NEWS AND VIEWS

OPINION

Navigating the pitfalls and promise of landscape genetics

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The field of landscape genetics has been evolving rapidly since its emergence in the early 2000s. New applications, techniques and criticisms of techniques appear like clockwork with each new journal issue. The developments are an encouraging, and at times bewildering, sign of progress in an exciting new field of study. However, we suggest that the rapid expansion of landscape genetics has belied important flaws in the development of the field, and we add an air of caution to this breakneck pace of expansion. Specifically, landscape genetic studies often lose sight of the fundamental principles and complex consequences of gene flow, instead favouring simplistic interpretations and broad inferences not necessarily warranted by the data. Here, we describe common pitfalls that characterize such studies, and provide practical guidance to improve landscape genetic investigation, with careful consideration of inferential limits, scale, replication, and the ecological and evolutionary context of spatial genetic patterns. Ultimately, the utility of landscape genetics will depend on translating the relationship between gene flow and landscape features into an understanding of long-term population outcomes. We hope the perspective presented here will steer landscape genetics down a more scientifically sound and productive path, garnering a field that is as informative in the future as it is popular now.

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The important gap filled by landscape genetics

Landscape genetics has emerged as one of the central topics of investigation in the field of molecular ecology (Sork *et al.* 1999; Manel *et al.* 2003; Selkoe *et al.* 2008; Balkenhol *et al.* 2016). Early efforts in landscape genetics were developed to explore spatial genetic patterns in a rigorous way and avoid some of the subjectivity with projecting population genetic patterns onto landscapes (Manel *et al.* 2003; Cushman *et al.* 2006; Balkenhol *et al.* 2009b). Much of its appeal then and now is in the capacity to address questions of broad interest to population geneticists and ecologists, such as how environmental variables impact the movement of organisms and how landscapes shape functional connectivity between populations. Further, with the capability to evaluate explicit landscape effects—including those associated with habitat conversion and modification—landscape genetics as a field has clear value for conservation biology (Segelbacher *et al.* 2010; van Strien *et al.* 2014).

Broadly speaking, the goal of landscape genetics is to identify environmental features that influence gene flow among populations. Ostensibly, meeting this goal is straightforward: molecular data coupled with geographic data (e.g. GIS layers) can be analysed in concert to infer relationships between gene flow and landscape characteristics. The rapid adoption of genetic tools (e.g. microsatellite loci, Single Nucleotide Polymorphisms) and a bevy of free and sophisticated software (e.g. R, Structure, GRASS GIS, Circuitscape) have increased the accessibility of landscape genetic techniques. This accessibility has, in turn, made landscape genetics a popular pursuit for many of us studying some aspect of population biology and conservation, resulting in an impressive breadth of published gene flow estimates across myriad species and landscapes.

All that glitters is not gold—acknowledging the limits and misapplication of landscape genetics

The efforts to date are commendable and foundational, and we laud the progress that has been made. However, we suggest that meeting the goal of landscape genetics is less tractable than typically acknowledged. This is because a number of complicating issues exist in both principle and practice, which are rarely considered (see Pitfalls below). One practical issue is that the field of landscape genetics is evolving so rapidly and new methods are being proposed (and criticized) with such regularity that it is difficult for researchers to identify the 'best practices' suitable to apply landscape genetics to their study system. As a result, we feel that important limitations and nuances are often overlooked, and that insights derived from such studies can lead to

potentially spurious conclusions. We will be the first to acknowledge that such mistakes can be difficult to perceive let alone avoid, having not been immune to them ourselves.

There are already many valuable articles that detail or critique specific aspects of landscape genetic methodology (Landguth *et al.* 2012; Cushman *et al.* 2013; Guillot & Rousset 2013; Hall & Beissinger 2014; Pflüger & Balkenhol 2014; Keller *et al.* 2015; Prunier *et al.* 2015; Balkenhol *et al.* 2016). Here, we take a broader perspective in describing four common pitfalls that researchers should prioritize avoiding when applying landscape genetic tools in their research. These pitfalls include (1) a myopic view of the role of gene flow in population health and viability, (2) the interpretation of results beyond what is supported by data or study design, (3) misinterpreting the biological relevance of genetic structure and (4) the potential for overconfidence in quantitative methods estimating landscape effects. Following a discussion of pitfalls, we outline practical alternative approaches designed specifically to help researchers avoid these pitfalls and advance the conceptual framework behind landscape genetics. It is our hope that by identifying these common pitfalls and highlighting ways to avoid them, we can improve landscape genetic-based understanding of wild populations while sharpening the accuracy and impact of this burgeoning discipline.

Common pitfalls in the application of landscape genetics

Pitfall 1: Gene flow is viewed as universally beneficial

There is no doubt that the magnitude of gene flow among populations can have a profound influence on both demographic and evolutionary outcomes. However, knowledge of gene flow alone only partially informs our understanding of how populations are ultimately influenced by the landscape. This is because gene flow has a variety of consequences for populations, which are dependent on ecological context and evolutionary history (Garant *et al.* 2007). In other words, identical levels of gene flow can have entirely different effects for different populations, species or landscapes (Figs 1 and 2). Ultimately, population genetic outcomes depend on drift and selection, in addition to gene flow (Haldane 1930; Yeaman & Otto 2011; Blanquart *et al.* 2012).

Yet despite our knowledge of these myriad effects, the typical view from much of the conservation and landscape genetics literature remains that increased gene flow is unequivocally beneficial for populations. Moreover, evidence for restricted gene flow seems to prompt an immediate sense of concern over population persistence. However, restricted gene flow among populations is not universally detrimental and can indeed have positive effects on populations (Fig. 2) (Rosenblum 2006; Nosil 2009; Richardson & Urban 2013). From a macroevolutionary perspective, this is evident in our understanding of the role genetic drift plays in species diversification (e.g. Knowles & Richards 2005). From a contemporary evolutionary perspective, gene flow that is restricted between divergent environments can allow for local adaptation in response to localized natural selection pressures by limiting the arrival of maladapted alleles (i.e. from genes that are locally adapted to different but connected environments) and reducing outbreeding depression (Frankham *et al.* 2011; Weeks *et al.* 2011) and migration load (Fig. 2) (Garcia-Ramos & Kirkpatrick 1997; Sexton *et al.* 2011; Richardson & Urban 2013). Thus, limited gene flow can lead to an increased response to selection, resulting in higher relative fitness of the local population.

Transmission of disease provides another example where gene flow might pose a risk rather than a benefit among connected populations (Fig. 1a). In this case, dispersal—a necessary precursor to gene flow—can serve as a vector of disease transmission (Park 2012). Here again, the relative advantages and disadvantages of different rates of dispersal appear to be context dependent. For example, some evidence suggests that the demographic benefit of connectivity outweighs the infectious risk of disease (McCallum & Dobson 2002; Heard *et al.* 2015), while other evidence points to beneficial fragmented populations experiencing refuge from disease (Becker & Zamudio 2011).

There are, however, many theoretical and empirical examples in which gene flow is beneficial. Evidence suggests that moderate rates of gene flow might generally be optimal for local adaptation because they facilitate the arrival of new, beneficial alleles (Fig. 1b) (Gomulkiewicz *et al.* 1999; Swindell & Bouzat 2006). Gene flow is also known to provide benefits through demographic rescue (Fig. 1c) (Brown & Kodric-Brown 1977), as well as genetic rescue (Ingvarsson 2001; Sexton *et al.* 2011) and restoration (Fig. 1d)(Hedrick 2005). The value of this potential benefit is thought to be most relevant in small, isolated populations (Thrall *et al.* 1998; Madsen *et al.* 2004) yet appears to be less important than increasing population size (Kenney *et al.* 2014). Dispersal, and hence gene flow, is similarly critical in populations that are characterized by high rates of local extinction–recolonization. In these circumstances, knowledge of gene flow alone can certainly aid conservation by identifying source and sink populations.

In conclusion, we underscore the need to recognize that gene flow is a process that can both positively and negatively influence a population's response to its environment. We therefore argue that gene flow should not be viewed as an end response. Instead, gene flow should be considered jointly along with population properties such as population size, growth and (mal)adaptation. Minimally, landscape genetic studies should address the implications of their findings in the light of these multifarious effects of gene flow. Testing such potential outcomes in tandem with landscape genetic inference will provide a more comprehensive understanding of the consequences of gene flow across the landscape (see Conceptual Framework section below).

Pitfall 2: Scale, inference and the risk of extrapolating results too broadly

An emerging theme in ecology and conservation is the need to understand patterns and processes across
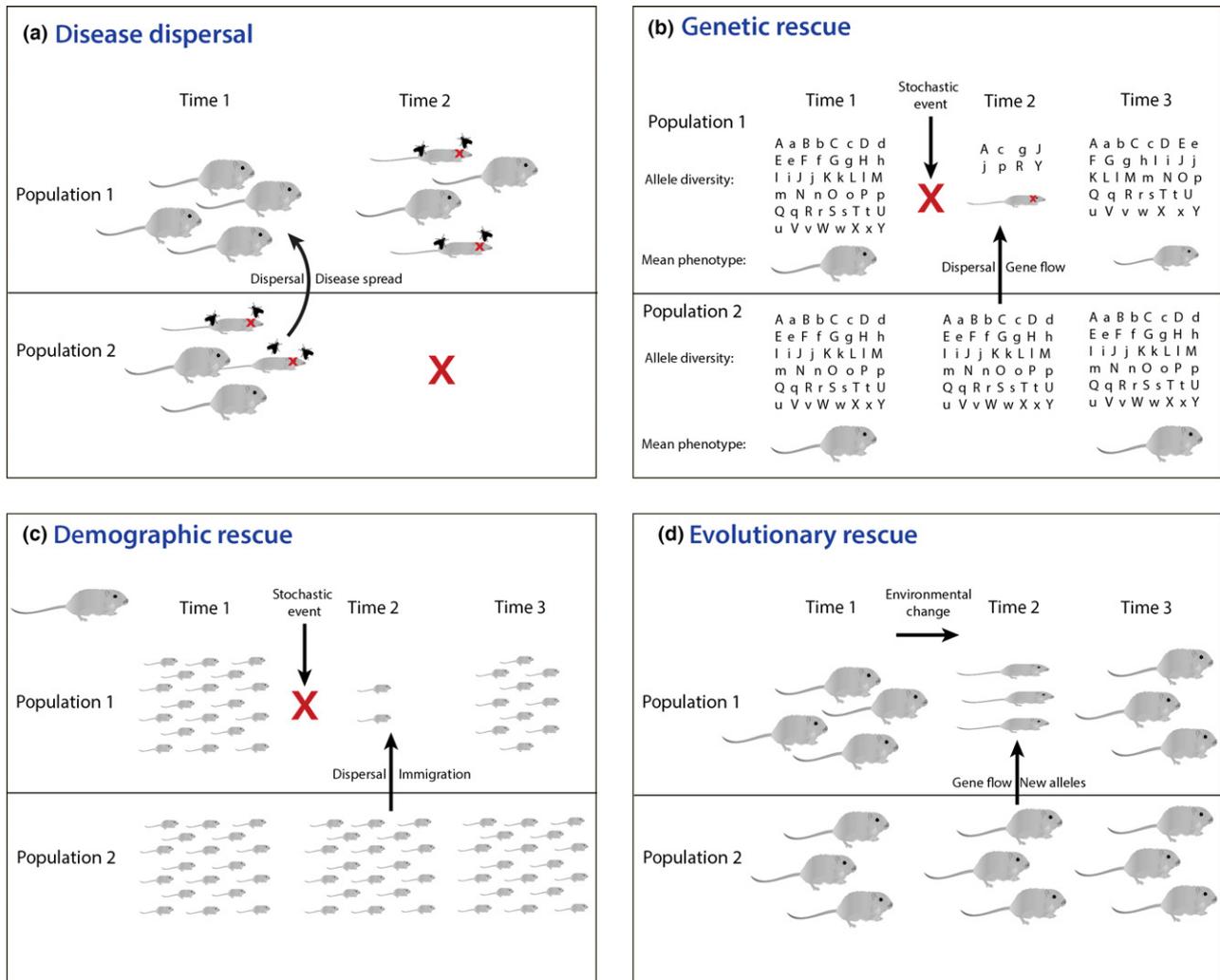
Fig. 1 The movement of individuals and gene flow between populations can have both positive and negative effects (both ecological and evolutionary) on the recipient population, as illustrated in these hypothetical mouse scenarios. (a) Dispersal can spread disease between populations, leading to lower population performance in population 1 over time. (b, c) When a population experiences a stochastic perturbation, both population size and genetic diversity can decrease correspondingly. Demographic rescue occurs when immigration via dispersal bolsters population numbers between time 2 and 3. Genetic rescue follows if the gene flow from other populations increases the genetic diversity to the point that the population is now viable after the genetic bottleneck resulting from the stochastic event. (d) When a well-adapted population 1 experiences an environmental change and is no longer well adapted to the new conditions (indicated by a smaller body size), evolutionary rescue occurs when gene flow comes from populations that are well adapted to the environmental condition that is novel for population 1. This gene flow provides alleles that were not in population 1 before but now provide an adaptive benefit under these new conditions.

taxonomic groups and geographic scales (Roberge & Angelstam 2004; Peters *et al.* 2008; Schwenk & Donovan 2011). This advancement of the field means that researchers need to move beyond single-species anecdotes in order to provide general inferences that are both geographically and taxonomically broad. With the capacity to map gene flow across large spatial scales, landscape genetics provides an appealing approach to generate geographically large-scale inference. Studies can also take advantage of collaborations to include multiple species within the same landscapes to increase relevance across taxonomic groups (see Conceptual Framework below).

Yet, we find that this goal of achieving broad relevance and applicability often leads to interpretations of data that extrapolate too far beyond the scope of a particular study, given its design and taxonomic focus. As a result, the relevance for studies is often overstated in both lofty titles and the conclusions drawn. For example, a common goal in landscape genetic studies is to relate findings to regional land conversion processes such as urbanization, logging and agricultural development (e.g. Spear and Storfer 2008; Gabrielsen *et al.* 2013; Reid & Peery 2014). Despite the fact that many studies estimate gene flow for just one species on a single landscape, results are often presented as
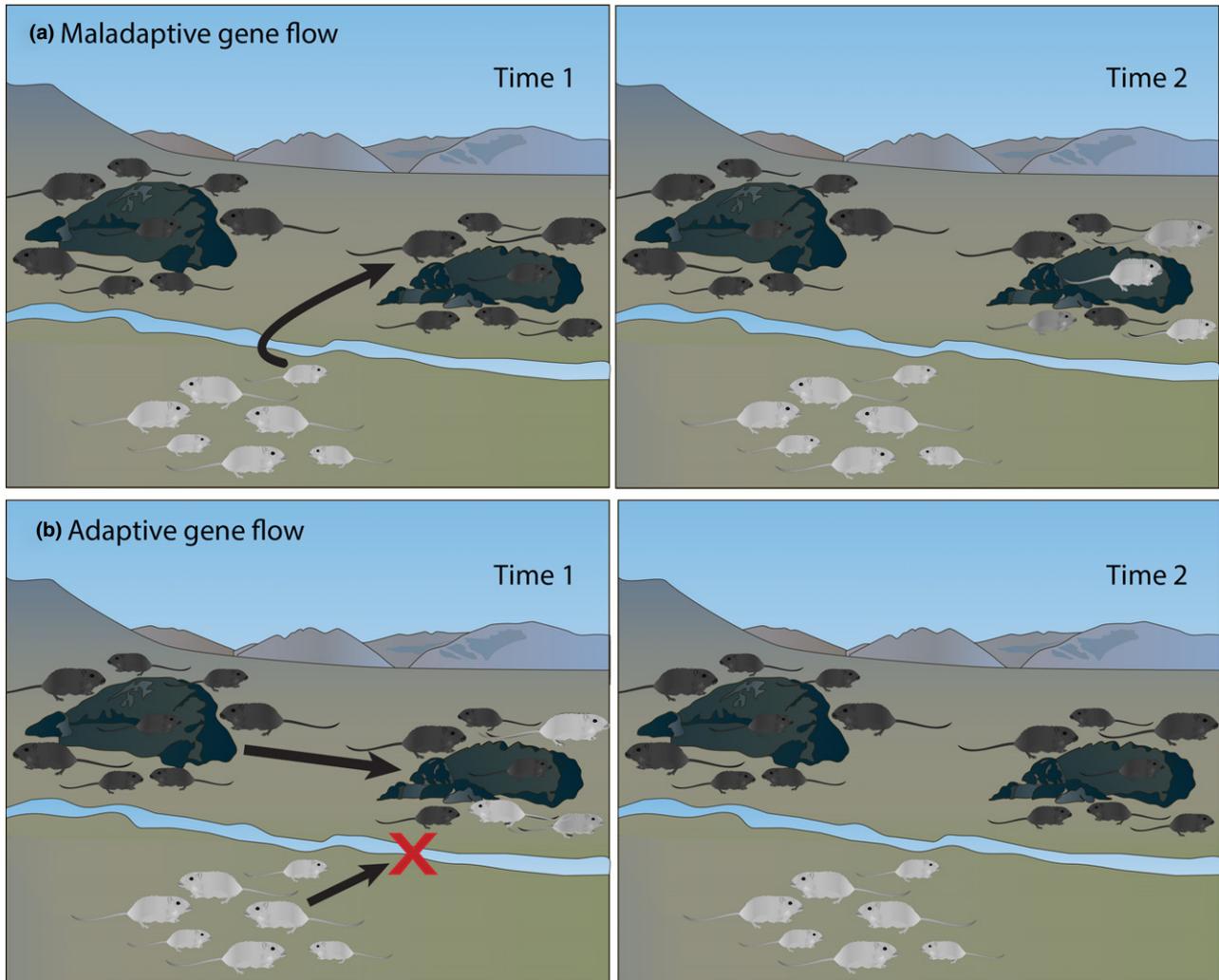
Fig. 2 Landscapes can directly impact how much movement and gene flow populations exchange, which has complex consequences for their adaptive potential. In the panels above, populations of mice can inhabit dark rocky surfaces or lighter soils. Visual predators ensure that mice with dark pelage have higher fitness and survival on dark substrate, while light colour mice are better adapted to light surfaces. (a) If the river does not substantially impede gene flow, the light-coloured population of mice could disperse and breed with the dark population. At time 2, their offspring will be of intermediate colour and decrease the mean fitness of the dark substrate population of mice. This decline in fitness indicates that genetic connectivity between the light and dark population contributes maladaptive gene flow, or migration load. (b) However, if the river inhibits gene flow markedly, maladapted alleles from the light-coloured population cannot increase the frequency of light-coloured mice on the dark rocks. If pelage colour already varies within the dark substrate area, gene flow from other, well adapted (i.e. dark pelage) will increase the frequency of well-adapted alleles and contribute adaptive gene flow that increases the mean fitness of the population in time 2.

broadly generalizable landscape effects likely to apply to areas outside of the study or across taxa. This connection may seem reasonable for landscapes with similar environments or species with similar ecological niches. However, the few studies that investigate multiple landscapes and species do not find consistent support for this extrapolation (e.g. Poelchau & Hamrick 2012; Richardson 2012; Whiteley *et al.* 2014).

The effect of roads is one example of this trend to generalize results. In cases where roads are found to affect gene flow, results are often communicated to suggest that in general, roads are important barriers to gene flow. Yet

evidence suggests that road effects are quite mixed. For example, in their review, Holderegger & Di Giulio (2010) found that among 32 studies reporting genetic effects of roads, 23 detected evidence for genetic differentiation while eight studies showed no effects whatsoever. For instance, one species of salamander showed very little genetic differentiation among populations separated by a divided highway (Prunier *et al.* 2014), whereas another species exhibited the opposite pattern in response to the same road class (Marsh *et al.* 2008). Further, geneflow patterns associated with roads can vary even among animals occupying identical habitats across the same landscapes

(Richardson 2012). These differential responses appear to also relate to phenotypic differentiation, wherein relative rates of gene flow across species correspond to the patterns of adaptation and maladaptation in populations influenced by road adjacency (Brady 2012, 2013). The specific mechanism behind road effects on population genetics may also contribute to the variation observed across studies. Simulation data suggest that increased mortality and genetic drift may be more important than decreased movements due to barrier effects in reducing genetic connectivity (Jackson & Fahrig 2011), while other studies find no such barrier effect for all but the busiest interstate highway (Shirk et al. 2010).

This variation in the genetic response to a single aspect of landscape development demonstrates the complexity that characterizes gene flow and its effects on populations. It also highlights the need for careful consideration of the inferential limits imposed by study designs. Further, because comparative studies are rare, we have very little understanding of how responses differ for multiple species on the same landscape. Developing such insight into the ways in which diverse taxa are affected by the same landscape is precisely the type of information that can lead to generalizable insights into landscape genetics.

Finally, we note that the tendency to aggrandize and overinfer results is often portended by the titles of papers, belying what in actuality might be a minor effect of a landscape feature, or an effect limited to the species and landscape in that particular study. This is not to discount the value of such studies. Indeed, this information can be highly relevant to local conservation interests and can provide valuable data needed for synthetic analyses. However, we advocate for a more measured degree of inference that is mindful of study design limits, so that results may be communicated appropriately. We also recommend that studies seeking to make broadly relevant inference carefully develop suitable study designs, such as those that utilize replicated landscapes that tailor sampling based on hypothesized landscape effects, and multispecies comparative approaches (see Conceptual Framework below).

Pitfall 3: (Mis)interpreting the biological meaning of genetic structure

Inferring gene flow has become the default goal for studies of applied landscape genetics. Yet, critically, gene flow is not the only process that influences population genetic structure. For example, high F_{ST} values based on neutral markers are typically interpreted as evidence of restricted gene flow between populations. Yet even alongside reduced migration rates, population differentiation in such cases could arise from large differences in effective population size leading to genetic drift (Whitlock & McCauley 1999). Demographic processes such as this—as compared to restricted gene flow—have very different implications for conservation (Pearse & Crandall 2004). In addition, the stability of gene flow levels and the amount of time that populations have been diverging can lead to patterns of genetic differentiation not caused directly by current geneflow levels. For example, one study on marine invertebrates found very little genetic divergence in a species with poor dispersal abilities, whereas a second species with highly dispersive pelagic larvae exhibited large genetic breaks in the same marine landscape. Analyses indicated that these counterintuitive genetic patterns between the two species were most likely due to dramatically different times since vicariance and colonization of the sampled populations (McGovern et al. 2010). In light of the multiple sources of genetic structure, it is critical that the evolutionary processes that may contribute to observed landscape genetic patterns are considered in advance of relating such patterns to landscape processes and to conservation objectives. Absent this inference, conclusions can be categorically wrong. Simulations can be useful in parsing these effects (see Conceptual Framework below), while Marko & Hart (2011) advocate the use of genealogical techniques (i.e. based on coalescent theory) to distinguish among these evolutionary processes (e.g. Dudaniec et al. 2012).

It is also not uncommon for landscape genetic studies to report low F_{ST} values indicating weak population divergence yet make strong claims about the meaning of such differentiation. Specifically, any F_{ST} that is statistically significant is often interpreted as biologically meaningful and said to deserve careful attention, especially in conservation settings. While 'biologically meaningful' bears no formal definition, the intention of such a claim seems to be to convey a sense of relevance for the influence of the landscape feature in question. This assertion of meaning is problematic because small changes in gene flow, while statistically significant, might have no effect on population performance. In other words, population differentiation—especially when it is slight—does not necessarily signal an effect or risk for population demography (Hedrick 1999).

Unfortunately, there is no clear threshold rule as to what constitutes a large effect on gene flow. For a small population whose persistence requires rescue effects and/or is prone to deleterious effects of inbreeding, a small but significant F_{ST} might be a serious threat. On the other hand, for species with evolutionary histories characterized by small population sizes, long lifespans and outbreeding avoidance, such differentiation might be entirely benign if not favourable (Holt & Gomulkiewicz 1997; Johnson et al. 2009). As mentioned earlier, this problem can be addressed by studies looking at multiple species and landscapes, along with complementary studies of the ecological and evolutionary status of populations (Aykanat et al. 2015). We suggest that as these ecology and evolution studies develop alongside landscape genetic inference, synthetic analyses can reveal how different levels of differentiation affect populations in different ecological and evolutionary contexts, and perhaps will help formally define what it means to be biologically meaningful.

Pitfall 4: Quantitative methods are mistaken for rigour and precision

There has been an important push in recent years to make landscape genetics a more quantitative field and less reliant

on descriptive patterns and expert opinion (Storfer *et al.* 2007; Guillot *et al.* 2009; Wang *et al.* 2013). In spirit, we support this effort and agree that inference of geneflow patterns benefits from quantitative investigation that can provide numerical estimates for landscape effects. However, more quantitative results and higher resolution models may appear to improve precision, but are not a substitute for robust study design and cautious inference. In our view, the abundance of data, software and new approaches under the banner of landscape genetics has increased the risk that studies will misapply these powerful methods and overextend the scope of inference for their data. We view this as particularly worrisome given the common application of landscape genetics to conservation efforts. For example, the relative ease with which resistance surfaces can be translated into models of biological corridors or in which a simulation programme can produce a scenario of future gene flow can lead to recommendations that either may be misguided or not supported when other data are considered. We caution that quantitative efforts not be viewed as unqualified indicators of rigour and study merit, particularly if independent validation studies are not conducted.

Avoiding the pitfalls and advancing the conceptual framework

Despite the pitfalls and potential misapplications highlighted above, the landscape genetics framework developed over the last 15 years comes with an immensely valuable set of tools and approaches and continues to transform the way we evaluate landscape effects in ecology, evolutionary biology and conservation (McRae *et al.* 2008; Segelbacher *et al.* 2010; Petren 2013). For this reason, here we advance the conceptual framework and provide practical guidance for incorporating landscape genetics into future studies, with an emphasis on a comprehensive perspective on gene flow, robust study design and proper applications of the associated methods. As with any emerging framework, the methods comprising landscape genetics are continually evolving, and new tools and tests are regularly developed to address specific questions or to take advantage of new data and genetic resources (e.g. Jones *et al.* 2013; Vincent *et al.* 2013; Galpern *et al.* 2014; Peterman 2014; Bradburd *et al.* 2016; Rellstab *et al.* 2015). With so much fluidity, it can be limiting to try to identify specific 'best' methods. However, there are important considerations regarding study design and types of analysis that are paramount for any landscape genetics study, regardless of the particular methods used. We outline those considerations below in the context of the pitfalls described above.

Taking a comprehensive view of gene flow and its influence on populations

Most landscape genetic studies to date, including our own, have overstated findings from estimates of gene flow and genetic structure without considering demographics (e.g.

N_e), natural selection or basic constraints imposed by study design. To move the field forward, we propose that spatial genetic patterns need to be interpreted with a more thorough consideration of ecological and evolutionary processes, including population demography, local adaptation and other factors that contribute to how populations respond to and persist within their landscapes. Conclusions in the absence of such information on population performance (and ultimately fitness) lack context. Ideally, well-studied systems would eventually pair landscape genetic inferences with studies of phenotypic traits and, ultimately, adaptive markers (Barrett & Hoekstra 2011; Barley *et al.* 2015). On this front, there are important approaches being developed using genomic data with many markers to identify genetic variation that is strongly correlated with environment variation across landscapes (e.g. environmental association analysis; Rellstab *et al.* 2015). While valuable, we view these association studies as first steps, but not as substitutes for in situ evaluations of population attributes (e.g. growth rates, population size, fitness proxies) or manipulative experiments testing for evolutionary status (e.g. local adaptation, divergent selection, degree of maladaptation). Inclusion of such population-level attributes would represent a valuable increase in the scope of landscape genetics and its relevance to evolution, ecology and conservation.

We suggest that statements advocating management strategies should be grounded in a more comprehensive understanding of these population responses. Simply reporting that genetic differentiation is significant or that gene flow is reduced in a given landscape is of limited value without understanding whether there are associated risks or benefits for population success. As one example, Bonin *et al.* (2007) developed the 'population adaptive index', a metric that attempts to evaluate several important genetic parameters of populations, including gene flow, genetic diversity and adaptive genetic variation. This measure can be modified for specific study systems or to include demographic and evolutionary information, and used to prioritize conservation efforts among populations using a much more comprehensive perspective than simple genetic differentiation (Bonin *et al.* 2007; Medugorac *et al.* 2009; Coleman *et al.* 2013). If such information was collected, it would be easy to incorporate demographics and fitness traits to connect gene flow, performance, and landscape context when evaluating population viability.

Developing hypotheses and a predictive framework

Landscape genetic methods are often treated as a means of exploratory analysis of population genetic patterns across space. While there is a role for exploratory applications (Kelling *et al.* 2009), we encourage researchers to pursue hypothesis-driven studies within the landscape genetics framework (Balkenhol *et al.* 2009a; Storfer *et al.* 2010). When studies are underpinned by a priori hypotheses, researchers can design sampling strategies that sufficiently target the variables of interest, produce more accurate parameter estimates and rigorously test the hypotheses

(e.g. Cushman *et al.* 2006; Amos *et al.* 2012). Put another way, if a researcher changes the study question from 'What is the landscape effect?' to 'What is the effect of landscape element x?', they are much more likely to design a sampling scheme that convincingly evaluates the effect of element x on genetic patterns and gene flow.

The alternative 'data-driven' studies often make unguided use of all landscape and environmental data layers available for a focal region. Added variables can increase the risk of finding spurious associations between those variables and the spatial genetic structure observed (Dormann *et al.* 2013). On the other hand, excluding variables that play a significant role can cause studies to overlook important relationships in that system (Kelling *et al.* 2009). Hypotheses developed using background data can help researchers design studies that are more likely to include the variables of interest and the sample sizes necessary to test the hypotheses while minimizing the risk of spurious results from model overfitting and an excess of variables with small effects.

One of the primary benefits of a hypothesis-driven approach is the ability to develop better predictive models (van Strien *et al.* 2014), which are the grist that determines how broadly applicable the results of any single study are. Hypotheses and predictive models will often combine genetic data and a deep understanding of a system, perhaps including data on the movement of individuals collected in the field (Lowe & Allendorf 2010) and how landscapes have changed over time or are expected to change in the future (Dudaniec *et al.* 2013; van Strien *et al.* 2014). The predictive value of a model is assessed in two ways: *internally*, using only a subset of the data to construct the model and quantify the predictive accuracy using the rest of the data set; and *externally*, by testing the accuracy of the model on a random sample from an independent data set. The degree of correspondence is typically evaluated by examining the residual variation between observed and predicted values (van Strien *et al.* 2014). A predictive modelling framework provides researchers and conservation managers with an understanding of the landscape effects on gene flow, as well as the predictive value of these models across different landscapes and under changing landscape and climate scenarios.

Selecting and replicating the focal landscape to expand the scope of inference

In our assessment, evaluation of multiple, independent landscapes is one of the most critical, and overlooked, components of a landscape genetics study. Some studies focus on a particular landscape based on information that is required expressly for a species inhabiting that landscape, as is often the case for imperilled populations (e.g. Wang 2009). However, replication of landscapes is required in order for the results to have broad relevance beyond just a single landscape (Holderegger & Wagner 2008; Amos *et al.* 2012) and for evaluating predictive models. Yet, examinations of multiple landscapes are exceedingly uncommon in

studies investigating landscape effects on gene flow (Segelbacher *et al.* 2010). In most other fields of biology, including ecology and evolution, an unreplicated study design would not be acceptable for drawing general conclusions about a variable of interest.

To illustrate the importance of replication, Bull *et al.* (2011) studied 12 landscapes and found very different landscape effects on gene flow in the American black bear. Importantly, the features affecting gene flow in each of the 12 landscapes were those that showed the most variation within a landscape (e.g. variation in elevation; topography), but were not consistent from one landscape to the next. Other replicated studies also indicate that it can be inaccurate to extrapolate landscape genetic inferences from one landscape to another (Dudaniec *et al.* 2012; Trumbo *et al.* 2013). We do not yet know whether these differences across focal landscapes result from heterogeneity in how landscapes influence organisms, low power to detect and quantify individual effects of each variable, or idiosyncrasies in the studied populations (e.g. departures from migration–drift equilibrium). Therefore, more than one noncontinuous landscape needs to be included in order to characterize the role of particular features and evaluate how consistent those effects are across landscapes. True replication may be difficult for continuously distributed species or habitats, in which case sampling should be performed in distant parts of the landscape or range where direct gene flow is unlikely.

Evaluating multiple species to expand the scope of inference

As conservation initiatives move towards comprehensive strategies targeting entire landscapes and communities of species (see Pitfall 2; Schwenk & Donovan 2011; Peters *et al.* 2008), landscape genetics studies will need to explicitly compare multiple species on the same landscape. However, to date most research on the effects of landscape structure on gene flow in plants and animals has been a collection of anecdotes—studies looking at a single species in one landscape. Fortunately, examples of multispecies comparative studies are increasing in the literature (e.g. Manier & Arnold 2006; Delaney *et al.* 2010; Goldberg & Waits 2010; Olsen *et al.* 2011; Aparicio *et al.* 2012; Poelchau & Hamrick 2012; Richardson 2012; Phillipsen *et al.* 2015). Given that conservation initiatives are rapidly moving away from single-species approaches, the best insights into gene flow for management strategies will come from studies that allow us to generalize across landscapes and biological systems. For example, studies that evaluate landscape resistance to gene flow for multiple species could examine the degree of overlap in these resistance surfaces among species in order to recommend candidate areas for protection as corridors of movement. We hope that regional-scale conservation initiatives (e.g. Natura 2000 and the Pan European Ecological Network in Europe; Yellowstone to Yukon and the Interstate-90 Wildlife Corridor Campaign in the U.S.) will stimulate the coordinated collection of genetic data from multiple species over the

same areas—something that may otherwise be logistically difficult for individual researchers.

Sampling strategies that provide strong inferences

General advice on sampling strategy is covered elsewhere (e.g. Schwartz & McKelvey 2009; Hale *et al.* 2012; Prunier *et al.* 2013); however, we note several important spatial and biological considerations here. First, as with any scientific study, hypotheses should dictate design; researchers should select landscapes that will allow them to convincingly assess how those landscape elements influence genetic patterns. For example, if high-order streams are predicted to impede dispersal and gene flow, the focal landscape studied would need to encompass multiple such streams with sampling sites both separated by and contiguous between these streams. It is also important to select an appropriate spatial scale for the questions being investigated. The landscape genetics framework is well-suited to investigating genetic patterns at small to moderate spatial scales. However, as the scale increases evolutionary lineages may vary across sampling sites, altering the inferences about landscape vs. phylogenetic effects that can be obtained (Vandergast *et al.* 2007; Wang 2010; Pante *et al.* 2015).

The appropriate number of sampling sites or populations will depend on both the spatial extent of the focal landscapes and the number of landscape elements being evaluated (Galpern *et al.* 2012). Unsampled populations or areas can alter landscape genetic inferences, depending on the metric of gene flow used and the amount of migration contributed by the unsampled populations (Beerli 2004; Naujokaitis-Lewis *et al.* 2012; Koen *et al.* 2013). Complex landscapes might require denser sampling to isolate the effects of particular landscape features (Prunier *et al.* 2013). While sampling specifically based on landscape variables may help detect an effect, sampling along a regular grid is the least biased approach (Schwartz & McKelvey 2009). Simulations also indicate that sampling along a uniform grid or randomly across the focal landscape provides the greatest power to identify the landscape processes generating spatial genetic patterns (Oyler-McCance *et al.* 2013). Of course, this may not always be feasible or practical. For studies exploring specific hypotheses, a stratified random sampling design can ensure that sites are selected in a way that allows specific landscape effects to be tested rigorously. Guided simulation methods may be an important step in study design for ensuring that the data set will have statistical power.

Additionally, as with any population-level analysis, the number of individuals sampled per site, as well as the type and number of genetic markers, are important considerations when applying landscape genetic methods (Wang 2011; Hale *et al.* 2012; Landguth *et al.* 2012). For studies with genomic data sets, the number of samples per population can be reduced if many unlinked loci are genotyped, because each locus represents an independent observation of the coalescent (Wang & Bradburd 2014). Nevertheless, investigations of fine-scale processes may still require greater sampling density.

An appealing alternative to population-level sampling is individual-based sampling using genetic dissimilarity between individuals rather than a collection of individuals grouped a priori into 'populations' (Rousset 1999). This approach has been used less frequently and has less analytical support at this point, because most current analyses are population-based and assume island–mainland models of gene flow (Dyer 2015). However, individual-based approaches allow for the sampling of more locations as fewer individuals need to be sampled from each 'site'. This permits higher resolution sampling within an area or inclusion of a wider sampling area of the landscape. Simulations suggest that the ability to detect landscape effects is similar or better using individual-based sampling, particularly as sampling is targeted around landscape features thought to disrupt gene flow (Prunier *et al.* 2013; Luximon *et al.* 2014). Finally, for studies based on opportunistic sampling, clustering of sampling sites can introduce bias because of spatial autocorrelation, making the sample non-independent and artificially inflating sample sizes (Fig. 3). In these cases, spatial rarefaction may be applied to reduce spatial dependency in the data and to avoid the introduction of sampling bias (Chiarucci *et al.* 2009; Brown 2014).

Identifying the appropriate scale of inference based on study design

Relative to more traditional ecological studies, contemporary studies of landscape genetics tend to be conducted across much larger spatial extents. It is therefore understandable that authors are inclined to infer observed patterns as reflecting general processes. While these interpretations may be warranted in some cases, most landscape genetic studies are performed for a single species in a single landscape. Given our emerging knowledge of how much variation occurs among even closely related species in the same landscape (Brady 2012, 2013; Richardson 2012), or identical species across different landscapes (Bull *et al.* 2011), it is critical that interpretations are carefully considered and communicated cautiously. We suggest that inference be clearly stated in each study, qualifying interpretations that relate to the study region versus those that speculate what might occur outside of the study area in similar landscape contexts. Ultimately, the capacity for larger scale inference that exceeds the spatial extent of a particular landscape can be made through a combination of replicated landscape/species designs and meta-analytic syntheses (e.g. Jenkins *et al.* 2010).

Selecting the appropriate scale to evaluate

GIS data are increasingly becoming available at finer spatial resolutions, and researchers are frequently taking advantage of these fine-scale data for localized landscape genetics studies. However, finer scale data are not always better, and both simulation and empirical studies have shown that the scale chosen can alter inferences (Anderson *et al.* 2010; Cushman & Landguth 2010; Angelone *et al.*
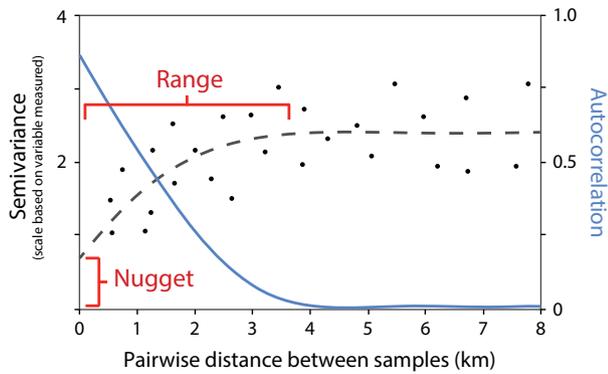
Fig. 3 Semivariograms plot the relationship between distance among samples and the degree of correlation in the response variable between each pair of points, and can be an important analysis in landscape genetics to determine the degree of autocorrelation across the landscape and the appropriate scale for analysing genetic data (Franklin & Mills 2003; King *et al.* 2010). This semivariogram displays a hypothetical relationship between pairwise distance (*x*-axis) and the semivariance (left *y*-axis) in a response variable between two points. Greater semivariance indicates less correlation between pairs of sampling points. Black dots represent measured data points, and the dashed black line is the model fitted to those points. Spatial autocorrelation (right *y*-axis) is a measure of covariance between sampling points, which decreases proportionally to semivariance, and is often estimated using Moran's *I*. In this example, pairs of samples that are farther than ~3.5 km apart are not spatially correlated for this variable. This distance where spatial autocorrelation is no longer observed is called the 'range'. The 'nugget' represents the y-intercept of the semivariance, representing small-scale variability in the data. This may be due to measurement error or, more interestingly, fine-scale variation in genetic or environmental variables that can facilitate genetic divergence and microgeographic adaptations. In other words, the nugget represents average variation within a site that might provide the basis for evolutionary change. Semivariograms provide a visual means to identify the appropriate spatial scale to sample in order to encompass environmental variation that is hypothesized to influence movement and gene flow across the landscape, or to ensure that independent samples are collected beyond the scale of autocorrelation.

2011; Galpern *et al.* 2012; Keller *et al.* 2013). Thus, it is critical for the scale to be chosen in an informed and methodical way. This is best accomplished a priori based on information about organismal biology, the environmental variables under study, or existing knowledge of the process being examined. In many cases, the optimal scale may not be known a priori; in these cases, model-fitting procedures and information theoretical approaches can be used to identify the optimal spatial scale from several alternatives (Cushman & Landguth 2010; Galpern *et al.* 2012). Additionally, in some cases, analysis at multiple scales may be necessary—for instance if different patterns or processes are operating at different scales (e.g. Keller *et al.* 2013). In these cases, examining semivariograms can help determine whether different processes are acting at different scales (Fig. 3).

Analytical and statistical options—choosing the right tool

The rise of landscape genetics has been fuelled by the steady development of analytical methods. The continued emergence of such methods is encouraging, but the plethora of options is also bewildering at times. Some important reviews exist highlighting the utility and limitations of some of these options (e.g. Balkenhol *et al.* 2009b; Guillot *et al.* 2009). These include evaluations of the Mantel test and its derivatives, which have been criticized for having high type I error rates and other drawbacks (Balkenhol *et al.* 2009b; Legendre & Fortin 2010; Guillot & Rousset 2013; Legendre *et al.* 2015) but may still provide useful initial tests for landscape genetic studies when complemented with other analyses (Cushman *et al.* 2013; Diniz-Filho *et al.* 2013). Fortunately, ongoing development of new methods has generated a suite of alternatives, and here, we highlight several new and promising analytical approaches that can make significant contributions to landscape genetics.

Moran's Eigenvector Maps to obtain orthogonal spatial data. One of the main criticisms of Mantel tests and related analyses is the nonindependence of values within the data set (Legendre & Fortin 2010; Guillot & Rousset 2013). Recently, Moran's eigenvector maps (MEM) and its precursor, principal coordinates of neighbour matrices (PCNM), have been developed and used for ecological data sets to create orthogonal variables and avoid the issues associated with nonindependent data (Dray *et al.* 2006; Legendre *et al.* 2015). MEMs are produced using a principal coordinate analysis of the same Euclidean distances among sampling sites that are typically used for Mantel tests (Dray *et al.* 2006; Diniz-Filho *et al.* 2009). MEM eigenvectors are obtained, which are used in subsequent analyses as new orthogonal variables. This means that the correlations of the new variables are zero, thereby avoiding the major nonindependence issue with matrix correlation tests where each element is correlated with each other value in its series. Regression analyses are then conducted using the new MEM variables as independent predictor variables. Genetic distances between sites are typically the dependent variable. This regression follows the dbRDA approach of McArdle & Anderson (2001). So it bears highlighting that the primary advantage in this approach is the new orthogonal spatial variables created with the MEM eigenvectors.

This approach has just recently been incorporated into studies of spatial genetic structure (Manel *et al.* 2010; Richardson & Urban 2013), and the MEMGENE package has been developed in R to facilitate the use of MEMs in landscape genetics (Galpern *et al.* 2014). This package produces new spatial variables that can be used directly to visualize the spatial patterns of genetic data, or as response variables in regression analyses with environmental predictor variables that are hypothesized to influence the spatial genetic structure of the focal species. Simulations suggest that this approach is particularly helpful in situations where gene flow is high and weaker genetic patterns are expected (Galpern *et al.* 2014).

Bayesian estimates of relative effect sizes. Alternative approaches have recently been developed and adapted for landscape genetic studies that overcome some of the limitations of earlier techniques. Bradburd *et al.* (2013) developed a Bayesian method that can simultaneously quantify the relative effect sizes of geographic and environmental distance on genetic divergence between samples. This approach uses geostatistical methods to explicitly model spatial autocorrelation and estimate the covariance structure of allele frequencies from multiple loci among sampling locations, thereby accommodating the nonindependence of pairwise data. Implemented in the R package BEDASSLE, the Bayesian framework allows one to estimate uncertainty in parameter estimates and evaluate how well each model fits empirical data, including nonlinear functions.

Structural equation modelling. Structural equation modelling (SEM) and the closely related path analysis have a long history in evolutionary biology (Wright 1921, 1934) but have only recently been applied in landscape genetics (Wang *et al.* 2013). Both approaches are extensions of multiple regression analysis and can therefore evaluate complex relationships between genetic patterns and multiple landscape and environmental variables (Urban & Richardson 2015). SEM can incorporate latent variables, which is particularly useful for landscape genetics studies in which there is often limited background data on the relative importance of various environmental predictor variables. SEM uses regressions and model-fitting to estimate the relative strengths of direct and indirect relationships between the variables of interest (Shipley 2002; Kline 2010). For example, Wang *et al.* (2013) used SEM to evaluate how geographic distance and 24 environmental variables contributed to spatial genetic structure in 17 *Anolis* lizard species. Environmental variation across the study area contributed significantly to genetic patterns; however, geographic isolation accounted for more than twice the genetic divergence observed, on average (Wang *et al.* 2013). Importantly, path analysis and SEM both rely on a set of hypotheses about the causal relationships between variables that are developed a priori by the investigators. This has been characterized as a limitation of SEM; however, we view this as a potential strength of the framework that encourages researchers to approach landscape genetics from a hypothesis-driven perspective (see discussion above).

Generalized linear mixed models. Another approach for dealing with issues of spatial autocorrelation is to utilize generalized linear mixed-effects models (GLMM), which account for both fixed and random effects in the data. While variables of interest can be analysed and inferred as fixed effects, variation associated with other levels of organization (e.g. spatial proximity) are estimated as random effects. Rousset & Ferdy (2014) recently developed a method, implemented in the R package spaMM, to use GLMM to quantify spatial correlations and demonstrate the performance of likelihood ratio tests for fixed effects under spatial autocorrelation. Yoder *et al.* (2014) recently showed how inverting the standard regression test (i.e. making environmental variation the response variable rather than genetic variation) can allow GLMM to overcome the potentially confounding effects of background spatial genetic structure. Linear mixed-effects models have recently been used convincingly for landscape genetic studies on aquatic insects, koalas and sage grouse to account for the nonindependence within distance matrices (van Strien *et al.* 2012; Dudaniec *et al.* 2013; Phillipsen *et al.* 2015; Row *et al.* 2015).

Population network topology. Other approaches have been developed to address the limitation of assuming linear responses of genetic distance to geographic and environmental distances. For instance, Dyer *et al.* (2010) showed how using conditional genetic distances, derived from network topology and that simultaneously takes the genetic covariance of all populations into account, can improve the sensitivity of analyses linking gene flow to landscape variables. They also suggest that examining pairwise distances between every pair of sampling sites, as is typically performed, neglects potential distance-weighted interactions between populations. As an alternative, they develop a framework that treats population pairs as direct or indirect links (based on patterns of gene flow), suggesting that this is more biologically realistic than treating all pairs as equally weighted in analysing genetic exchange (Dyer *et al.* 2010).

The GeNetIt package in R has also been developed to create population genetic networks using gravity models that estimate the strength of interaction between 'nodes' (i.e. sampling sites) based on geographic distance, as well as site-specific and between-site variables (e.g. landscape resistance; Murphy *et al.* 2010; Evans & Murphy 2016). This approach can estimate both within-site (nodes) and among-site (node connections) influences on connectivity, and both straight-line and least cost path connections can be evaluated. Using gravity models, Murphy *et al.* (2010) found local (e.g. predator density, heat load) and between-site (e.g. topography, climate) factors associated with gene flow among montane frog populations.

Optimizing landscape resistance models. It is often useful to model landscapes as resistance surfaces where GIS is used to reclassify raster pixels of landscape attributes (e.g. land cover, slope) as costs to movement. The association between the cost to traverse these resistance surfaces and genetic distances are then evaluated (Spear *et al.* 2010). Accurately parameterizing the costs within these resistance models is a challenge that has been discussed previously (Zeller *et al.* 2012; Graves *et al.* 2013). While ecological tracking and experimental data are the most direct way to understand movement in nature, those data are rarely available to identify landscape costs (Lowe & Allendorf 2010; Nowakowski *et al.* 2015) and movement is not the same as successful gene flow.

To avoid subjectivity with costs assigned by expert opinion, researchers sometimes use genetic data to assign cost values to each landscape variable. This can be somewhat circular when later applying those costs to evaluate the rela-

tionship between cumulative resistance models and genetic distances (e.g. Richardson 2012). However, promising new approaches are being developed to optimize resistance surfaces by simultaneously evaluating multiple resistance surfaces and a range of cost values for each. Implemented in R, the ResistanceGA package uses linear mixed models and information criteria (Burnham & Anderson 2002) to assess the best-fitting landscape resistance surfaces (Peterman 2014). This approach was used to combine ecological and genetic data to parameterize models that were better supported than models based on habitat suitability or organism abundance (Peterman et al. 2014). The 'mgLandscape' function in MEMGENE can also evaluate alternative resistance surfaces using variation partitioning against the estimated genetic distances between sites (Peres-Neto & Galpern 2015).

The value of simulations for landscape genetics

There are constraints for any landscape genetics study in the number of populations and landscapes that can feasibly be evaluated. Given these limitations, simulations provide a complementary tool that allows one to model various scenarios describing potential landscape effects on dispersal (Epperson et al. 2010; Shirk et al. 2012). Consequently, implementing these simulations requires hypotheses on how particular landscape elements might affect gene flow. Simulation results are evaluated against data from real-world landscapes, and results that closely match the empirical data provide support for the hypothesized landscape effects and the parameter estimates comprising those simulations (Epperson et al. 2010; Balkenhol & Landguth 2011). Many programmes have been developed or adapted to facilitate simulations of genetic patterns across landscapes, often at the individual rather than population level (Balloux 2001; Landguth & Cushman 2010; Hoban et al. 2012; Schumaker 2013).

Simulations have been used effectively to assess complex landscape genetic scenarios that would be difficult to isolate empirically. For example, McCulloch et al. (2013) simulated gene flow in a Neotropical bat species to evaluate the potential genetic effects of habitat fragmentation in the Atlantic Forest of South America. Castillo et al. (2014) used simulations to identify the landscape and climate factors associated with gene flow in American pikas, a montane species that is particularly vulnerable to warming climates. Simulations have been used to evaluate important analytical aspects of landscape genetics, including the power and accuracy of statistical methods frequently used in the field (Balkenhol et al. 2009b; Jaquiéry et al. 2011) and the suitability of specific sampling designs for detecting the effects of individual landscape variables (Schwartz & McKelvey 2009; Kierepka et al. 2012; Prunier et al. 2013). Landguth et al. (2010) simulated a range of dispersal strategies to estimate how many generations must elapse before a new landscape barrier is detectable using genetic data.

Simulations have also proven valuable for exploring the effects of historical landscape structure no longer available for study (Dudaniec et al. 2012), and for predicting the effects of future landscape changes and evolution on genetic patterns (Wasserman et al. 2012; Rebaudo et al. 2013). The latter, implemented in SimAdapt, could represent an important approach to connecting predictive models (parameterized by careful empirical studies) to conservation efforts by examining how populations and species will respond to land-use, land-cover and climate change scenarios on a given landscape. We view this type of modelling—which can incorporate both neutral and adaptive genetic variation into explicit landscape scenarios—as a key example of how landscape genetics can be more specific and predictive about the effects of gene flow (e.g. Forester et al. 2016). Rather than assuming a universally positive effect of gene flow, modelling approaches such as SimAdapt provide a way to quantify the potential outcomes of different levels of gene flow under hypothetical landscape and movement contexts.

Conclusions

Landscape genetics is a new field of study for molecular ecology, and the regular development of new methods and analyses means that it is evolving rapidly. This pace of development is encouraging, but also means that 'best' methods are difficult to identify and track. More importantly, the rapid expansion has also allowed serious flaws to be propagated related to interpretation of spatial genetic patterns, overextension of inference beyond what is permitted by the study design, and limited use of hypothesis-testing frameworks. However, foremost among the pitfalls we highlight here is the often singular focus on genetic differentiation and ensuring that gene flow is high and supported. Landscape genetic applications generally lose sight of fundamental ecological and evolutionary principles, namely that gene flow has complex consequences that can both enhance or jeopardize the success of populations (i.e. growth, persistence, fitness). An important transition for the field of landscape genetics will be to provide management recommendations founded on a more comprehensive understanding of these varied population responses to connectivity on the landscape.

We acknowledge that inferring population consequences and conservation implications of gene flow is no small task, especially when past demographic and/or evolutionary history is unknown or not incorporated for comparison (e.g. Larson et al. 2012). Similarly, identifying adaptive genetic diversity remains challenging in nonmodel organisms and even inaccessible for many of the endangered species we study. Yet ultimately, the utility of landscape genetics for conservation will depend on translating the relationship between gene flow and landscape features into an understanding of long-term population outcomes. For example, how much gene flow is needed to sustain populations? Does reduced gene flow pose a challenge to population persistence, or might differentiation be a beneficial process aiding adaptation in certain landscapes? Answering questions such as these will help deliver the insights of landscape genetics in a way that is more valuable for conservation objectives.

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