Conservation of adaptive potential and functional diversity: integrating old and new approaches

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Abstract

Continuing advances in whole genome scale approaches integrated with other ‘omic’ technologies promise to revolutionise understanding about the relevance of genetic variation to risks of species declines and extinctions. In the face of the vastly increased accessibility of such approaches, it is important that we advance beyond descriptive genetics to developing a more functional perspective on whether enhancing genetic variation is the most effective strategy for conservation management. Rather than a comprehensive review of the field, this paper focuses on several key issues that have been discussed since the dawn of “conservation genetics” and that warrant re-assessment based on emerging “omics” data, combined with new analytical approaches to ecological niche modelling and population genomic analyses. Specifically, the following inter-related issues are discussed: (1) the relative impacts of inbreeding and outbreeding on fitness and adaptive potential, particularly in relation to genetic rescue; (2) how “species” should be defined for conservation management; (3) deciding on how much and what type of genetic variation should be preserved; and (4) how we can move from descriptive genetics to actually understanding adaptive processes in the wild. None of the ideas presented are new; the purpose here is to serve as a reminder that many of the issues raised 30 years ago are still relevant but not completely resolved and would benefit from tackling afresh with modern tools, but considering historical perspectives.

Keywords Conservation genetics · Adaptive potential · Population genomics · Inbreeding · Species concepts · Genetic rescue

Introduction

As evident from the papers presented in this special issue, it is an exciting time to be a conservation geneticist. Continuing advances in sequencing technologies and analytical pipelines means that we are on the brink of a step change in understanding the functional role that genetic variation plays in adaptation to changing environments. Population geneticists and systematists have always been at the forefront of exploiting new developments, often using new technologies to test much older theories. Integrating molecular genetics into conservation began with allozymes in the 1970s, followed in the 1980s by DNA sequences and restriction fragment length polymorphisms based on high copy number

molecules such as mitochondria (mtDNA) and ribosomes (rDNA). However, it was automation of the polymerase chain reaction (PCR) made possible by use of a thermostable polymerase in the late 1980s (Mullis and Faloona 1987; Saiki et al. 1988) that really revolutionised accessibility and affordability of DNA sequencing and fragment analyses to inform conservation decisions across a wide range of species.

In the midst of the current “omics” revolution, it is worthwhile revisiting perspectives from the brink of this PCR revolution (Lande 1988; O’Brien and Evermann 1988; Ralls et al. 1988; Simberloff 1988; Avise 1989). What is striking is that, despite a monumental increase in knowledge about patterns of genetic variation across a wide range of captive and wild populations, many of the same fundamental issues are still under debate. Avise (1989) envisioned that: “As increasingly sophisticated methods of descriptive molecular genetics are applied to natural populations (or as more DNA sequence data become available), opportunities for finer distinctions will result, and in the extreme, virtually

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every local population, family unit, and even individual may prove distinguishable from all others by some recently derived genetic trait.” However, while he promoted the use of sequence data to identify genetically unique populations or cryptic species (e.g. defining Evolutionarily Significant Units, or ESUs: Ryder 1986; Moritz 1994b) he was against using only molecular data to make management decisions. Lande (1988) argued that demographic and behavioural considerations would have more immediate consequences for population declines than genetics; individuals in many species show decreased reproduction at low population densities for non-genetic reasons, such as restricted mate availability (i.e. the Allee effect: reviewed in Avise 1989). Similarly, in response to arguments that loss of genetic variation and inbreeding depression could seriously increase extinction risk in highly endangered species like cheetahs (O’Brien 1994), field ecologists made a plea that genetics should not replace detailed ecological assessments of drivers of population declines because factors such as predation, poaching or habitat loss would result in more immediate effects than slower genetic declines (Caro and Laurenson 1994). Simberloff (1988) comprehensively reviewed the contribution of population and community biology to the field of conservation and emphasised that populations are threatened not only by genetics, demography, and environmental stochasticity but also by behavioural and physiological effects. Thus, even 30 years ago, there was concern that as molecular variation became an arguably easier quantity to measure than ecological factors, there was a risk that descriptive genetics would replace detailed assessments of other drivers of population declines.

Frankham (2010) reiterated this concern as whole genome approaches started to be applied to non-model organisms: “It is to be hoped that genomic tools will be wisely used to address important issues in conservation genetics, rather than becoming a bandwagon with a substantial proportion of trivial work, as happened subsequent to the introduction of allozymes.” What the “omics” revolution offers is a real opportunity to shift from cataloguing patterns of variation at a finer scale across even more organisms to combining different techniques to fully understand adaptive processes that might be compromised by anthropogenic or natural habitat changes.

The purpose of this paper is to highlight ongoing conservation-related debates where we now have the potential to make real progress in directly relating genetic variation at the scale of whole genomes to phenotypic, fitness, and ecological consequences and using this information to make predictions about adaptive potential in changing environments. Rather than a comprehensive review, the aim is to focus on some recurring issues, both from historical perspectives and using some recent examples to highlight how genome-scale approaches are starting to contribute to altered

understanding. The ultimate objective is to promote discussion of what we still don’t know and how we might fill those gaps in knowledge, to ensure that the powerful set of tools now at our disposal are used most effectively to inform conservation management decisions.

Consequences of inbreeding

Even before it was practical to use genetic markers to quantify variation in natural populations, there has been concern that human-mediated changes in habitat availability would increase risk of extinction of threatened populations by reducing effective population size and increasing rates of inbreeding. Despite critical discussion of these issues for the past 30 years, remarkably little consensus still persists today. Franklin and Frankham (1998) discussed the difficulty of establishing and making generalisations about how large populations must be to retain evolutionary potential, and the concept of a minimum viable effective population size (Nunney and Campbell 1993) and how this relates to heritability and selection (Wood et al. 2016) and the adaptive potential of small populations (Willi et al. 2006) has long been discussed. Avise (1989) pointed out that there is extensive variation among species in the fitness costs of inbreeding (Ralls et al. 1988) but that many species naturally have breeding systems (e.g. self-fertilisation or mating with siblings) or geographic population structures that reduce heterozygosity below what would be predicted under neutral expectations for high outcrossing and unrestricted gene flow. In such circumstances, purging of negative deleterious mutations in highly inbred individuals could alter the fitness consequences of increased habitat fragmentation and reductions in population size. However, the rate and effectiveness of purging the genetic load without an increase in extinction is dependent on the genetic basis of inbreeding depression (Charlesworth and Charlesworth 1999), which is not known for many species (Hedrick 1994). Keller and Waller (2002) predicted that purging should be strongest for slightly inbred plants with restricted gene flow. This could explain lack of strong fitness differences between populations of the plant *Arabidopsis lyrata* that have recently undergone a shift to inbreeding compared to their outcrossing sibling populations (Stift et al. 2013; Carleial et al. 2017), despite substantial loss of heterozygosity and diversity across the genome (Foxe et al. 2010; Buckley et al. 2018). Heterozygosity-fitness correlations have long been used to investigate the consequences of inbreeding in wild populations (David 1998) but strong correlations are sometimes restricted to a few traits that arguably could reduce competitiveness (e.g. traits related to growth in white-tailed deer: Brommer et al. 2015; and steelhead trout: Naish et al. 2013), rather than drive population-level extinctions. Persistence and divergence

in parts of the genome associated with adaptive processes, despite the presence of detrimental anatomical and physiological effects associated with inbreeding (e.g. in brown bears: Benazzo et al. 2017), also suggests that genetic load should be considered in relation to important functional loci rather than global patterns of heterozygosity.

Thirty years ago, Simberloff (1988) and Lande (1988) questioned the effects of inbreeding and loss of genetic diversity as a major factor affecting the persistence of populations in the wild. While inbreeding and loss of heterozygosity results in individual fitness costs, what they thought was lacking were concrete demonstrations that inbreeding caused any wild populations to decline; connections between heterozygosity and population viability are complex and hard to predict *a priori*. In contrast, although recognising that most information at the time was based on laboratory experiments and domesticated populations, Lacy (1997) suggested that, even in the wild, no species of mammal had been shown to be unaffected by inbreeding and that there was no evidence for effective purging. On the surface this might seem to be a dichotomous debate between mammal and plant-centric viewpoints. However, actual evidence to test whether reduced heterozygosity and genetic diversity of inbred individuals increases risks of extinction at the population level (Newman and Pilson 1997) and the functional implications of heterozygosity–fitness correlations (David 1998) have been somewhat limited by the focus on highly variable but neutral genetic markers (Ouborg et al. 2010). A major contribution emerging from genome-scale analyses is the identification of particular loci associated with inbreeding depression, rather than focusing on overall heterozygosity (e.g. Steiner et al. 2013). Classic examples of long-term persistence despite extremely low levels of genome-wide variation (e.g. Island foxes: Robinson et al. 2016) questions the dogma that lack of overall genetic variation will mean inevitable extinction and suggests that assessing variation at loci associated with adaptation could be more informative. Inferring an extinction to be attributed to inbreeding based on low genome-wide heterozygosity of the few remaining individuals in a population (e.g. the Sierra Morena wolf population: Gómez-Sánchez et al. 2018) also risks confounding factors originally causing the loss of genetic variation with those resulting in low population viability. Thus, even based on more recent genomic evidence, disentangling whether loss of genetic diversity *per se*, inbreeding depression, or other factors associated with population declines or habitat fragmentation drive extinction (Ouborg et al. 2010) remains a challenge.

Nevertheless, for species perceived to be at high risk of extinction through genetic erosion, “genetic rescue” by augmenting populations from captive bred sources or translocations between isolated populations (Storfer 1999; Weeks et al. 2011) has frequently been suggested. However,

opponents have questioned the relative value of alleviating the negative effects of inbreeding depression and inducing beneficial effects of heterosis through genetic supplementation compared to potentially unknown consequences of outbreeding depression (Edmands 1999). Mating between dissimilar individuals, while increasing genetic variation in the resulting progeny, can disrupt favourable gene combinations and reduce fitness under some circumstances (Templeton 1986; Avise 1989). For plants with limited dispersal, for example, an intermediate genetic distance has been suggested to be optimal for outcrossing, due to local adaptation (Price and Waser 1979). It is also important to distinguish between short-term benefits and increases in long-term adaptive potential (Lynch and O’Hely 2001). Even if short-term local adaptation is reduced, the benefits of supplementation if only divergent immigrants are available could be preferable to doing nothing (Kronenberger et al. 2017) and it has been questioned whether outbreeding depression has been overestimated (Ralls et al. 2017). Frankham (2015) performed a meta-analysis demonstrating the success of genetic rescue across generations for the limited number of examples available but demonstrated consistent benefits of outcrossing for inbred populations in both stressful and benign environments. Establishing the genetic basis of inbreeding depression, heterosis and outbreeding depression from a genome-wide scale is now achievable but requires time consuming accompanying fitness studies performed under ecologically realistic conditions.

Common garden or laboratory experiments are powerful tools for quantifying the effects of inbreeding depression but have demonstrated the complexity of interpreting fitness consequences that could be generalised across species. Fitness can be context dependent, with the magnitude of inbreeding depression increasing under stressful conditions (e.g. Fox and Reed 2011) and differing between life history stages (e.g. Eckert and Barrett 1994). Variation in the genetic basis for inbreeding depression (Charlesworth and Charlesworth 1999), for example, could alter effects in natural populations. Despite demonstration of strong inbreeding depression, mixed mating appears to be a common and sustainable strategy in flowering plants (Goodwillie et al. 2005), which could reflect the dynamic nature of fitness consequences. Aguilar et al. (2008) suggested that shifts in mating systems (i.e. increased selfing) in plants are associated with habitat fragmentation; however, inbreeding depression is not always apparent in populations of normally outcrossing species with recent habitat-associated shifts in mating system (Carleial et al. 2017). Amos and Balmford (2001) commented that populations that have gone through a severe bottleneck can show a remarkable ability to respond to novel environmental changes. Frankham (1995) was concerned that despite the fundamental assumption underlying many conservation genetics strategies that inbreeding increases

risks of extinction, there was a lack of information on the shape of the relationship or how to distinguish genetic from nongenetic effects. Experiments in *Drosophila*, for example, suggested that a threshold level of inbreeding could tip the balance toward extinction (Frankham 1995) but the shape of the curve changes upon exposure to stressors such as toxins and pathogens. More recently, common garden experiments combined with genomics in *Drosophila* (Schou et al. 2017) has revealed that the consequences of inbreeding might also vary across the genome: they explained a slower rate of loss of genetic diversity in small populations than theoretically expected by associative overdominance, with homozygosity of deleterious recessive alleles selected against in regions of low recombination. What is required are more studies like this that investigate the mechanisms underlying genetic diversity (Fraser 2017) rather than assuming that low levels of genetic diversity due to inbreeding mean inevitable extinction of small populations.

Species concepts

The incorporation of molecular markers into systematics (reviewed in Hillis et al. 1996) altered perspectives on species designations compared to morphological studies alone but how this should be used in conservation has been the subject of continuous debate. Based on discussions at a conference of the American Association of Zoological Parks and Aquariums (AAZPA), the concept of Evolutionarily Distinct Units (ESUs) for conservation was proposed as an alternative to the controversial exercise of naming subspecies (Ryder 1986). What has been debated subsequently is how to define what these units are and how they should be used for practical management (Moritz 1994b; Vogler and DeSalle 1994; Fraser and Bernatchez 2001). Even some of the original proponents of the idea emphasise that preserving habitats and focusing on ecological or evolutionary processes will ultimately be preferable to conservation of particular phenotypes or genotypes (Moritz 1999, 2002); process-oriented approaches, for example, might recommend restricting translocation of animals between ESUs but allow for mixing among Management Units (MSUs) within ESUs, to preserve adaptive potential (Moritz 2002). Focusing on evolutionary potential of ecosystems based on phylogenetic diversity in hotspots rather than individual species is also worthy of broader consideration (Forest et al. 2007).

However, there are sometimes practical reasons to focus conservation efforts on defined populations; for example, the US endangered species act incorporates the idea of evolutionary distinctiveness, based on demonstration of the importance for conserving wild salmon populations (Waples 1991). This can have dramatic impacts for the ability of conservation managers to gain government support

for conservation programmes targeting particular focal populations at risk, rather than whole species that might have wider distributions and could help to bridge the gap between scientists and conservation practitioners (Taylor et al. 2017). Nevertheless, concern remains that lack of consensus on species definitions will inhibit conservation efforts (Frankham 2010), with some promoting return to the biological species concept rather than evolutionary based definitions for making conservation management decisions (Ralls et al. 2017) and others asserting that phylogenetic distinctiveness better describes the evolutionary process of speciation (Groves et al. 2017). There is also increasing evidence that hybridisation might represent a creative rather than destructive force in evolution. For example, based on RFLPs, Whitham et al. (1999) found more hybridisation than expected among species of cottonwoods but predicted that introgression was restricted to particular parts of the genome; they also suggested that plant hybrid zones might support a higher diversity of other organisms. Genomic studies have dramatically expanded on such views; signatures of introgression have been found more widely than expected and hybrid speciation even in diploids has been resurrected as a driving force in evolution that could have important conservation implications (e.g. Robinson et al. 2016; vonHoldt et al. 2016, 2017; Quilodran et al. 2018; Smith et al. 2018).

The type of genetic markers used to define units for conservation has also been debated. Original approaches were based on mtDNA variation (Moritz 1994a, b), but the use of genes that could be used as a proxy for adaptation, such as immune genes at the Major Histocompatibility Complex (MHC), have also been promoted for conservation and captive breeding programmes (e.g. Hughes 1991; Aguilar et al. 2004; Luo et al. 2004; Ujvari and Belov 2011; Marsden et al. 2012; Savage et al. 2018). Neutral and selected genes also provide different types of information relevant for predicting adaptive potential and so combined perspectives could be most informative (Funk et al. 2012; Pauls et al. 2013). Pluralistic approaches to defining independently evolving units (e.g. Fennessy et al. 2016) are also preferable to definitions based on single genes but questions about what impacts this might have on small threatened populations and on interpretation of congruence (Bercovitch et al. 2017) and fit to a multispecies coalescent model (Barley et al. 2018) have been questioned. Shifts towards genome-wide Single Nucleotide Polymorphisms (SNPs) will be particularly useful to provide a comprehensive assessment of genetic distinctiveness and will allow more precision in targeting of what deserves special efforts for conservation (Morin et al. 2004; Desalle and Amato 2017). Holistic perspectives that consider genome-wide variation, ecological factors and historical contexts from fossils will also become more practical and in some cases might open new debates about species boundaries (e.g. for wolves: Rutledge et al. 2012; vonHoldt

et al. 2017). Sampling design also remains a critical issue for interpreting patterns of variation; although the increased power provided by genomic scale data technically allows inferences based on fewer individuals per population than less informative markers, adequate sampling is still critical (e.g. Galapagos tortoises: Gaughran et al. 2017). However, even with increased precision, the question remains about how definition of genetically distinct units should be used most effectively to inform conservation management decisions. Critical to progress will be to develop mechanisms to ensure that genomic developments are translated into practical interventions through effective communication between academic researchers and conservation practitioners (see discussion in Shafer et al. 2015, 2016; Garner et al. 2016).

How much genetic variation is enough?

An important issue to consider if genetic variation is used as a central criterion to set conservation priorities is how do we determine when appropriate levels of diversity, heterozygosity and connectivity between populations exist and when interventions might be warranted? Simberloff (1988), for example, emphasized that genetics is equivocal about the value of preserving connectivity between refuges; maintaining connectivity promotes gene flow but this might prevent local adaptation to changing environmental conditions or enhance spread of diseases between populations. What constitutes barriers to connectivity also could be misinterpreted; for example, fragment boundaries might not reflect real ecological boundaries for trees that exhibit long-distance pollination or seed dispersal (Kramer et al. 2008). As with original debates about phenetic-based classification systems for naming species (Farris 1977) and more recent discussions about thresholds of divergence to classify a broad range of species based on DNA barcoding (e.g. Hebert et al. 2003; Vences et al. 2005; Mattio and Payri 2010; Schoch et al. 2012), or for interpreting diversity of operational taxonomic units (OTUs) in microbiome studies (Konstantinidis and Tiedje 2005; Goodrich et al. 2014), it is highly unlikely that a single threshold could be set that would apply across a wide range of taxonomic groups. For example, Smith and Donoghue (2008) demonstrated that rates of molecular evolution vary widely among angiosperms and are more related to life history traits than taxonomy. Thus, even within taxonomic groups, setting a single threshold that would describe optimal patterns of variation would be difficult to establish.

It is also difficult to predict how much heterozygosity should be maintained to achieve genetically “healthy” populations. Avise (1989) suggested that relationships between heterozygosity and population viability are complex but also that organisms with different types of mating systems will vary in how much heterozygosity is “normal”. For example,

despite concerns that low levels of genetic variation and homozygosity in cheetahs reflected genetic erosion due to habitat fragmentation and a historical bottleneck in the Pleistocene (O’Brien et al. 1985, 2017), this has not resulted in higher impacts of disease in wild populations compared to other carnivores (Caro and Laurenson 1994; Thawitser et al. 2010; Castro-Prieto et al. 2011). In plants, a shift from outcrossing to inbreeding is one of the most frequent evolutionary transitions (Barrett 2003), with heterozygosity decreasing more rapidly in the few first generations after selfing than genetic diversity (Charlesworth and Charlesworth 1979). Nevertheless, many highly successful invasive plant species are highly inbred or clonal (Barrett et al. 2008). The history of inbreeding or other demographic parameters within a given lineage could thus alter interpretation of when “healthy” levels of genetic variation have been compromised by habitat changes or isolation.

The type of genetic variation also could be more important than how much overall variation is maintained; adaptive significance rather than just phylogenetic distinctiveness could be more relevant for conservation (Crandall et al. 2000; Holderegger et al. 2006). Amos and Balmford (2001) reiterated the common view that habitat fragmentation threatens slow erosion of genetic variability by drift and short-term reductions in fitness due to inbreeding depression, but pointed out that there is also evidence that at least some species appear to have mechanisms to maintain higher than expected levels of variability. They suggested that this could be enhanced, for example, by increased relative fitness of more outcrossed individuals rather than severe inbreeding depression in inbred individuals. Maintenance of variation at adaptively important genes has been found even for species where isolation and inbreeding predict low levels of genetic variation at neutral markers (e.g. Aguilar et al. 2004; Castro-Prieto et al. 2011; Funk et al. 2016; Robinson et al. 2016; Benazzo et al. 2017). Just as for neutral genes, this has led to discussions about the value of quantifying “diversity thresholds” for important adaptive processes; for example, to predict relative susceptibility to disease (King and Lively 2012). Genome-scale perspectives will allow a much more quantitative assessment of what types of genetic variation are most relevant for understanding risks of population declines.

There is also an outstanding question of whether variation should be preserved within isolated populations that show reductions in diversity or in more of a metapopulation framework to maintain diversity over larger geographic regions. For example, Charruau et al. (2011) advocate that conservation strategies should be implemented that can simultaneously facilitate conservation priorities of preserving locally adapted ecotypes and genetic diversity across the range of a species. Such an approach has proven effective, for example, for highly endangered Tasmanian devils, but relied on using

captively bred individuals rather than just wild populations (Hogg et al. 2017). Developments in forensic approaches to working with ancient DNA also will be useful for establishing a longer time scale over which neutral and adaptive variation can be considered within species, to establish historical information on how much variation is “normal” and to identify the most appropriate source populations to use for reintroductions or translocations (Marr et al. 2018). However, even with more fine-scale information based on genome-wide SNPs, setting thresholds for how much diversity to preserve and over what proportion of the range of a species remains a substantial challenge.

Genetics of adaptation

Genomic approaches will allow unprecedented opportunities to precisely determine the amount, distribution and functional significance of genetic variation in natural populations across a wide range of organisms (Allendorf et al. 2010; Fuentes-Pardo and Ruzzante 2017). However, in order to be able to use this detailed genetic information as a predictive tool to mitigate the consequences of changing environments, it is important that an eco-evolutionary perspective is maintained, considering both short-term ecological consequences of genetic interventions and long-term evolutionary processes related to adaptation (Keyghobadi 2007; Kinnison and Hairston 2007; Schwartz et al. 2007; Frankham 2010; Ouborg et al. 2010; Eizaguirre and Baltazar-Soares 2014; Shafer et al. 2015). Genetic diversity can affect ecological processes such as primary productivity, population resilience to disturbance, interspecific competition, community composition, and energy and nutrient fluxes at the population, community and ecosystem levels but the relative importance of genetics to other factors is not often assessed (Hughes et al. 2008). A recent meta-analysis of factors that limit animal movements found that the vast majority of studies (77%) focused on restrictions to gene flow, and few investigated consequences for restricted demographic exchange (17%) and limited resource access (10%) (Cosgrove et al. 2018). There is also increasing evidence that variation in the biotic environment can be critical for determining fitness; for example, community ecology of microbes can have large effects on adaptation (Guo et al. 2018) but understanding interactions with “host” genetics is an open question. Combining “omic” approaches also might reveal new insights into consequences of population bottlenecks beyond reduction in genetic variation; for example, combining genome-wide association studies (GWAS) to identify quantitative trait loci (QTLs) related to adaptive traits that could be tested for evidence of selection or differential expression (through transcriptomics) in different environmental contexts, with metabolomics or proteomics to

assess resulting physiological differences. Taking a GWAS approach to investigating changes in metabolomes has been applied to investigate the genetic architecture of secondary metabolites affecting human nutrition in crops (Matsuda et al. 2014), to uncover the functional basis of production-reducing traits in livestock (Welzenbach et al. 2016) and in relation to metabolic costs of human disease (e.g. Adamski 2012) but has not yet been commonly applied in conservation settings. For conservation applications, combining such big data approaches with detailed ecological assessments about limits to adaptation would be particularly powerful to assess relative risks to declining populations.

Advances in analytical approaches also provide more potential to efficiently combine genomic tools with field experiments to test adaptive potential (Savolainen et al. 2013). Reciprocal transplant experiments and common garden experiments are powerful tools for quantifying the relationship between population size and local adaptation (Leimu and Fischer 2008); combined with genomics they provide the potential to robustly assess the relationship between genetic variation and adaptation. Such approaches can also be applied to multiple species inhabiting common environments (Bucharova et al. 2017). For example, even closely related species inhabiting the same environments can show differences in genetic variation and adaptive potential at fine local scales (Lobo et al. 2018), which should be accounted for in multi-species based conservation. Landscape genomics, combining phylogeographic patterns with detailed environmental data (Gugger et al. 2018) also could aid in the restoration and preservation of either particular threatened species or larger communities (Montalvo et al. 1997; Funk et al. 2008), by informing practical decisions about what to preserve, how and over what geographic scales (McKay et al. 2005). Relating genomic variation to critical phenotypic responses to environmental stress (Bustos-Salazar et al. 2017; Vangestel et al. 2018) can be used to inform selection of individuals to use for restoration or breeding programmes for sustainably harvested populations. Combining remote sensing (Turner et al. 2003; Vihervaara et al. 2017) and ecological niche modelling (May et al. 2011; De La Torre et al. 2014) with conservation genetics is also a powerful way to predict future adaptation. Such approaches demonstrate, for example, that land availability could be more important than genetic diversity in range shifts (Broadhurst et al. 2018) and highlight that climate change could also create new habitats, as species expand into climatically previously inaccessible locations (Luoto et al. 2006). However, it is also important to assess whether rapid changes in climate risk overwhelming the capacity for adaptation (Jump and Penuelas 2005). Thus, integrating advances in ecology and geography with genomics will increase potential to establish predictive frameworks for the consequences of conservation management decisions.

It is also becoming apparent that rapid adaptation can happen in the absence of substantive genetic variation. For example, Willoughby et al. (2018) found that introduced populations of steelhead trout showed very low genome-wide diversity compared to their native range but showed signatures of rapid adaptation at several loci related to transition to an anadromous to freshwater restricted lifestyle. The changing views of epigenetics that have come from genomic studies (Jablonka and Lamb 2002) and evidence that differences in phenotypic plasticity could be important for determining species distributions in changing climates (Valladares et al. 2014) or explaining success of invasive species (Parker et al. 2003) suggest that just studying underlying genomic variation will not be sufficient to predict responses to climate change. Managing phenotypes rather than genotypes has been suggested for habitat restoration (Watters et al. 2003) and transcriptome studies using gene expression as a phenotype (DeBiasse and Kelly 2016; Elmer 2016) have revealed important insights into the genomic control of immediate responses to environmental stress. However, such studies have also questioned whether phenotypic plasticity results in long-term adaptation rather than rapid responses to environmental stress (Ho and Zhang 2018). It is also increasingly apparent that local adaptation and adaptive divergence can happen even with high gene flow (Attard et al. 2018; Shih et al. 2018). Advances could also be made in how we compare phenotypic and genotypic variation that go beyond correlations (e.g. Q_{st} vs F_{st} : McKay and Latta 2002) and more directly test the functional consequences of genetic changes. There is also the chicken and the egg type question of whether genetic variation is caused by local adaptation or whether local adaptation relies on pre-existing genetic variation (Taylor 1991). For example, a recent study on birds found a positive correlation between the magnitude of changes in allele frequencies necessary to keep up with changing climatic conditions and the magnitude of population declines, suggesting that lack of adaptation may already have had a negative effect on genetic variation and adaptive potential (Bay et al. 2018). Similarly, a low level of MHC variation in a vulnerable frog species was concluded to be a consequence rather than the cause of selection for alleles promoting survival in the face of the continual presence of important disease agents (Savage et al. 2018); local adaptation to a prevalent disease threat can actually reduce genetic variation. Focusing on preservation of adaptive phenotypes rather than genotypes could thus be important to consider as we learn more about the regulation of adaptive processes at the genomic level.

We could also learn from successful adaptation examples rather than just firefighting to predict what is limiting adaptation of threatened species. Although the majority of studies on invasive species attempt to determine what can be done to restrict invasiveness (Pagad et al. 2018), using

invasive species as models to understand the genomic basis of successful colonization of new environments and resilience to climatic change (Suarez and Tsutsui 2008) has potential for predicting strategies for management of endangered species as well. Since invasive species are often colonising new habitats with a small number of founders, almost by definition they have to be able to adapt to altered environmental conditions without substantial genetic variation (Caron et al. 2014). Investigating the genetic architecture of adaptive traits in the face of this limited variation (Puzey and Vallejo-Marin 2014; Dlugosch et al. 2015) and on the reproductive and phenotypic strategies associated with successful establishment in new environments (Barrett et al. 2008; van Kleunen et al. 2008) could provide important insights for conservation management. Determining the genomic basis for changes in physiological and behavioural traits associated with adaptation could be particularly important.

Conclusions

The increasing accessibility of genome scale “omics”, combined with advances in ecological niche modelling and population genomic analyses hold great promise for developing more functional perspectives about adaptive potential than was possible using previous technologies. However, it is important that we don’t use these approaches simply to add more fine-scale details to our catalogue of genetic variation but think about what we can learn about the circumstances in which this variability “matters” for conservation. Arguably, the largest recent advances have been made in understanding the genomic basis of adaptation but the difficult part will be to incorporate this knowledge into active management plans. We also might need to rethink some long-standing perspectives on the relative importance of genetic variation to conservation. Genome-scale analyses question whether our views have been too simplistic: for example, genomic signatures of phenotypic plasticity, epigenetics, hybridisation, and maintenance of adaptive variation despite high inbreeding are all more apparent than previously suspected. The relative fitness consequences of inbreeding versus outbreeding, focus on “species” as the units of conservation, determining how much variation should be the target of genetic interventions, and strategies for genetic rescue and restoration ecology all could be tackled from new perspectives based on combining genome scale “omics” with ecological scale experiments.

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