Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION

OPINION ARTICLE

Making the connection: expanding the role of restoration genetics in restoring and evaluating connectivity

Kirstin M. Proft[1,2], Menna E. Jones[1], Christopher N. Johnson[3], Christopher P. Burridge[1]

The success of restoration activities is affected by connectivity with the surrounding landscape. From a genetic perspective, landscape connectivity can influence gene flow, effective size, and genetic diversity of populations, which in turn have impacts on the fitness and adaptive potential of species in restored areas. Researchers and practitioners are increasingly using genetic data to incorporate elements of connectivity into restoration planning and evaluation. We show that genetic studies of connectivity can improve restoration planning in three main ways. First, by comparing genetic estimates of contemporary and historical gene flow and population size, practitioners can establish historical baselines that may provide targets for restoration of connectivity. Second, empirical estimates of dispersal, landscape resistance to movement, and adaptive genetic variance can be derived from genetic data and used to parameterize existing restoration planning tools. Finally, restoration actions can also be targeted to remove barriers to gene flow or mitigate pinch-points in corridors. We also discuss appropriate methods for evaluating the restoration of gene flow over timescales required by practitioners. Collaboration between restoration geneticists, ecologists, and practitioners is needed to develop practical and innovative ways to further incorporate connectivity into restoration practice.

Key words: adaptive variation, connectivity, conservation genetics, landscape genetics, monitoring, restoration genetics

Implications for Practice

- Genetic estimates of contemporary and historical gene flow and population size can be used to establish targets for restoration of populations where connectivity and genetic diversity have been lost.
- Existing restoration planning tools and frameworks can be parameterized with empirical genetic data about dispersal, landscape resistance and barriers, gene flow, and adaptive variation, rather than expert opinion, increasing the likelihood of achieving restoration goals.
- The impacts of restoration on connectivity should be explicitly evaluated, using genetic analyses and markers that are able to quantify gene flow over short timescales or where there is limited genetic differentiation among locations.
- Collaboration between restoration practitioners and geneticists is needed to provide new tools to guide restoration of gene flow and connectivity.

Introduction

The outcomes of restoration projects for biodiversity are influenced by the surrounding landscape. Recruitment and maintenance of a plant or animal population at a restored site may be affected by the geometry and area of the restoration patch (e.g. Lindenmayer et al. 2007; Lindenmayer et al. 2010), its connectivity to remnants or other restored patches (e.g. Damschen et al. 2008; Lindenmayer et al. 2010; Cosentino et al. 2014), and the composition of the landscape matrix (e.g. Damschen et al. 2008; Mabry et al. 2010). Where restoration patches are too small to support an independent population (or even a single home range), and thus form part of a larger mosaic of habitat for a regional population, landscape factors that affect connectivity will be especially significant in determining success (Brudvig 2011). From a genetic perspective, the connectivity of a restoration area to habitat patches in the surrounding landscape influences local population size and genetic diversity (Weeks et al. 2011). Small, isolated populations are at elevated extinction risk from inbreeding depression (Frankham 2005) or reduced adaptive potential to future environmental change (Hoffmann et al. 2015; Weeks et al. 2016). These three interrelated elements—connectivity, population size, and genetic diversity—are all keys to ensuring the long-term fitness and adaptive potential of restored species (Fig. 1).

Author contributions: KP, CB conceived and planned this article and created the figures; KP led the writing; CB, CJ, MJ contributed to drafting and editing the manuscript.

[1] School of Natural Sciences, University of Tasmania, Private Bag 55, Hobart, Tasmania 7001, Australia
[2] Address correspondence to K. M. Proft, email kirstin.proft@utas.edu.au
[3] School of Natural Sciences and Australian Research Council Centre of Excellence for Australian Biodiversity and Heritage, University of Tasmania, Private Bag 55, Hobart, Tasmania 7001, Australia

doi: 10.1111/rec.12692

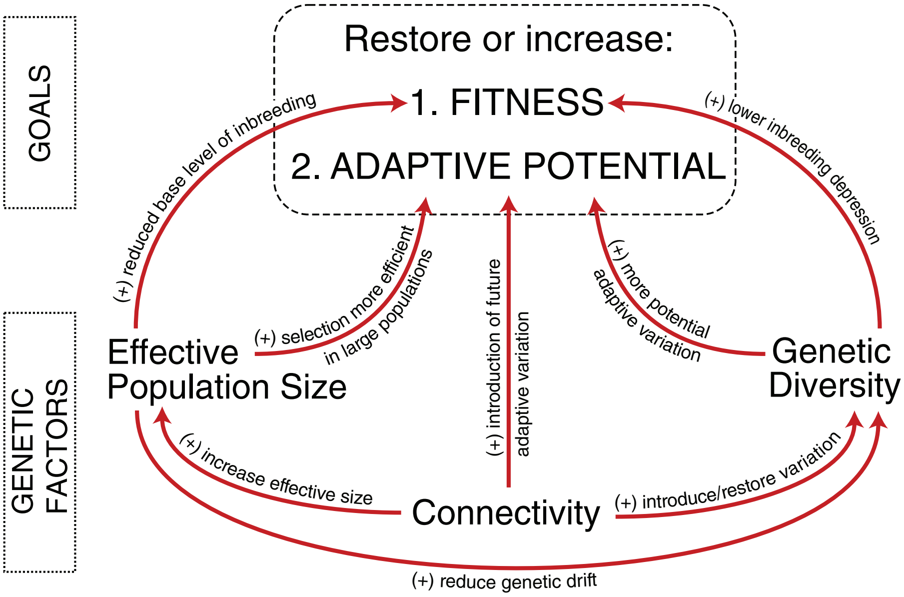

Figure 1. Illustration of three interrelated genetic factors that can influence restoration goals, which should be considered in an integrated genetic approach to restoration practice.

Historically, the application of genetic techniques to restoration ecology has been limited in scope, focusing on associations between genetic diversity and fitness with respect to translocation activities, rather than considering natural connectivity (Mijangos et al. 2015). The lack of focus on genetic connectivity may have had a number of causes, including a failure of many landscape genetic studies to choose appropriate spatial scales and statistical techniques to support conservation questions (Keller et al. 2015), and challenges in obtaining and processing genetic data for sensitive or highly mobile taxa in restored landscapes. However, next-generation sequencing techniques are now making extensive datasets available for conservation genetic and genomic studies at relatively low cost, even for nonmodel organisms (Narum et al. 2013). Current techniques for non-invasive genetic sampling techniques make it possible to collect genetic data for elusive species (e.g. black bears, Pelletier et al. 2017), and can even provide DNA suitable for next-generation sequencing (Russello et al. 2015).

There has been a recent increase in studies applying population and landscape-genetic techniques to link connectivity and restoration planning in novel ways. These include identifying barriers to gene flow (McRae et al. 2012) or spread of adaptive genetic variation (Apgar et al. 2017); mapping gradients of adaptive variation in species (Shryock et al. 2017); and setting genetic targets for restored populations that reflect diversity and connectivity in reference populations (Drury et al. 2017). Connectivity of restored populations to the surrounding landscape is also becoming an important metric of restoration success, both for translocated (Aavik et al. 2013; Reynolds et al. 2013) and naturally recolonizing species (Cosentino et al. 2015; Isselin-Nondedeu et al. 2017; Mijangos et al. 2017). Given the rapid development of sequencing technology and analytical approaches to assessing genetic connectivity, and increasing interest in incorporating this into restoration genetics, we feel that it is timely to synthesize current and emerging genetic techniques that can support decision-making in ecological restoration. We highlight ways in which genetic data can inform restoration (Fig. 2), and provide recommendations for practice.

Quantifying and Understanding Connectivity in Restored Areas

The establishment of connectivity between populations in restored areas and neighboring patches and the natural recolonization of restored habitat are heavily dependent on species' dispersal capabilities. Relative or absolute contemporary rates of dispersal among populations can be estimated using programs such as BayesAss+ (Wilson & Rannala 2003) or BIMr (Faubet & Gaggiotti 2008). Alternatively, individual dispersal can be genetically estimated using individual population assignment approaches (e.g. Berry et al. 2004), parentage analyses (e.g. Peery et al. 2008), or sibling analyses (e.g. Feutry et al. 2017). Historically, the most common genetic markers used for ecologically focused genetic studies were microsatellites, amplified fragment length polymorphisms (AFLPs), and allozymes. Affordable next-generation sequencing is now allowing the increasing use of single nucleotide polymorphism (SNP) datasets, which can provide many neutral markers as well as information about adaptive variation (Narum et al. 2013).

Landscape genetics, a field which integrates approaches from landscape ecology and population genetics (Manel et al. 2003), provides tools for quantifying the relationships between gene flow and environmental factors. Many landscape genetic studies utilize resistance surfaces, which are spatial layers that quantify the "resistance" of landscape and environmental variables to movement and gene flow by organisms (Zeller et al. 2012).

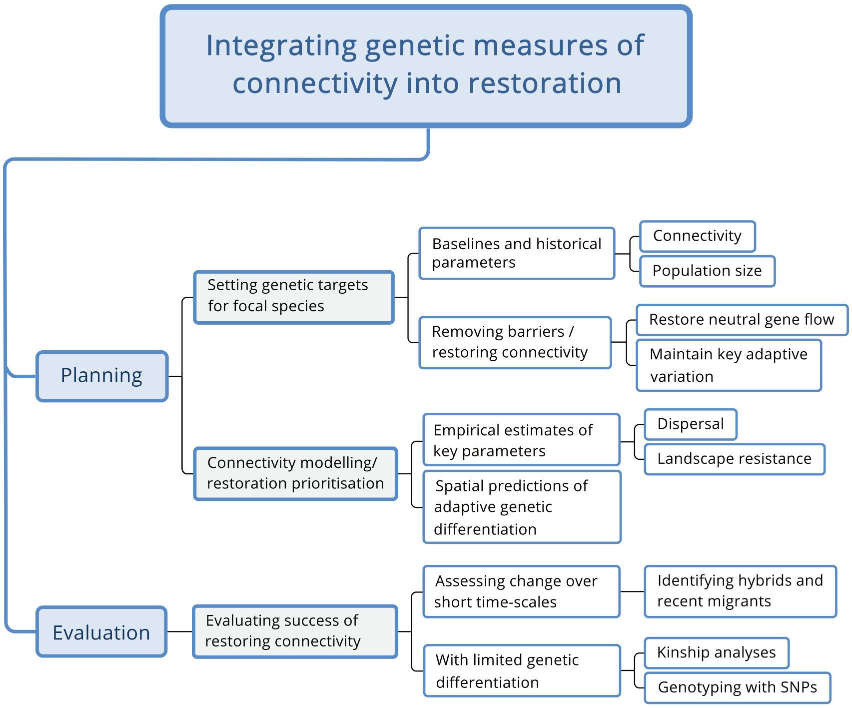

Figure 2. Schematic illustrating ways in which genetic research addressing connectivity can be incorporated into practice. A range of different techniques and products of connectivity research (white boxes) can inform key stages of restoration (gray boxes).

In a typical resistance surface, cells with low resistance represent areas—such are core habitat types—that are easy for an organism to move through, whereas those with higher resistance represent features that impede movement. Resistance surfaces can be optimized using empirical genetic data, either by using model selection to choose which of several predefined surfaces best explains the genetic data or by optimizing resistance surface parameters to maximize fit with observed genetic distances (Zeller et al. 2012). Alternatively, generalized dissimilarity modeling (GDM; Ferrier et al. 2007) provides a two-step procedure that can be used to model nonlinear effects of environmental variables on genetic structure, and then predict and visualize genetic differentiation as landscape maps. Both the resistance surfaces and the outputs of GDM can be used in restoration planning to visualize and predict the connectivity of a restored area within a specific landscape configuration. Landscape genetic studies can also be used to derive parameters or address questions that may inform a restoration project, such as quantifying the influence of habitat gaps on long-term dispersal rates (Coulon et al. 2012), modeling the effects of restoration and land use change on gene flow (van Strien et al. 2014), or comparing the importance of different habitat patches for genetic connectivity in co-occurring species (Fortuna et al. 2009).

Establishing Historical Baselines

Genetic studies have the capacity to establish historical baselines with respect to population connectivity and effective population size, thus indicating if restoration is necessary, and suggesting targets for improvement or metrics for evaluation. Differences in mutation rates and inheritance patterns of genetic markers can be exploited to estimate and contrast patterns of historical and contemporary genetic connectivity. For example, Mijangos et al. (2017) used a mitochondrial DNA marker and microsatellites to reconstruct regional historical migration rates and population sizes of a small marsupial across a landscape containing restored mine sites. They then used microsatellite markers to assess whether postmining rehabilitation restored contemporary connectivity to recolonizing populations at a local scale.

For projects with a limited budget, a single marker type can be analyzed using several measures of gene flow representing different time frames. Historical gene flow can be inferred using coalescent methods implemented in programs like MIGRATE (Beerli & Felsenstein 2001) and IM (Hey & Nielsen 2004), or estimates of F_{ST}, which may take hundreds of generations to show a response to changes in connectivity (Landguth et al. 2010). These can then be contrasted with contemporary dispersal rates. For instance, Apodaca et al. (2012) found that contemporary gene flow (inferred with genetic assignment methods) in a threatened salamander species was significantly less than historical gene flow (inferred with coalescent methods), suggesting a strong impact of habitat fragmentation, and recommended habitat restoration to increase the gene flow between populations to historical levels. If historical landscape data are available, another approach is to test whether the observed genetic structure is best explained by contemporary or historical landscape patterns (e.g. Zellmer & Knowles 2009; Epps et al.

Table 1. Opportunities to integrate empirical genetic connectivity data into recent restoration planning tools.

Aspect of Connectivity	*Representative Studies*	*Connectivity Data Used*	*Opportunities to Integrate Genetic Data*	*Associated Planning Tools*
Removing barriers to gene flow	McRae et al. (2012)	Uses landscape resistance surfaces to identify key barriers to connectivity, and assess benefits of removing them.	Use genetic data to derive empirical habitat resistance surfaces as inputs.	"Barrier mapper" module within "Linkage Mapper" tool. Available at http://www.circuitscape.org/linkagemapper
Identifying movement corridors and bottlenecks	Ribeiro et al. (2017)	Uses landscape resistance surfaces to simulate ecological corridors between source and target patches, for conservation and restoration planning.	Use genetic data to derive empirical habitat resistance surfaces as inputs.	LandScape Corridors software package for corridor design. Available at https://github.com/LEEClab/LS_CORRIDORS
	Pelletier et al. (2014)	Creates landscape-wide, omnidirectional connectivity maps from circuit-theory analyses on landscape resistance surfaces.	Use genetic data to derive empirical habitat resistance surfaces as inputs.	Protocol for making connectivity maps for a landscape, including masking nontarget areas to highlight pinch-points where restoration should be prioritized.
Optimizing patch connectivity for restoration prioritization at landscape scale	Bortoleto et al. (2016)	Classifies distance between patches into categories (e.g. close, far) based on hypothesized species dispersal capabilities; maps resistance of surrounding matrix to dispersal.	Use genetic data to derive both dispersal distance classes and habitat resistance surfaces for target species.	Mathematical index describing suitability of habitat patches for restoration within a landscape, incorporating probability of dispersal to a site, and success of establishment.
	Foster et al. (2016)	Estimates local and regional connectivity using gap crossing and maximum dispersal distances for target species, and least cost path analyses.	Incorporate estimates of dispersal capabilities derived from genetic data.	Multiscale methodology to prioritize areas for investment in revegetation.
Designing reserves to protect genetic differentiation	Thomassen et al. (2011)	Uses GDM to model environmental variables predicting genetic divergence between populations, and creates landscape prediction of classes of genetic similarity.	Already integrated in GDM modeling; use similar methods and data to create maps of genetic structure for other species	Genetic similarity maps used as input for ResNet reserve selection algorithm (Sarkar et al. 2009); could be used in other restoration/conservation planning tools to ensure genetic variation is conserved or linked.
Linking areas with different adaptive genetic variation	Shryock et al. (2017)	Identifies loci under selection; uses GDM to model environmental variables predicting adaptive variation and create landscape-wide maps of adaptive differentiation.	Already integrated in GDM modeling; use similar methods and data to create maps of adaptive distance/connectivity for other species.	Adaptive distance mapping tool for study area, designed for seed provenancing. Available from http://datadryad.org/resource/doi:10.5061/dryad.d48r5, could also be used to prioritize restoration that protects under-represented divergence, or connects adaptively divergent populations.

2013). A third technique uses genetic simulations to reflect several hypothesized past conditions, and tests which simulation most closely matches the empirical genetic data (Pelletier et al. 2017).

Similarly to estimating past gene flow, historical effective population sizes can be estimated using coalescent methods, and contrasted with other genetic approaches that provide estimates of contemporary population size, such as temporal linkage methods (reviewed by Gilbert & Whitlock 2015). These approaches also allow prediction of population persistence, and future consequences of population size for adaptive potential. Evidence for survival through periods of historical population size change may indicate a species' resilience to such fluctuations (Hoffmann et al. 2015), and likewise, long-term, low population sizes may suggest a high likelihood of success in restoration activities despite a potentially low number of individuals to be reestablished (Lankau & Strauss 2011). However, the importance of effective population size for maintaining adaptive potential of populations in the face of unprecedented environmental change (Sgrò et al. 2011) highlights the potential benefits of increasing effective population size regardless of historical baselines or dynamics.

Protecting Adaptive Potential

Evolution can facilitate persistence of restored populations during rapid climatic and environmental change if sufficient genetic variation is present (Sgrò et al. 2011; Hoffmann et al. 2015). It is therefore important to maintain or increase adaptive potential within restored populations. There are a range of genetic techniques that enable us to measure adaptive diversity. Common garden and controlled environment experiments have been widely used to identify adaptation to local conditions (e.g. Sinclair et al. 2015). However, for taxa less amenable to direct manipulation (e.g. many animals), adaptive variation can be identified by screening genomic markers such as SNPs or AFLPs for loci that show unusually high geographic structuring of variation (e.g. Beaumont & Balding 2004; Foll & Gaggiotti 2008). Environment-association analyses, which identify loci strongly correlated with environmental gradients independent of neutral population genetic structure, can also identify potentially adaptive loci (e.g. Joost et al. 2007; Frichot et al. 2013). While these techniques do not specifically identify the variant underlying the adaption, and interpretations of biological significance are often vague (Shafer et al. 2015), this is an area of active research with great potential for ongoing development (Garner et al. 2016).

Once adaptive variation has been identified, there are a number of practical ways that it can be preserved or enhanced in the restoration planning process. One approach involves translocating individuals into a restoration site, with the aim of enhancing the adaptive potential of the population. For instance, when sourcing seed for restoration planting, some practitioners advocate translocating a mixture of different genotypes that may be better adapted to disturbance (Lesica & Allendorf 1999) or future climates (e.g. Sgrò et al. 2011; Prober et al. 2015) at a restoration site. These approaches form part of a broader movement toward climate adaptation through assisted gene flow (Aitken & Whitlock 2013). Translocations may also be particularly important for rare, dispersal-limited species (Baur 2014).

A second approach to protecting and improving adaptive diversity is by restoring natural connectivity between populations through landscape restoration, corridor creation, or removal of barriers to gene flow. In particular, increasing connectivity between areas that have different levels of adaptive diversity or span environmental gradients may help to improve adaptive potential of a species (Sgrò et al. 2011).

Strategically restoring natural connectivity may be a useful approach in many circumstances, as it can avoid several potential risks of translocations. If populations of a species are adapted to their local conditions, translocations may result in individuals being maladapted to their new environments. Evidence of local adaptation has been found in many plant species (Oduor et al. 2016), and this may lead to fitness decreases in individuals translocated to sites that are geographically or climatically distant from their origins, which is a key argument for the use of local provenancing in restoration (Bucharova et al. 2017). Translocations of nonlocal individuals with different phenotypes may also result in complex impacts on coevolved species. For example, oaks of different provenances in a common garden experiment had different abundances of gallwasps (Sinclair et al. 2015), and, similarly, different ecotypes of the perennial grassland species *Centaurea jacea* in common garden conditions have substantial differences in the frequencies of seed herbivores and their associated parasitoids (Bucharova et al. 2016). Local biotic factors such as soil fungal assemblages at restoration sites may also be correlated with species distributions (Pellissier et al. 2013), and could affect the fitness of translocated individuals. Another reason to favor restoration of connectivity as opposed to translocation is to reduce the risk of outbreeding depression, which may reduce fitness when divergent populations are crossed (Weeks et al. 2011). However, the long-term negative consequences of outbreeding depression from translocations appear to have been overstated, except where divergence is sufficient to result in reproductive failure (Weeks et al. 2011) or population sizes are very small (Aitken & Whitlock 2013).

Managers should weigh up the relative costs and likelihood of success when using assisted gene flow or habitat restoration to protect adaptive diversity. Genetic simulations may assist managers in choosing an optimal strategy; for instance, Pelletier et al. (2017) simulated the future genetic trajectory of an isolated population of black bears (*Ursus americanus*) with and without translocations, and concluded that, due to the likelihood of allelic diversity declining rapidly without intervention, and socioecological barriers making habitat restoration impractical, an ongoing translocation program was necessary to conserve this population. In some cases, both strategies may be appropriate, beginning with assisted gene flow to reestablish healthy populations, followed by landscape restoration to promote expansion into new habitats and maintain connectivity without ongoing intervention (e.g. Robichaux et al. 2017).

Translation Into Practice

To ensure the integration of connectivity into restoration practice, we need clear methods for incorporating genetic data into planning and evaluation. Table 1 highlights examples of recent tools or methodologies for restoration planning that could incorporate genetic data in different ways. There are a number of different tools that can assist managers to increase connectivity through restoration, by identifying connectivity corridors, barriers, and pinch-points. Additionally, regional restoration planning frameworks may include estimates of patch connectivity among other key variables (Table 1). Expert opinion is commonly used to parameterize connectivity models and resistance surfaces, but this can be less reliable than empirical approaches (Beier et al. 2008; Zeller et al. 2012). Thus, using genetic data to provide empirical dispersal estimates or resistance surfaces for use in these planning tools could improve the accuracy of models and hence restoration success.

For managers aiming to maintain or connect adaptive diversity through habitat restoration, GDM could be a particularly useful tool, as it generates spatial predictions of putatively adaptive genetic structure that is linked to environmental variables (Table 1). These can then be used to manually select restoration sites that link differently adapted populations, or conserve under-represented adaptive variance. Alternatively, these surfaces can furnish inputs for reserve or restoration-network planning algorithms.

A key challenge for environmental managers wishing to restore connectivity for a wide range of species will be deciding upon an appropriate subset of taxa for targeted genetic research. One approach is to select several umbrella species with relatively high requirements for connectivity, design a network of managed areas for each species based on gene flow and population size, and then “stack up” these networks to produce the final landscape management plan (Baguette et al. 2013). However, this approach may be complicated by the fact that even ecologically and phylogenetically similar species may respond differently to landscape variables (e.g. Poelchau & Hamrick 2012). Alternatively, species might be selected if they provide important ecological functions, such as seed dispersal and pollination, which may be critical to ecosystem recovery (Montoya et al. 2012).

To better integrate connectivity into restoration practice, it is also important to explicitly evaluate the impacts of restoration projects on genetic connectivity, not only during translocations (Aavik et al. 2013; Reynolds et al. 2013), but also in species that naturally recolonize restored habitat (Cosentino et al. 2015; Isselin-Nondedeu et al. 2017; Mijangos et al. 2017). When evaluating the restoration of habitat for connectivity, it is important to note that “gene flow” should be considered as the incorporation via reproduction of genes into another population; “movement” of genes alone is insufficient to realize the fitness benefits of gene flow. Therefore, documented use of a habitat corridor, or movement into or away from a restoration area (e.g. germination of a seed dispersed from elsewhere), need not indicate gene flow (Horskins et al. 2006); genetic confirmation of reproductive contribution to the population is required.

To allow timely monitoring of restoration success, assessment of gene flow associated with restoration activities should employ methods sensitive to changes over short timescales. Assignment methods that can identify hybrids and recent migrants between populations (e.g. Anderson & Thompson 2002; Piry et al. 2004) may provide the most rapid assessments. For example, Isselin-Nondedeu et al. (2017) successfully employed assignment methods to detect migration of palmate newts (*Lissotriton helveticus*) into and between a network of ponds within 2 years of restoration. Where there is little genetic differentiation between populations, methods based on kinship analysis (e.g. Peery et al. 2008; Jones & Wang 2010; Feutry et al. 2017) may prove most successful for detecting gene flow (Palsbøll et al. 2010). Additionally, using even moderate numbers of SNP markers may allow more sensitive detection of genetic differentiation and admixture than microsatellite markers (Gärke et al. 2012).

Conclusion

Ecological restoration will play a critical role in conserving biodiversity and ecosystem function in the future. We have synthesized emerging ways in which genetic research into connectivity, population size, and genetic diversity can improve the planning and evaluation of restoration actions, as summarized in Figure 2. We hope that this article inspires collaborations among geneticists, restoration ecologists, and decision makers to develop new tools that can incorporate a greater variety of genetic data into restoration practice, and guide the restoration and evaluation of gene flow and connectivity.

Acknowledgments

We thank N. Davidson, S. Burgess, and five anonymous reviewers for constructive comments on previous versions of this manuscript. This research was supported by an Australian Research Council Linkage Grant (LP130100949) in partnership with Greening Australia, with collaborators Bush Heritage Australia, the Tasmanian Land Conservancy, and the Department of Primary Industries, Parks, Water and Environment, Tasmania. K.P. is supported by the Holsworth Wildlife Research Endowment and the Ecological Society of Australia, and an Australian Government Research Training Program Scholarship.

LITERATURE CITED

Aavik T, Holderegger R, Edwards PJ, Billeter R (2013) Patterns of contemporary gene flow suggest low functional connectivity of grasslands in a fragmented agricultural landscape. Journal of Applied Ecology 50:395–403

Aitken SN, Whitlock MC (2013) Assisted gene flow to facilitate local adaptation to climate change. Annual Review of Ecology, Evolution, and Systematics 44:367–388

Anderson EC, Thompson EA (2002) A model-based method for identifying species hybrids using multilocus genetic data. Genetics 160:1217–1229

Apgar TM, Pearse DE, Palkovacs EP (2017) Evolutionary restoration potential evaluated through the use of a trait-linked genetic marker. Evolutionary Applications 10:485–497

Apodaca JJ, Rissler LJ, Godwin JC (2012) Population structure and gene flow in a heavily disturbed habitat: implications for the management of the imperilled Red Hills salamander (*Phaeognathus hubrichti*). Conservation Genetics 13:913–923

Baguette M, Blanchet S, Legrand D, Stevens VM, Turlure C (2013) Individual dispersal, landscape connectivity and ecological networks. Biological Reviews 88:310–326

Baur B (2014) Dispersal-limited species – a challenge for ecological restoration. Basic and Applied Ecology 15:559–564

Beaumont MA, Balding DJ (2004) Identifying adaptive genetic divergence among populations from genome scans. Molecular Ecology 13:969–980

Beerli P, Felsenstein J (2001) Maximum likelihood estimation of a migration matrix and effective population sizes in *n* subpopulations by using a coalescent approach. Proceedings of the National Academy of Sciences of the United States of America 98:4563–4568

Beier P, Majka DR, Spencer WD (2008) Forks in the road: choices in procedures for designing wildland linkages. Conservation Biology 22:836–851

Berry O, Tocher MD, Sarre SD (2004) Can assignment tests measure dispersal? Molecular Ecology 13:551–561

Bortoleto LA, Figueira CJM, Dunning JB, Rodgers J, da Silva AM (2016) Suitability index for restoration in landscapes: an alternative proposal for restoration projects. Ecological Indicators 60:724–735

Brudvig LA (2011) The restoration of biodiversity: where has research been and where does it need to go? American Journal of Botany 98:549–558

Bucharova A, Frenzel M, Mody K, Parepa M, Durka W, Bossdorf O (2016) Plant ecotype affects interacting organisms across multiple trophic levels. Basic and Applied Ecology 17:688–695

Bucharova A, Michalski S, Hermann JM, Heveling K, Durka W, Hölzel N, et al. (2017) Genetic differentiation and regional adaptation among seed origins used for grassland restoration: lessons from a multispecies transplant experiment. Journal of Applied Ecology 54:127–136

Cosentino BJ, Schooley RL, Bestelmeyer BT, Kelly JF, Coffman JM (2014) Constraints and time lags for recovery of a keystone species (*Dipodomys spectabilis*) after landscape restoration. Landscape Ecology 29:665–675

Cosentino BJ, Schooley RL, Bestelmeyer BT, McCarthy AJ, Sierzega K (2015) Rapid genetic restoration of a keystone species exhibiting delayed demographic response. Molecular Ecology 24:6120–6133

Coulon A, Fitzpatrick JW, Bowman R, Lovette IJ (2012) Mind the gap: genetic distance increases with habitat gap size in Florida scrub jays. Biology Letters 8:582–585

Damschen EI, Brudvig LA, Haddad NM, Levey DJ, Orrock JL, Tewksbury JJ (2008) The movement ecology and dynamics of plant communities in fragmented landscapes. Proceedings of the National Academy of Sciences of the United States of America 105:19078–19083

Drury C, Schopmeyer S, Goergen E, Bartels E, Nedimyer K, Johnson M, Maxwell K, Galvan V, Manfrino C, Lirman D (2017) Genomic patterns in *Acropora cervicornis* show extensive population structure and variable genetic diversity. Ecology and Evolution 7:6188–6200

Epps CW, Wasser SK, Keim JL, Mutayoba BM, Brashares JS (2013) Quantifying past and present connectivity illuminates a rapidly changing landscape for the African elephant. Molecular Ecology 22:1574–1588

Faubet P, Gaggiotti OE (2008) A new Bayesian method to identify the environmental factors that influence recent migration. Genetics 178:1491–1504

Ferrier S, Manion G, Elith J, Richardson K (2007) Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. Diversity and Distributions 13:252–264

Feutry P, Berry O, Kyne PM, Pillans RD, Hillary RM, Grewe PM, et al. (2017) Inferring contemporary and historical genetic connectivity from juveniles. Molecular Ecology 26:444–456

Foll M, Gaggiotti O (2008) A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. Genetics 180:977–993

Fortuna MA, Albaladejo RG, Fernández L, Aparicio A, Bascompte J (2009) Networks of spatial genetic variation across species. Proceedings of the National Academy of Sciences of the United States of America 106:19044–19049

Foster E, Love J, Rader R, Reid N, Dillon M, Drielsma MJ (2016) Planning for metapopulation persistence using a multiple-component, cross-scale model of connectivity. Biological Conservation 195:177–186

Frankham R (2005) Genetics and extinction. Biological Conservation 126:131–140

Frichot E, Schoville SD, Bouchard G, François O (2013) Testing for associations between loci and environmental gradients using latent factor mixed models. Molecular Biology and Evolution 30:1687–1699

Gärke C, Ytournel F, Bed'hom B, Gut I, Lathrop M, Weigend S, et al. (2012) Comparison of SNPs and microsatellites for assessing the genetic structure of chicken populations. Animal Genetics 43:419–428

Garner BA, Hand BK, Amish SJ, Bernatchez L, Foster JT, Miller KM, et al. (2016) Genomics in conservation: case studies and bridging the gap between data and application. Trends in Ecology & Evolution 31:81–83

Gilbert KJ, Whitlock MC (2015) Evaluating methods for estimating local effective population size with and without migration. Evolution 69:2154–2166

Hey J, Nielsen R (2004) Multilocus methods for estimating population sizes, migration rates and divergence time, with applications to the divergence of *Drosophila pseudoobscura* and *D. persimilis*. Genetics 167:747–760

Hoffmann A, Griffin P, Dillon S, Catullo R, Rane R, Byrne M, et al. (2015) A framework for incorporating evolutionary genomics into biodiversity conservation and management. Climate Change Responses 2:1–24

Horskins K, Mather PB, Wilson JC (2006) Corridors and connectivity: when use and function do not equate. Landscape Ecology 21:641–655

Isselin-Nondedeu F, Trochet A, Joubin T, Picard D, Etienne R, Le Chevalier H, et al. (2017) Spatial genetic structure of *Lissotriton helveticus* L. following the restoration of a forest ponds network. Conservation Genetics 18:853–866

Jones OR, Wang J (2010) COLONY: a program for parentage and sibship inference from multilocus genotype data. Molecular Ecology Resources 10:551–555

Joost S, Bonin A, Bruford MW, Després L, Conord C, Erhardt G, et al. (2007) A spatial analysis method (SAM) to detect candidate loci for selection: towards a landscape genomics approach to adaptation. Molecular Ecology 16:3955–3969

Keller D, Holderegger R, van Strien MJ, Bolliger J (2015) How to make landscape genetics beneficial for conservation management? Conservation Genetics 16:503–512

Landguth EL, Cushman SA, Schwartz MK, McKelvey KS, Murphy M, Luikart G (2010) Quantifying the lag time to detect barriers in landscape genetics. Molecular Ecology 19:4179–4191

Lankau RA, Strauss SY (2011) Newly rare or newly common: evolutionary feedbacks through changes in population density and relative species abundance, and their management implications. Evolutionary Applications 4:338–353

Lesica P, Allendorf FW (1999) Ecological genetics and the restoration of plant communities: mix or match? Restoration Ecology 7:42–50

Lindenmayer DB, Cunningham R, Crane M, Michael D, Montague-Drake R (2007) Farmland bird responses to intersecting replanted areas. Landscape Ecology 22:1555–1562

Lindenmayer DB, Knight EJ, Crane MJ, Montague-Drake R, Michael DR, MacGregor CI (2010) What makes an effective restoration planting for woodland birds? Biological Conservation 143:289–301

Mabry CM, Brudvig LA, Atwell RC (2010) The confluence of landscape context and site-level management in determining Midwestern savanna and woodland breeding bird communities. Forest Ecology and Management 260:42–51

Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. Trends in Ecology & Evolution 18:189–197

McRae BH, Hall SA, Beier P, Theobald DM (2012) Where to restore ecological connectivity? Detecting barriers and quantifying restoration benefits. PLoS One 7:e52604

Mijangos JL, Pacioni C, Spencer PBS, Craig MD (2015) Contribution of genetics to ecological restoration. Molecular Ecology 24:22–37

Mijangos JL, Pacioni C, Spencer PBS, Hillyer M, Craig MD (2017) Characterizing the post-recolonization of *Antechinus flavipes* and its genetic implications in a production forest landscape. Restoration Ecology 25:738–748

Montoya D, Rogers L, Memmott J (2012) Emerging perspectives in the restoration of biodiversity-based ecosystem services. Trends in Ecology & Evolution 27:666–672

Narum SR, Buerkle CA, Davey JW, Miller MR, Hohenlohe PA (2013) Genotyping-by-sequencing in ecological and conservation genomics. Molecular Ecology 22:2841–2847

Oduor AMO, Leimu R, van Kleunen M (2016) Invasive plant species are locally adapted just as frequently and at least as strongly as native plant species. Journal of Ecology 104:957–968

Palsbøll PJ, Zachariah Peery M, Bérubé M (2010) Detecting populations in the 'ambiguous' zone: kinship-based estimation of population structure at low genetic divergence. Molecular Ecology Resources 10:797–805

Peery MZ, Beissinger SR, House RF, Bérubé M, Hall LA, Sellas A, Palsbøll PJ (2008) Characterizing source-sink dynamics with genetic parentage assignments. Ecology 89:2746–2759

Pelletier D, Clark M, Anderson MG, Rayfield B, Wulder MA, Cardille JA (2014) Applying circuit theory for corridor expansion and management at regional scales: tiling, pinch points, and omnidirectional connectivity. PLoS One 9:e84135

Pelletier A, Obbard ME, Harnden M, McConnell S, Howe EJ, Burrows FG, et al. (2017) Determining causes of genetic isolation in a large carnivore (*Ursus americanus*) population to direct contemporary conservation measures. PLoS One 12:23

Pellissier L, Pinto-Figueroa E, Niculita-Hirzel H, Moora M, Villard L, Goudet J, et al. (2013) Plant species distributions along environmental gradients: do belowground interactions with fungi matter? Frontiers in Plant Science 4:1–9

Piry S, Alapetite A, Cornuet JM, Paetkau D, Baudouin L, Estoup A (2004) GENECLASS2: a software for genetic assignment and first-generation migrant detection. Journal of Heredity 95:536–539

Poelchau MF, Hamrick JL (2012) Differential effects of landscape-level environmental features on genetic structure in three codistributed tree species in Central America. Molecular Ecology 21:4970–4982

Prober S, Byrne M, McLean E, Steane D, Potts B, Vaillancourt R, et al. (2015) Climate-adjusted provenancing: a strategy for climate-resilient ecological restoration. Frontiers in Ecology and Evolution 3:1–5

Reynolds LK, Waycott M, McGlathery KJ (2013) Restoration recovers population structure and landscape genetic connectivity in a dispersal-limited ecosystem. Journal of Ecology 101:1288–1297

Ribeiro JW, dos Santos JS, Dodonov P, Martello F, Niebuhr BB, Ribeiro MC (2017) LandScape Corridors (LSCORRIDORS): a new software package for modelling ecological corridors based on landscape patterns and species requirements. Methods in Ecology and Evolution 8:1425–1432

Robichaux RH, Moriyasu PY, Enoka JH, McDaniel S, Loh RK, Bio KF, et al. (2017) Silversword and lobeliad reintroduction linked to landscape restoration on Mauna Loa and Kilauea, and its implications for plant adaptive radiation in Hawai'i. Biological Conservation 213:59–69

Russello MA, Waterhouse MD, Etter PD, Johnson EA (2015) From promise to practice: pairing non-invasive sampling with genomics in conservation. PeerJ 3:e1106

Sarkar S, Fuller T, Aggarwal A, Moffett A, Kelley CD (2009) The ConsNet software platform for systematic conservation planning. Pages 235–248. In: Moilanen A, Wilson KA, Possingham HP (eds) Spatial conservation prioritization: quantitative methods and computational tools. Oxford University Press, New York

Sgrò CM, Lowe AJ, Hoffmann AA (2011) Building evolutionary resilience for conserving biodiversity under climate change. Evolutionary Applications 4:326–337

Shafer ABA, Wolf JBW, Alves PC, Bergström L, Bruford MW, Brännström I, et al. (2015) Genomics and the challenging translation into conservation practice. Trends in Ecology & Evolution 30:78–87

Shryock DF, Havrilla CA, DeFalco LA, Esque TC, Custer NA, Wood TE (2017) Landscape genetic approaches to guide native plant restoration in the Mojave Desert. Ecological Applications 27:429–445

Sinclair FH, Stone GN, Nicholls JA, Cavers S, Gibbs M, Butterill P, et al. (2015) Impacts of local adaptation of forest trees on associations with herbivorous insects: implications for adaptive forest management. Evolutionary Applications 8:972–987

van Strien MJ, Keller D, Holderegger R, Ghazoul J, Kienast F, Bolliger J (2014) Landscape genetics as a tool for conservation planning: predicting the effects of landscape change on gene flow. Ecological Applications 24:327–339

Thomassen HA, Fuller T, Buermann W, Milá B, Kieswetter CM, Jarrin P, et al. (2011) Mapping evolutionary process: a multi-taxa approach to conservation prioritization. Evolutionary Applications 4:397–413

Weeks AR, Sgrò CM, Young AG, Frankham R, Mitchell NJ, Miller KA, et al. (2011) Assessing the benefits and risks of translocations in changing environments: a genetic perspective. Evolutionary Applications 4:709–725

Weeks AR, Stoklosa J, Hoffmann AA (2016) Conservation of genetic uniqueness of populations may increase extinction likelihood of endangered species: the case of Australian mammals. Frontiers in Zoology 13:31

Wilson GA, Rannala B (2003) Bayesian inference of recent migration rates using multilocus genotypes. Genetics 163:1177–1191

Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landscape Ecology 27:777–797

Zellmer AJ, Knowles LL (2009) Disentangling the effects of historic vs. contemporary landscape structure on population genetic divergence. Molecular Ecology 18:3593–3602

Coordinating Editor: Siegy Krauss

Received: 12 September, 2017; First decision: 20 October, 2017; Revised: 2 February, 2018; Accepted: 7 February, 2018