Adaptive introgression: a resource for management and genetic conservation in a changing climate

Running head: Adaptive introgression and conservation

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Abstract

Current rates of climate change require organisms to respond through migration, phenotypic plasticity, or genetic changes via adaptation. Here we focus on questions regarding species’ and populations’ ability to respond to climate change through adaptation. Specifically, the role adaptive introgression, movement of genetic material from the genome of one species into the genome of another through repeated interbreeding, may play in increasing species’ ability to respond to a changing climate. Such interspecific gene flow may mediate the consequences of limited adaptive potential from standing genetic variation and mutation alone, and has been shown to enable adaptive responses to changing environments. Despite the near dismissal of the potential benefits of hybridization in a conservation framework, we conclude with the proposition that gene flow between sympatric or parapatric sister species or within species that exhibit strong ecotypic differentiation may represent an underutilized management option to conserve evolutionary potential in a changing environment. This will be particularly true where advanced-generation hybrids exhibit adaptive traits outside the parental phenotypic range, a phenomenon known as transgressive segregation. We hope these ideas provoke discussion regarding how we maintain evolutionary potential, the conservation value of natural hybrid zones, and consideration of their important role in adaptation to climate.
Introduction

One of the single largest threats to populations globally is climate change. Current rates of climate change have been associated with community and ecosystem-level changes in composition and functioning, temporal shifts in development and spatial shifts in geographic distributions (Franks & Hoffmann 2012; Hoffmann & Sgro 2011; McCarty 2001; Shaw & Etterson 2012; Visser 2008; Walther 2010). The ability of species to track changes in climate requires a combination of strategies, including the capacity to migrate to favorable conditions, plasticity to enable shorter term responses to environmental change, and longer term adaptive evolutionary responses that may result in allelic and associated phenotypic changes (Aitken et al. 2008; Alberto et al. 2013; Franks et al. 2013; Savolainen et al. 2013; Schiffers et al. 2014). Populations unable to respond to changing conditions are at increased risk of extinction or reduced fitness (Aitken et al. 2008). Here we focus on questions regarding populations’ abilities to respond to climate change through adaptation, and the role adaptive introgression may play in increasing species’ abilities to respond to changing climates. We discuss how hybridization may mediate the consequences of limited adaptation potential from standing genetic variation and mutation alone, and provide case studies where hybridization and introgression have enabled adaptive responses. We conclude with the proposition that interspecific gene flow between sister species, or intraspecific gene flow between populations that exhibit strong ecotypic differentiation, may represent an underutilized management option to conserve evolutionary potential in changing environments.

Adaptation to a changing climate

One of the major challenges to populations in a changing climate is adapting to new environments within an appropriate timeframe. While phenotypic plasticity and migration may permit more immediate responses to environmental change, in the long term an adaptive
evolutionary response, or ‘evolutionary rescue’, is likely necessary to avoid or limit the negative consequences of maladaptation under changed environmental conditions (Gonzalez et al. 2013; Schiffers et al. 2014; Table 1). ‘Genetic rescue’ describes the introduction of variation to counter the demographic and genetic consequences of small population size, providing a rescue from the genetic load (Carlson et al. 2014). ‘Evolutionary rescue’, however, attributes a change in the genetic composition of a population to increased frequency of adaptive alleles, resulting in an adaptive evolutionary response (Anderson et al. 2013; Franks et al. 2013). For populations experiencing a rapidly changing climate the initial stages of this adaptive evolutionary response may be associated with declines in fitness and population size as maladaptive alleles are purged from the population. This decline offers a limited opportunity for genotypes that exhibit phenotypes appropriate to the changing selective pressures to reproduce at a rate sufficient to stimulate population recovery (Gonzalez et al. 2013). In its simplest form, if successful, this process produces a U-shaped trajectory where population decline is followed by an exponential increase (Figure 1).

However, the probability that a population will experience an evolutionary rescue of this sort is dependent on the interaction of a number of factors including population size, mutation rate, the strength of natural selection, and the standing genetic variation (Bell & Gonzalez 2009; Gonzalez et al. 2013; Schiffers et al. 2014).

Recent simulations by Orr and Unckless (2014) suggest that evolutionary rescue is more likely to occur from standing genetic variation than through de novo mutations. The time to population rebound and the demographic consequences of initial maladaptation increase for rescues from new mutations versus those from standing variation (Orr & Unckless 2014). Thus the ability to adapt may be limited where standing genetic diversity is reduced, leading to a reduced capacity of populations to respond to changing environments (Bijlsma &
Loeschcke 2012; Millar & Libby 1991; Sgro et al. 2011). Conservation priorities should therefore consider strategies that mediate the potential risks to populations’ persistence and future adaptive potential (Hellmann & Pineda-Krch 2007; Hoffmann & Sgro 2011). This should include mechanisms that maintain evolutionary resilience: the ability of a species or population not only to maintain its current state, but also undergo evolutionary adaptation in response to environmental change (Eizaguirre & Baltazar-Soare 2014; Sgro et al. 2011).

One potential avenue to increase evolutionary resilience is to harness natural hybridization to augment genetic diversity already present (Carlson et al. 2014). Where genetic variation is limited, hybridization and introgression may recombine variation to allow rapid evolution in response to changing selective pressures. We assume that combinations of favorable alleles adapted to the new environment will be present in recombinant introgressed genotypes, increasing the rate of demographic recovery. Thus, hybridization and introgression may bridge or fill in the U-shaped adaptation trajectory (Figure 1), enabling a quicker recovery or entirely avoiding the negative consequences of population decline. This represents a simple model regarding the role of adaptive introgression in evolution independent of density-dependent effects, and we acknowledge the potential of alternative outcomes. These will be species and context-specific and may include increased risk of disrupting local adaptation or intrinsic coadaptation or potential for introgressed genotypes to exhibit unfavorable allele combinations. However, given the current rate of climate change the positive consequences of hybridization may outweigh the negatives in some cases, and adaptation within an appropriate timeframe may require production of new genetic and phenotypic combinations (Kremer et al. 2012).

The role of hybridization and introgression in evolution
Views on the role of hybridization in evolution have changed over time. Some considered hybrids the ‘raw materials’ of evolution and a creative source of functional novelty (Arnold 1997; Rieseberg & Wendel 1993), while others argued hybridization was an evolutionary dead-end (Mayr 1963). This debate derives from the fact plant biologists considered hybridization to be an important source of new variation and a frequent component of the evolutionary history of many plant species (Harrison 1993), whereas hybridization had been traditionally viewed as a rare occurrence within the animal kingdom, and hybrids are more often observed to be less fit than either parent species (Mayr 1963). Both Anderson (Anderson 1949) and Stebbins (Anderson & Stebbins 1954) emphasized the importance of reshuffling segregating genetic variation via hybridization. Recent research indicates hybridization provides an important source of genetic variation on which selection might act, and its adaptive role is more widespread—among both plants and animals—than previously believed (Abbott et al. 2013; Arnold 1997; Dowling & Secor 1997; Grossen et al. 2014; Hedrick 2013; Jeong et al. 2014; Larsen et al. 2010; Rieseberg & Wendel 1993; Rius & Darling 2014; Twyford & Ennos 2012).

Hybridization is broadly defined as the successful mating between individuals from two genetically differentiated lineages, and introgression as the permanent infiltration of genes from one genetic lineage into the genome of another through repeated backcrossing (Stebbins 1959; Wheeler & Guries 1987). Introgression may act to extend a species’ gene pool, where movement of genetic material from one lineage into the genetic background of another creates novel recombinant genotypes that may exhibit modifications of existing adaptations, rather than de novo production through mutation (Rweyungeza et al. 2007; Stebbins 1959). This produces a wide array of variation upon which natural selection may act. Thus, natural hybrids, particularly advanced-generation hybrids (backcrosses, F2s, and beyond) that carry
introgressed alleles, may exhibit a range of fitness characteristics relative to either parental species (Rieseberg 1995; Rieseberg & Ellstrand 1993); or exhibit adaptive characteristics outside the natural parental range, termed transgressive segregation (Dittrich-Reed & Fitzpatrick 2013; Hamilton et al. 2013; Welch & Rieseberg 2002; Figure 2). These heritable transgressive phenotypes can permit rapid niche or habitat divergence among hybrid lineages (Rieseberg et al. 1999).

**Hybridization, introgression, and conservation of evolutionary potential**

From a conservation standpoint, hybridization provides a mechanism to release populations from adaptive limits. This is important in the face of increasing environmental stochasticity. Increased genetic variation through hybridization can provide additional adaptive capacity (Bridle & Vines 2006; Pereira et al. 2013; Rius & Darling 2014) or generate transgressive traits (Chunco et al. 2012; Pereira et al. 2013; Seehausen 2013) enabling rapid population recovery in response to changing conditions. Both mechanisms have direct implications in terms of species’ evolutionary potential and their ability to adapt (Rweyongeza et al. 2007), particularly where parental species’ habitat becomes limited or degraded (Dittrich-Reed & Fitzpatrick 2013).

However, hybridization is often dismissed in a conservation context due to multiple risks, including: (i) the potential for genetic assimilation of ‘pure’ species or spread of invasive genotypes, (ii) the potential for outbreeding depression (the reduction in fitness of offspring between genetically divergent lineages), and (iii) the murky legal status of hybrids under laws such as the Endangered Species Act (Allendorf et al. 2010; Allendorf et al. 2001b; Muhlfeld et al. 2014; Rhymer & Simberloff 1996a). Re-examination of these views may be required given rapid climate change, increased knowledge of the evolutionary value of hybridization,
and incorporation of new experimental and modeling approaches to evaluate the likelihood of evolutionary rescue due to hybridization and adaptive introgression.

Although examples of extinction and displacement through invasion via hybridization have been documented (Hovick & Whitney 2014; Kleindorfer et al. 2014; Levin 2002; Rhymer & Simberloff 1996b), so too have instances in which a parental genome has remained relatively intact despite long histories of association and possible interbreeding (Fitzpatrick et al. 2008; Steeves et al. 2010), along with cases of stable hybrid zone formation (Arnold 1997; Harrison 1993). Furthermore, a contrasting view on the risk of genetic swamping is taken if one adopts a ‘gene-centric’ over ‘species-centric’ view (Petit 2004). With this view, rather than signaling species collapse, hybrids are considered repositories of their respective parental genomes, particularly at loci important to adaptation (Crispo et al. 2011).

Risks of outbreeding depression may not be as universal as they are often perceived to be (Frankham 2015; Hoffmann et al. 2015). Few examples in the wild have been documented and simple criteria can be used to predict the likelihood of outbreeding depression in management settings (Frankham et al. 2011). Aitken and Whitlock (2013) conducted simulation studies examining the fitness consequences of introducing migrants to a population with alleles maladapted to local conditions, resulting in genetic incompatibilities. These simulations showed that although reduced fitness was initially observed due to outbreeding depression, populations rebounded over time. Furthermore, they noted that if introduced individuals had novel alleles pre-adapted to the change in conditions, the duration of the drop in mean fitness was reduced, and was followed by a significant increase in fitness, or evolutionary rescue (Aitken & Whitlock 2013). Evidence from long-term experimental hybrid swarms provide empirical evidence to support to these observations (Hwang et al.)
This suggests that the effects of outbreeding depression are likely temporary, and the benefits of facilitating gene flow between genetically divergent populations, or even sister species, might outweigh the costs and can be maintained beyond the first generation (Whitely et al. 2015; Willi et al. 2007).

Challenges based on the legal status of hybrids may be harder to overcome, as laws effectively dealing with hybrids remain unclear (Garnett et al. 2011; Haig & Allendorf 2006). Both ‘intercross policies’ and ‘propagation policies’ have been suggested to provide managers with flexibility and guidelines to deal with different hybridization scenarios (Haig & Allendorf 2006). Although these policies have not been adopted, it will be important to bear in mind that the rate of natural hybridization may increase where climate change causes shifts to species distributions (Garroway et al. 2010; Mortiz & Agudo 2013; Pauls et al. 2012). Furthermore, cases in which interspecific hybridization provides adaptive genetic variation necessary to rescue native species at risk of extinction may become increasingly frequent (Baskett & Gomulkiewicz 2011). In any case, there will not be a one-size-fits-all legislative solution to address hybrids, and it has been argued that the consequences of natural hybridization should be considered separately from human-mediated (e.g. controlled crosses, or ‘genetic-rescues’) or anthropogenic hybridization (e.g. unintentional introduction of exotics; (Allendorf et al. 2001a; Shafer et al. 2015).

With regard to introgression in conservation scenarios an important factor to consider is the time frame within which adaptation and evolutionary rescue must occur. Introgression results from several generations of backcrossing and selection where segregating genetic variation is reshuffled. In the shorter term, early hybrid generations may contribute to demographic decline following hybrid breakdown (Fenster & Galloway 2000). The rate of demographic
recovery, and the potential for successful evolutionary rescue depends on species-specific life-history characteristics. Theoretical work of Baskett and Gomulkiewicz (2011) suggest an adaptive evolutionary response is dependent upon the level of assortative mating, the fitness of introgressed loci, and the mating system. While this work presents a significant step forward, it will be important to empirically validate these results. Evidence for successful evolutionary rescue on a short time-frame can be seen in several cases of interpopulation genetic rescue (Madsen et al. 1999; Miller et al. 2012; Pickup et al. 2013; Weeks et al. 2011) where intentional release of unrelated individuals of the same species into small populations resulted in rescues attributed to increased fitness of admixed genotypes (Broadhurst et al. 2008; Vander Wal et al. 2013).

**Case studies of hybridization, adaptive introgression, and transgressive segregation in changing environments**

*Hybridization and adaptive introgression in changing environments*

Experiments specifically testing the potential for evolutionary rescue from hybridization under changing environments remain limited. Stelkens et al. (2014) present an elegant study where crosses between yeast strains were assessed for survival across increasingly stressful environments. They observed increased survival of interspecific hybrids following transfer to increased salt solutions compared to parental strains or intraspecific crosses, noting that F2 hybrids performed better than F1 hybrids in increasingly severe conditions. They concluded that the likelihood of evolutionary rescue in response to rapidly changing environmental conditions was greater where interspecific recombination augmented genetic diversity, even between distant relatives (Stelkens et al. 2014).
Evidence of evolutionary rescue through adaptive introgression has been observed in cases of the rapid spread of pesticide resistance. Warfarin resistance in the western European house mouse (*Mus musculus domesticus*) was traced to a single introgressed gene from the Algerian mouse (*M. spretus*) (Song et al. 2011). This variant is now widespread as increased rodenticide use provided strong selection for the introgressed gene. This result is all the more notable given that hybrid sterility is common between these species. A parallel case of adaptive introgression was observed in *Anopheles* mosquitoes. Introgression of a suite of insecticide-resistant alleles, alongside changing selective pressures, favored the survival and spread of hybrid mosquitoes with introgressed insecticide-resistance genes (Norris et al. 2015).

*Transgressive segregation opens new environments*

Heritable transgressive traits play an important role in increasing the niche breadth of individuals, enabling adaptation to novel environments. Transgressive phenotypes, produced from F2, backcross or advanced-generation hybrids, are attributed to complementary gene action where segregating variation between parental taxa recombine in hybrids at multiple loci to produce extreme phenotypes (Figure 2). In their study of salt tolerance in the hybrid species *Helianthus paradoxus*, Welch and Rieseberg (2002) found that hybrids exhibited extreme values for traits associated with salt tolerance when compared with either of the parental species (*Helianthus annuus* x *Helianthus petiolaris*). Similarly, an examination of spruce species and their hybrids by Hamilton et al. (2013) found that hybrid genotypes displayed greater cold tolerance within a certain temperature range than either parental species.
While transgressive segregation is more often ascribed to plant species (Rieseberg et al. 1999; Rieseberg & Carney 1998; Stelkens & Seehausen 2009; Yakimowski & Rieseberg 2014), it has also been a key source of adaptation for many animal species. Hybridization between the butterflies *Lycaeides anna* and *L. melissa* has resulted in hybrid taxa that exhibit unique habitat preferences and morphologies that have led to novel evolutionary trajectories of hybrids distinct from parental populations (Gompert et al. 2006; Nice et al. 2013). Likewise, alpine *Lycaeides* species, products of introgression between *L. melissa* and *L. idas*, exhibit adaptive traits that enable persistence in more extreme alpine habitats, pointing towards the role of adaptive introgression as a mechanism to conserve evolutionary potential (Gompert et al. 2006). Pereira et al. (2013) developed multi-generation interspecific crosses between populations of the copepod *Tigriopus californicus* with varying levels of thermal tolerance. Interestingly, the authors found that crosses between ecologically and genetically similar populations lead to introgressed genotypes that exhibited extreme tolerance to warmer environments relative to parents, with little evidence of hybrid breakdown. These results suggest that even where parental taxa may be ecologically or genetically similar, segregating variation underlying polygenic traits may result in transgressive segregation, thus allowing admixed individuals to occupy fitness peaks on the adaptive landscape outside of that used by parental taxa (Pereira et al. 2013). These examples assert the important role introgressive hybridization and transgressive segregation play influencing the evolutionary trajectory and adaptive potential of populations (Yakimowski & Rieseberg 2014).

*Facilitated admixture to prevent extinction*

In a few cases, genetic rescue via human-mediated hybridization has been undertaken to not only conserve genetic diversity and evolutionary potential, but also as a means to maintain parental genomes at risk of extinction (Crispo et al. 2011). While potentially controversial,
documented cases such as the Florida panther (*Puma concolor coryi*) and Norfolk Island boobook owl (*Ninox novaeseelandiae undulate*) have demonstrated that increased fitness and preservation of parental genomes can follow from human-mediated hybridization (Benson et al. 2011; Garnett et al. 2011; Hostetler et al. In press; Johnson et al. 2010). Thus, in the context of evolutionary resilience and persistence, these cases of intraspecific gene flow between genetically differentiated subspecies or subpopulations enable an ‘*in situ*’ response to changing environments, and provide examples of successful evolutionary rescues (Vander Wal et al. 2013).

**Conclusions and future directions**

These case studies suggest hybridization can offer an increased capacity for adaptation, potential range expansion in a changing climate, and in extreme cases the persistence of genes at risk of extinction due to loss of parental species (Allendorf et al. 2001b; Lewontin & Birch 1966; Rius & Darling 2014; Seehausen 2013). This will have important implications where species are genetically depauperate, exhibit adaptational lag, or have not been able to migrate in response to changing environments (Aitken et al. 2008; Wilczek et al. 2014).

Recent work has provided the theoretical framework to test the role of adaptive introgression in response to climatic shifts, however additional experimental studies will be required to elaborate current models (Baskett & Gomulkiewicz 2011; Bell & Gonzalez 2009).

As the field of conservation evolves, combining conservation management with evolutionary theory is required (Eizaguirre & Baltazar-Soare 2014). We suggest that genetic variation which persists within natural hybrids can have conservation value, and natural introgression between sympatric or parapatric sister species could be considered an ‘*in situ*’ conservation strategy, particularly where ‘pure’ species are at risk of extinction or where adaptive potential
in admixed populations have been observed (Becker et al. 2013). Inclusion of hybridization and introgression in conservation may require a shift in conservation framework to a ‘gene-centric’ view (Crispo et al. 2011; Petit 2004) and inclusion of evolutionary processes contributing to the maintenance of adaptive evolutionary potential (Eizaguirre & Baltazar-Soare 2014; Sgro et al. 2011; Weeks et al. 2011). In order to maximize adaptive potential in response to changing environmental conditions purposeful propagation of genetic variation via human-mediated hybridization may be necessary for species at risk (Shafer et al. 2015).

Conservation managers first need to identify populations that may benefit from evolutionary rescue. These will likely be a combination of threatened species where traditional management options have failed or failure is imminent (Hoffmann et al. 2015). Following this, evaluation of the potential outcomes of hybridization and introgression are required to validate theoretical models. Restoration projects provide an excellent opportunity to experimentally evaluate these outcomes, which may include actively managing and maintaining advanced-generation recombinant genotypes, monitoring captive breeding programs including hybrids, or assessing fitness consequences of assisted gene flow programs. Additionally, the development of these programs can be informed by genomic data, which can reveal the extent of introgression and its impact on genetic variation underlying adaptive traits, providing the opportunity to tease apart the genetic variation contributing to adaptive introgression (Hoffmann et al. 2015).

We suggest managers need to consider hybrids and hybrid species alongside parental species when formulating conservation strategies. The benefits of adaptive introgression are multifaceted including: increased genetic diversity (through genetic rescue) and formation of new recombinant genotypes that may have increased capacity to respond to changing
selective pressures, resulting in an adaptive evolutionary response that limits demographic
decline under rapidly changing conditions. This will be important where hybrids exhibit
adaptive potential outside the parental range, or where recombinant genotypes have an
increased ability to track changing fitness optima. Ultimately, managers should prioritize
conservation of variation that increases the potential for evolutionary change in response to
rapidly changing climates. We hope the ideas represented here provoke a discussion
regarding the conservation value of hybridization, and consideration of its potential role in
adaptation to climate.
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Literature Cited


usage of insecticide-treated bed nets. Proceedings of the National Academy of Science USA.


Figure 1 – Simplified U-shaped trajectory of population demography over time in response to an environmental stress across three scenarios: (i) population decline where maladaptation results in extirpation once populations fall below an extinction threshold (light grey), (ii) population decline due to maladaptation followed by evolutionary rescue from standing genetic variation (medium grey), and (iii) population decline and recovery where interspecific gene flow reduces the demographic consequences of maladaptation and enables rapid population growth (black; adapted from Carlson et al. 2014). Asterisks indicates the point at which interspecific gene flow is introduced in scenario (iii).
Figure 2 – Schematic crossing design between two parental tree species and their first (F1) and second generation (F2) hybrids. The shading in F1 and F2 generations reflects the percentage of alleles inherited from the black and white tree. The pluses and minuses represent segregating genetic variation in parental populations that positively (+) or negatively (-) influence tree height. Recombination in advanced-generation hybrids (F2 and beyond) have generated extreme phenotypes (trees on the far right and left of the row) relative to parent phenotypes from complementary gene action, termed transgressive segregation.
Table 1. Glossary of terms

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<tr>
<th>Term</th>
<th>Definition</th>
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<tr>
<td>Hybridization</td>
<td>Successful mating between individuals from two genetically differentiated lineages</td>
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<td>Introgression</td>
<td>Movement of genetic material from the genome of one species into the genome of another through repeated interbreeding</td>
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<td>Transgressive segregation</td>
<td>Formation of extreme phenotypes in recombinant hybrids relative to parental species due to complementary gene action of segregating genetic variation between parent species</td>
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<tr>
<td>Genetic Rescue</td>
<td>Introduction of variation to counter the demographic and genetic consequences of small population size</td>
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<tr>
<td>Evolutionary Rescue</td>
<td>Change in the genetic composition of a population to an increased frequency of adaptive alleles following an adaptive evolutionary response</td>
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<tr>
<td>Evolutionary Resilience</td>
<td>The ability of a species to not only maintain its current state, but also undergo evolutionary adaptation in response to environmental change</td>
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<td>Hybrid Swarm</td>
<td>A population containing multiple generations of hybrids that are actively backcrossing or mating with other hybrid genotypes</td>
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<tr>
<td>F1 hybrid</td>
<td>First generation hybrid progeny resulting from mating between two parental species; see Figure 2</td>
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<tr>
<td>F2 hybrid</td>
<td>Second generation hybrid progeny resulting from mating between two F1 hybrids; see Figure 2</td>
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