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The application of genetic indicators in wild populations: potential and pitfalls for genetic monitoring

Jennifer Pierson, Gordon Luikart and Michael Schwartz

Things we know

1. Genetic diversity is the foundation of all biodiversity but is seldom considered in studies of biodiversity surrogates.
2. Genetic monitoring may soon be more tractable than many traditional ecological approaches.
3. Genetic indicators are influenced by multiple ecological and evolutionary processes.
4. Genetic indicators can be difficult to interpret.
5. *A priori* criteria and/or thresholds for interpreting indicators are important to define.

Knowledge gaps

6. Determining the limits of non-genetic surrogates for assessing genetic diversity.
7. How will genomics change our understanding of patterns of diversity?
8. Ecologists and geneticists need to work together to define objectives and interpret indicators.
9. How do spatial processes influence metrics derived from idealised populations?
10. Identifying generalisations about how indicators perform.

Introduction

> *'Nothing in biology makes sense except in the light of evolution'*
>
> – Theodosius Dobzhansky

> *'Nothing in evolution makes sense except in the light of population genetics.'*
>
> – Michael Lynch

The genetic aspects of biodiversity and conservation have been long recognised as important to the viability of populations and evolutionary potential of species (Lande 1988). Yet incorporating genetic considerations into conservation, management, and decision making has lagged behind this recognition (Mace *et al.* 2003; Laikre *et al.* 2010). Gene-level (genetic) diversity is required for maintaining fitness and for future evolution and consequently is fundamental to conservation of past and future biodiversity. Thus far, indicators of gene-level diversity have concentrated mostly on agricultural populations, such as food crops (Brown 2008) and forestry products (Boyle 2000). In wild populations, the primary application has been conservation of genetic diversity in the wild relative of crop plants (Laikre *et al.* 2010).

The lack of genetic markers and data on a wide variety of species has contributed to the use of non-genetic surrogates (Mace *et al.* 2003). However, genetic data have become increasingly more feasible to attain through non-invasive sampling techniques, reduced costs for laboratory analyses, and improved data analysis approaches (Schwartz *et al.* 2007; Beja-Pereira *et al.* 2009; Luikart *et al.* 2010). The era of genomics will continue to increase the ease with which large quantities of genetic information are obtained (Allendorf *et al.* 2010). Therefore, applying genetic metrics as indicators is becoming more realistic in natural resource management.

The increase in genetic monitoring of wild populations has spurred interest in the application and evaluation of genetic metrics as indicators used to describe patterns of genetic diversity (Schwartz *et al.* 2007; Robert 2011; Hansen *et al.* 2012; Graudal *et al.* 2014; Hoban *et al.* 2014). The same caveats generally apply to using genetic indicators as to any other indicator in that it is important to outline objective(s) and have a clear benchmark or criteria for identifying biologically significant change (Schwartz *et al.* 2007). In this chapter, we focus on the application of common genetic metrics as genetic indicators, or measures of patterns of genetic diversity, genetic erosion, or genetic vulnerability (Brown 2008). We outline five things we have learned regarding the current application of genetic indicators and their use in natural resource management, and five areas of research that will be most fruitful in moving the field forward.

What we know

1. Genetic diversity is the foundation of all biodiversity, but is seldom considered in studies of biodiversity surrogates

In 1992 at the Earth Summit in Rio de Janeiro, 190 of the world's leaders signed the Convention on Biological Diversity (CBD) in which they recognised the need to conserve three levels of biological diversity – ecosystems, species within ecosystems, and genes within species – while providing economic opportunities to use these biological resources sustainably. According to article 7 of the CBD, each member nation is required to identify and monitor important components of biological diversity. Yet, only approximately one fifth of the National Biodiversity Strategic and Action Plans acknowledged the need for monitoring at the gene level. This is despite approximately two-thirds of the plans recognising the importance of genetic diversity in wild plant and animal species (Laikre *et al.* 2010). Laikre and colleagues (2010) suggest that this is partially a human perception problem, where degradation of ecosystems or loss of species is observable to the 'human eye', deterioration of the gene pool is largely invisible.

At the national level, the critical environmental laws that protect biodiversity are also primarily focused on the protection and monitoring at the ecosystem and species level. For instance, *The United States Endangered Species Act (1973)* is a law with the goal of conserving two levels of biodiversity – species and ecosystems – while *Canada's Species at Risk Act 2002* (SARA) is more focused on species. In contrast, Australia has passed the *Environment Protection and Biodiversity Conservation Act (1999)*, which focuses on all levels of biodiversity including 'species, habitats, ecological communities, genes, ecosystem and ecological processes,' although processes for protecting gene level biodiversity appear lacking. Thus, while many national acts are established to protect and monitor biodiversity, there is a deficiency of considering the most fundamental unit – the gene.

2. Genetic monitoring may soon be more tractable than many traditional ecological approaches

Genetic monitoring is becoming more tractable than traditional ecological and demographic approaches in several species and scenarios. This is primarily due to: (1) increased feasibility of genotyping poor-quality DNA; (2) developments in genomics that allow rapid, inexpensive genotyping; and (3) improved data analysis approaches that allow estimates of important population parameters.

Large sample sizes or more representative samples of individuals can often be collected from non-invasive genetic samples, such as faeces, hair or feathers (Waits and Paetkau 2005; Beja-Pereira *et al.* 2009). Therefore, many parameters, including presence–absence, abundance, effective population size (N_e), number of breeders (spawners), population structure and connectivity (gene flow), can be more easily or reliably estimated using non-invasive genetic samples for species that are secretive or elusive. Certain single nucleotide polymorphism (SNP) chip technologies allow simultaneous genotyping of tens to hundreds of SNPs on tens to hundreds of individuals using low quantity DNA (Campbell and Narum 2008). Concurrent advances in data analysis techniques can provide improved estimates of several commonly used genetic metrics. As an example, the use of genetic indicators to assess and monitor spatial patterns of connectivity, in the context of landscape or climate related features, is increasingly feasible thanks to landscape genetic modelling approaches and software (Sork and Waits 2010).

3. Genetic indicators are influenced by multiple interacting ecological and evolutionary processes

Genetic indicators are often used to assess one aspect of a population (e.g. loss of genetic diversity) that is being influenced by multiple ecological and evolutionary processes (Fig. 15.1). Genetic drift, gene flow, selection and mutation are the primary evolutionary processes. Population size, dispersal behaviour, breeding behaviour, and selective pressures are the primary ecological processes. Many of these processes interact with each other, which can add greatly to the complexity of selecting and interpreting the appropriate indicator and associated criteria. For instance, the loss of genetic diversity over time could be affected by the evolutionary processes of genetic drift, gene flow, selection and the ecological processes of population size, dispersal behaviour and breeding behaviour as well as the interactions between processes (e.g. interaction between gene flow and drift). Careful thought regarding the particular processes that might be under pressure (e.g. habitat loss leads to reduced population size and increased drift) can lead to improved selection of an appropriate metric. Multiple genetic indicators (e.g. metrics) should be used. Simultaneous consideration of different indicators can often help understand causes of genetic changes and also help avoid misinterpretation, such as falsely concluding a population size decline when none occurred (Luikart *et al.* 1998).

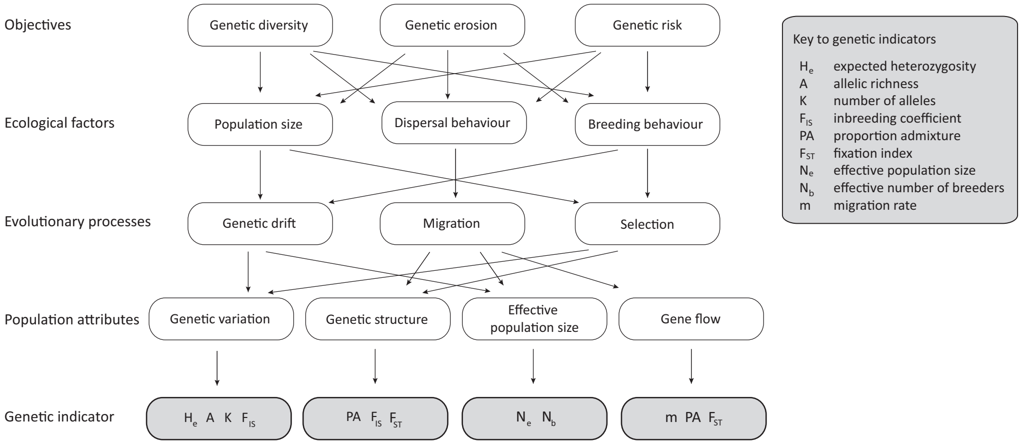

Fig. 15.1. The overarching objectives of an assessment or monitoring program and the connections to ecological factors, evolutionary processes, the subsequent population attributes of interest, and the common population genetic metrics that can be used as genetic indicators for these objectives, as connected through the population attributes.

4. Genetic indicators can be difficult to interpret

The use of genetic indicators as an index of population change can be extremely powerful (e.g. Tallmon *et al.* 2010, 2012). Although genetic data have been widely used to monitor changes in populations of plant and animal species, there has been some reluctance by managers to employ genes as indicators of change. There are many reasons for this hesitation, but a prominent reason may be that changes in genetic signals can be difficult to interpret. For example, the classic population genetics metric F_{IS} is a measure of non-random mating. This measure can become significantly positive if parents on average are more closely related than two mates chosen at random: a phenomenon that can occur in small populations. Similarly, not accounting for underlying population substructure (or a high number of immigrants) can lead to F_{IS} being positive. Other population genetic metrics have the same types of problems, where the signal can be interpreted in multiple, often conflicting, ways. Although this argues for setting genetic questions in a hypothesis testing framework with clear expectations, this is seldom done in genetic assessments and monitoring programs.

5. *A priori* criteria and/or thresholds for interpreting indicators are important to define

Genetic indicators are used to assess either the current status of a population or to detect trends over time. Therefore, the choice of an appropriate indicator, and subsequent criteria for interpreting the indicator, are inherently tied to the objective of the program. Initial design of a program to assess or monitor patterns of genetic diversity should include clear objectives connected to a sampling design and appropriate analytical methods (Schwartz *et al.* 2007). Criteria are important to set *a priori* to ensure the sampling and experimental design are at the correct scale and have the power to detect trends when they exist. Criteria outline what specific conditions need to be met, for the program objectives to be met. This can represent a substantial, but essential, task in the application of genetic indicators in an assessment or monitoring program.

For example, a common objective of genetic monitoring programs is to determine if genetic erosion is occurring. This requires selecting an appropriate indicator of genetic diversity and criteria for what constitutes genetic erosion. Criteria may include a consistent decline in allelic richness over a minimum of three sampling periods. General criteria have been proposed for several applications of genetic indicators (Boyle 2000; Hansen *et al*. 2012; Graudal *et al*. 2014). Hansen and colleagues (2012) outline criteria for detecting adaptive genetic responses to environmental change and suggested several approaches that can be used to demonstrate the criteria have been met. These criteria include six steps: (1) demonstrate adaptive genetic variation exists; (2) link this genetic variation with a specific environmental stress; (3) test for genetic change over time; (4) test that selection has occurred; (5) link observed genetic changes due to selection to environmental factors; and (6) rule out population replacement. Although each application of genetic indicators may require specific criteria, the examples here guide how simple criteria can be applied to give specific requirements of how patterns in the indicator will relate to the program objective.

Knowledge gaps

6. Determining the limits of non-genetic surrogates for assessing genetic diversity

Surrogates of genetic diversity that do not require genetic data from molecular markers (i.e. non-genetic surrogates) have been proposed as indicators of genetic diversity (Brown *et al.* 1997; Boyle 2000; Graudal *et al.* 2014). Boyle (2000) suggest obtaining genetic estimates of gene-level diversity as a last resort, and recommend demographic verifiers as a first step (e.g. population size, population isolation, mating system, species distribution, ecological amplitude). In practice, non-genetic indicators, such as a shift in species range or extent of occupation, are often used to assess genetic diversity and potential for genetic erosion (Forest Practices Authority 2012; Pauls *et al.* 2013; US Fish and Wildlife Service 2013). For example, the Australian Government's most recent State of the Environment Report (State of the Environment 2011 Committee 2011) states that genetic diversity is 'at the heart of biodiversity'. Yet, threats to genetic diversity are primarily assessed through reductions in species distributions (State of the Environment 2011 Committee 2011) and loss of populations (Forest Practices Authority 2012).

The theoretical relationships between these non-genetic surrogates and genetic diversity are well understood (Frankham 1996). However, multiple ecological and evolutionary processes that shape patterns of genetic diversity (e.g. population supplementation, habitat fragmentation, dispersal patterns, population history) may be acting on wild populations that complicate these simple predicted relationships (Jackson and Fahrig 2014; Last *et al.* 2014). For example, the relationship between population size and genetic diversity can be complicated by population supplementation (e.g. the release of hatchery fish). Therefore population size may perform poorly as an indicator of genetic diversity in some cases (Osborne *et al.* 2012). An important issue with using shifts in species distributions as the sole indicator of genetic erosion is the likely oversight of cryptic diversity, or structured genetic diversity that may represent different lineages that may be on different evolutionary trajectories, within morphospecies (Pauls *et al.* 2013). This loss of cryptic diversity may result in large underestimates of predicted biodiversity loss (Bálint *et al.* 2011). As such, the use of coarse non-genetic indicators of genetic diversity in isolation can lead to incorrect management decisions.

We recommend the use of genetic indicators in conjunction with non-genetic indicators when assessing genetic diversity status and risks (e.g. Alsos *et al.* 2012). A combined approach may require less molecular data, therefore provide the ease of non-genetic indicators, yet still include the minimum genetic information necessary to minimise incorrect management decisions. Pfenninger and colleagues (2012) outline a methodology that uses a combined approach. Their approach includes assessing genetic diversity and evaluating species distribution models to assess the risk of the loss of genetic diversity due to global climate change. Additionally, more empirical work in wild populations is needed to refine our understanding of the relationship between non-genetic metrics and patterns of genetic diversity, especially in situations that do not meet the assumptions of predicted theoretical relationships (e.g. spatially structured populations, moderate specialists) (Habel and Schmitt 2012; Neel *et al.* 2013).

7. How will genomics change our understanding of patterns of diversity?

Genomics will allow more precise estimates of most population genetic metrics, such as mean $F_{ST,}$ N_e and *Nm* (gene flow), using neutral markers (Allendorf *et al.* 2010). Genomics also has the potential to dramatically improve our basic understanding of processes such as inbreeding depression and local adaptation through examining gene expression, epistasis and genomic architecture (Kardos *et al.* 2015; Narum and Campbell 2015). By looking at many genes across the genome, studies have been able to separate adaptive genetic diversity from neutral genetic diversity. Local adaptation can be evaluated by the identification of adaptive genes using high F_{ST} outlier loci as an indicator of genome regions that are putatively under directional selection, such as for local adaptation (Allendorf *et al.* 2010).

From a conservation management perspective, an important application is defining management units based on both neutral and adaptive diversity (Funk *et al.* 2012; Moore *et al.* 2014). For example, Limborg and colleagues (2012) analysed 281 transcriptome derived SNPs in Atlantic herring (*Clupea harengus*), a highly migratory small pelagic fish, for elucidating neutral and selected genetic variation among populations. They analysed 607 individuals from 18 spawning locations in the north-east Atlantic, including two temperature clines (5–12°C) and two salinity clines. They found approximately nine loci that had excessively high F_{ST} (genetic differentiation) and also significant correlations with temperature and salinity differences among populations. In a cluster analysis used to identify population groups (conservation units), they identified only three genetically distinct groups of herring when using only the neutral loci. However, four distinct populations were identified when considering the putatively adaptive loci. This is just one example of how genomics can enhance our ability to apply and interpret genetic metrics for conservation management by providing deeper information about wild populations.

8. Ecologists and geneticists need to work together to define objectives and interpret indicators

There is a need for ecologists and population geneticists to work together to understand what are biologically meaningful indicators to monitor in the context of set objectives. There is a long history of debate regarding the importance of genetic considerations in short-term conservation efforts (Lande 1988) and subsequently the fields of ecology and population genetics have developed in parallel until fairly recently. A growing consensus contends that ecological and evolutionary processes, and the interactions between them – termed eco-evolutionary dynamics – are difficult, if not impossible, to separate (Schoener

2011). Indeed, eco-evolutionary dynamics are fundamental to consider to design effective conservation efforts (Hendry *et al.* 2010).

Eco-evolutionary dynamics is a swiftly emerging field, bringing ecologists and evolutionary biologists, including population geneticists, together to work on biodiversity conservation (Pierson *et al.* 2015). The effective use of genetic indicators relies on the combined knowledge of the ecological attributes of the system being evaluated and how these ecological attributes may affect evolutionary processes. This combined knowledge informs which population genetic indicators may inform objectives given the interaction of ecological and evolutionary processes likely acting on the particular system. Thus, collaborative efforts between ecologists and geneticists are essential.

9. How do spatial processes influence metrics derived from idealised populations?

Population genetics has much to offer the field of biodiversity assessments. However, much of population genetics theory has revolved around idealised (i.e. Wright-Fisher) populations, which are basically classical urn models, ideal for sampling and statistics. One of the biggest challenges in using population genetics to monitor natural or wild populations of plants and animals is to understand how spatial processes influence these models and their results.

The notion that space can strongly influence our understanding of population genetics is not new. Phenomenon such as the Wahlund effect, which is the reduction of observed heterozygosity in a population caused by substructure, was first coined by Sten Wahlund in 1928. Despite the recognition that many of the classic population genetic metrics are influenced by spatial processes, this fact is often ignored, which can result in highly biased parameter estimates. For example, recent work by Neel and colleagues (2013) shows that N_e estimated from linkage disequilibrium is highly influenced by spatial dynamics. In fact, the interaction between the sampling frame, breeding dynamics and sample size can produce wildly different estimates of N_e on the same landscape. This is because the local spatial genetic structure, or neighbourhood dynamics, can create small-scale Wahlund effects. Currently, we treat these spatial processes as nuisances in our ability to use classic population genetics models. We hope future research will allow us to better describe the processes and use this autocorrelation structure to inform management decisions.

10. Identifying generalisations about how indicators perform

Population genetic metrics perform differently as indicators in different situations (Hoban *et al.* 2014), which can contribute to difficulty in their interpretation. Theoretical, experimental and empirical work can elucidate when general patterns emerge based on attributes or combinations of attributes such as life history or population history. A few generalisations have emerged in recent years that have been supported by a combination of theoretical and empirical work. For example, the number of alleles (K) and allelic richness (A) have consistently performed better than heterozygosity (H_e) as an indicator of genetic erosion often caused by population decline (Hoban *et al.* 2014; Pinsky and Palumbi 2014) because alleles are lost faster than heterozygosity declines (Luikart *et al.* 1998).

An active area of research is on effective population size (N_e): a concept central to conservation management as it represents the population size that genetic drift acts upon. Genetic drift is a stochastic process that changes allele frequencies and reduces genetic diversity in small populations. As such, N_e can be a good indicator of the 'genetic risk' a population suffers. In theory, N_e represents the number of individuals that influence genetic change (or loss) in the population. In practice, N_e is notoriously difficult to estimate.

The effective number of breeders (N_b), an annual estimate of the number of individuals contributing to the genepool, is more tractable to estimate than N_e in species with overlapping generations (Waples *et al.* 2013, 2014). However, the genetic indicator of interest is often N_e and the relationship between estimates of N_b and N_e can vary among species making interpretation of estimates of N_b difficult. Waples and colleagues (2013) examined N_b/N_e ratios across a wide variety of plants and animals (including invertebrates) and found that, although N_b/N_e varied widely (~0.3–1.6), two life history traits explained 67% of the variation in this ratio. Thus, these life history traits can be used to improve interpretation of $N_{b.}$

Another area of research that will improve interpretation of genetic indicators is how the choice of molecular markers affects different metrics. For example, high throughput sequence data are an increasingly common choice that have some fundamentally different properties to microsatellites, which have been the most commonly used marker in recent years. These different properties, such as mutation rate, will likely influence estimates of popular genetic indicators such as heterozygosity and allelic richness (Lozier 2014). As such, research is needed to understand how to select and interpret genetic indicators in light of the type of molecular markers.

Conclusions

As anthropomorphic pressures (fragmentation, habitat loss, introduced species and diseases, and climate change) on populations continue to increase, conserving genetic diversity will become more central to conserving the ability of species to rapidly adapt and persist (Barrett and Schluter 2008; Stuart *et al.* 2014). Increased capacity to readily obtain and analyse large amounts of genetic data from wild populations means this is an exciting time to carefully consider how best to apply genetic metrics as indicators of the genetic 'health' of populations. Many of the challenges in effectively applying genetic metrics in wild populations can be tackled with careful *a priori* objectives and criteria set in a hypothesis testing framework. Indeed, the next decades hold incredible promise for the application of genetic monitoring methods to tackle challenging aspects of biodiversity conservation (Beatty *et al.* 2014; Ficetola *et al.* 2015).

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