailable. Consistent reporting of all of these data collection methods can help reviewers as well as readers assess the appropriateness of the spatial data for the study species, the question(s) being asked, and statistical analysis methods employed. Reporting of data sources can also inform readers as to availability data for studies on similar species or in similar geographic regions.

Future directions

Our analysis of empirical trends identified a number of future directions for landscape genetic studies. One of the largest discrepancies we observed was that the vast majority of studies took place in temperate locations while tropical environments, well known as hotspots of biodiversity (Myers *et al.* 2000), were underrepresented. This trend has also been noted for ecological studies in general (Fazey *et al.* 2005; Gardner *et al.* 2007) and likely reflects both the lower-income status and lower proficiency in English of many tropical countries, which, taken together, constrain initiation and publication of scientific research (May 1997; Fazey *et al.* 2005). Tropical areas are currently experiencing high rates of deforestation and landscape modification (Carnaval *et al.* 2009) and are also a major focus of landscape scale corridor efforts (Kaiser 2001). Thus landscape genetic approaches may be especially valuable in the tropics for quantifying effects of landscape change and evaluating the effectiveness of corridors for maintaining functional connectivity.

We found that only one-third of studies presented a clear sampling design. While many landscape genetic studies may, by necessity, rely on opportunistic sampling (i.e. hunter collected tissues), employing robust study designs is critical for many analytical methods and to test specific hypotheses (Storfer *et al.* 2007). For example, failure to capture the range of variation in an environmental (e.g. temperature) or landscape variable (e.g. elevation) may over- or under-estimate the importance of the influence of that variable on gene flow and genetic structure (Storfer *et al.* 2007). Stratified sampling designs help to capture the range of variation in a variable of interest. Overall, authors should carefully design sampling that is matched to research questions and clearly report this design in the resulting publication (reviewed in Storfer *et al.* 2007).

Another general trend was that studies often tended to address general or exploratory questions related to barriers or overall connectivity. For example, visual inspection of overlays of landscape data on genetic clusters for spatial coincidences of cluster boundaries with (obvious) landscape structures was commonly used (Fig. 6). Few studies addressed specific hypotheses of connectivity or more specific objectives, such as identifying source-sink processes or identifying corridors. As landscape genetics is a relatively young discipline (Manel *et al.* 2003), it is not surprising that initial studies have often been exploratory as opposed to hypothesis-driven, as such studies are necessary before more specific questions can be asked. However, landscape genetics has been moving toward testing specific hypotheses of how environmental and landscape features influence the spatial distribution of neutral genetic variation (Cushman *et al.* 2006;

Balkenhol *et al.* 2009a), as well as that of adaptive markers and traits (Holderegger & Wagner 2008; Manel *et al.* 2010). To this end, Guillot *et al.* (2009) provide a comprehensive review of spatial statistics that can be applied in genetics studies.

As we look to the future, recent technological advances will lead to the availability of vast amounts of molecular and even complete genomic data available for landscape genetics studies (Holderegger & Wagner 2008). Landscape geneticists should begin to consider how to incorporate new types of genetic data into landscape genetic analyses, and spatial analysis of genomic data in particular will likely require new methods and approaches (see Manel *et al.* 2010). In addition, understanding the spatial distribution of molecular markers under selection is becoming increasingly important to assess the adaptive potential of natural populations in the face of global change (Holderegger & Wagner 2008; Manel *et al.* 2010). As human development continues to increase across most landscapes (Sanderson *et al.* 2002), it will be important to understand how these converted landscapes influence disease spread, genetic diversity, gene flow and population viability in a diversity of taxa. To assist in these goals, we suggest that data from landscape genetics studies be made freely available via a web-based database to facilitate higher level analyses and interpretations.

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Supporting Information

Additional supporting information can be found in the online version of this article.

Table S1 Description of data fields entered into database

Table S2 Categorization of journal types as ecology/conservation versus genetics

Table S3 Mean sample, number of loci and ratio (mean sample size per year/mean number of loci per year) in landscape genetic studies by year

Fig. S1 Trends in analytical methods over time.

Fig. S2 Percent of terrestrial versus percent of aquatic studies using a particular analysis method.

Fig. S3 Percent of publications using each type of landscape variable over time.

Fig. S4 Percentage of landscape genetic studies per taxonomic category using a particular analytical method.

Fig. S5 (a) Molecular markers used by journal type. (b) Percentage of landscape genetic studies that used multiple molecular markers by journal type.

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