



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

Jill A. Hamilton\*†‡¶ and Joshua M. Miller‡

\*Department of Evolution and Ecology, University of California, Davis, CA, 95616, U.S.A.

†Department of Biological Sciences, North Dakota State University, Fargo, ND, 58102, U.S.A.

‡Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9, Canada

**Abstract:** *Current rates of climate change require organisms to respond through migration, phenotypic plasticity, or genetic changes via adaptation. We focused 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 1 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 extinction risk or consequences of limited adaptive potential that result from standing genetic variation and mutation alone, enabling a quicker demographic recovery in response to changing environments. Despite the near dismissal of the potential benefits of hybridization by conservation practitioners, we examined a number of case studies across different taxa that suggest 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. The ideas presented in this essay are meant to 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.*

**Keywords:** adaptive management, evolution, evolutionary potential, genetics, hybridization

La Introgresión Adaptativa como Recurso para el Manejo y la Conservación Genética en un Clima Cambiante

**Resumen:** *Las tasas actuales de cambio climático requieren que los organismos respondan a través de migraciones, plasticidad fenotípica o cambios genéticos por medio de la adaptación. Nos enfocamos en cuestiones respectivas a la habilidad de las poblaciones y las especies para responder al cambio climático por vía de la adaptación. En específico, nos enfocamos en el papel adaptativo que puede tener la introgresión, que es el movimiento de material genético del genoma de una especie al de otra por medio de la cruce repetida entre ellas, en el incremento de la habilidad de una especie para responder al clima cambiante. Dicho flujo génico entre especies puede mediar el riesgo de extinción o las consecuencias del potencial adaptativo limitado que resultan solamente de la variación genética permanente y la mutación, lo que permite una recuperación demográfica más rápida en respuesta a los ambientes cambiantes. A pesar del rechazo de los beneficios potenciales de la hibridación por parte de quienes practican la conservación, examinamos estudios de caso en diferentes taxones que sugirieron que un flujo génico entre especies hermanas simpátricas y parasimpátricas o dentro de especies que exhiben una fuerte diferenciación ecotípica podría representar una opción de manejo subutilizada para conservar el potencial evolutivo en un ambiente cambiante. Esto será particularmente cierto donde los híbridos de generación avanzada exhiban caracteres fuera del rango fenotípico parental, un fenómeno conocido como segregación transgresiva. Las ideas presentadas en este ensayo tienen la intención de provocar discusiones con respecto a cómo mantenemos el potencial evolutivo, el valor de conservación de las zonas de híbridos naturales y la consideración de la importancia de su papel en la adaptación al clima.*

¶email [jill.hamilton@ndsu.edu](mailto:jill.hamilton@ndsu.edu)

Paper submitted January 13, 2015; revised manuscript accepted June 17, 2015.

**Palabras Clave:** evolución, genética, hibridación, manejo adaptativo, potencial evolutivo

## Introduction

One of the single largest threats to populations globally is climate change. Current rates of climate change are associated with community and ecosystem-level changes in composition and functioning (Walther 2010; Franks & Hoffmann 2012), temporal shifts in development (Visser 2008), and spatial shifts in geographic distributions (McCarty 2001; Hoffmann & Sgro 2011; Shaw & Etterson 2012). The ability of species to track changes in climate requires a combination of strategies, including the capacity to migrate to favorable conditions (Schiffers et al. 2014), plasticity to enable shorter term responses to environmental change (Franks et al. 2013), and longer term adaptive evolutionary responses that may result in allelic and associated phenotypic changes (Aitken et al. 2008; Alberto et al. 2013; Savolainen et al. 2013). Populations unable to respond to changing conditions are at increased risk of extinction or reduced fitness (Aitken et al. 2008). We focused on the role adaptive introgression may play in increasing species' abilities to respond to changing climates. We considered how hybridization may mediate the consequences of limited adaptation potential from standing genetic variation and mutation alone and examined case studies where hybridization and introgression have enabled adaptive responses to changing environmental conditions. We concluded 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.

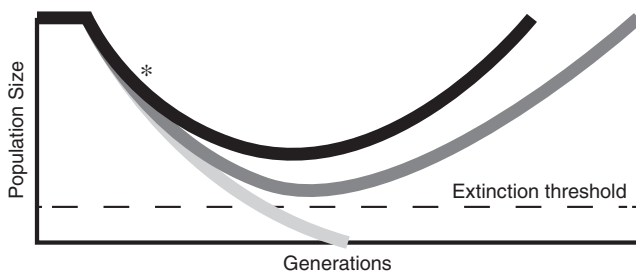
## Adaptation to a Changing Climate

One of the major challenges to populations in a changing climate is adapting to new environments within an appropriate time frame. 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). Genetic rescue involves 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, results in a change in the genetic composition of a population to increased frequency of adaptive alleles and leads to an adaptive evolutionary response (Pertoldi

et al. 2007; 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 in the population (Fig. 1). However, the probability that a population will experience an evolutionary rescue of this sort depends 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. Thus, the ability to adapt may be limited where standing genetic diversity is reduced and may lead to a reduced capacity of populations to respond to changing environments (Millar & Libby 1991; Sgro et al. 2011; Bijlsma & Loeschcke 2012). Conservation priorities should therefore consider strategies that mediate the potential risks to a population's persistence and future adaptive potential (Hellmann & Pineda-Krch 2007; Hoffmann & Sgro 2011). Strategies should maintain evolutionary resilience: the ability of a species or population to maintain its current state and to undergo evolutionary adaptation in response to environmental change (Sgro et al. 2011; Eizaguirre & Baltazar-Soare 2014).

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 and thus increase the rate of demographic recovery. In this way, hybridization and introgression may bridge or fill in the U-shaped adaptation trajectory (Fig. 1) and enable a quicker recovery or completely avoid the negative consequences of population decline. This represents a simple model regarding the



*Figure 1. Simplified trajectory of population demography over time in response to environmental stress: population decline where maladaptation results in extirpation once populations fall below an extinction threshold (light gray), population decline due to maladaptation followed by evolutionary rescue from standing genetic variation (medium gray), and population decline and recovery where interspecific gene flow reduces the demographic consequences of maladaptation and enables rapid population growth (black) (asterisk, point at which interspecific gene flow is introduced in this scenario) (adapted from Carlson et al. 2014).*

role of adaptive introgression in evolution, independent of density-dependent effects, and therefore there may be alternate outcomes. These outcomes 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 negative consequences in some cases, and adaptation within an appropriate time frame may require production of new genetic and phenotypic combinations (Kremer et al. 2012).

### 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 (Rieseberg & Wendel 1993; Arnold 1997), whereas others argued that hybridization was an evolutionary dead end (Mayr 1963). This debate derives from the fact plant biologists considered hybridization 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 (1949) and Anderson and Stebbins (1954) emphasized the importance of reshuffling segregating

genetic variation via hybridization. Recent research indicates that hybridization provides an important source of genetic variation on which selection might act and that its adaptive role is more widespread—among both plants and animals—than previously believed (Rieseberg & Wendel 1993; Dowling & Secor 1997; Hedrick 2013; Rius & Darling 2014).

Hybridization is broadly defined as the successful mating between individuals from 2 genetically differentiated lineages, and introgression is defined as the permanent infiltration of genes from 1 genetic lineage into the genome of another through repeated backcrossing (Table 1; Stebbins 1959; Wheeler & Guries 1987). Introgression may act to extend a species' gene pool, where movement of genetic material from 1 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 (Stebbins 1959; Rweyongeza et al. 2007). This produces a wide array of variation upon which natural selection may act. Thus, natural hybrids, particularly advanced-generation hybrids (backcrosses, F<sub>2</sub>s, and beyond) that carry introgressed alleles, may exhibit a range of fitness characteristics relative to either parental species (Rieseberg & Ellstrand 1993; Rieseberg 1995) or exhibit adaptive characteristics outside the natural parental range, termed transgressive segregation (Welch & Rieseberg 2002; Dittich-Reed & Fitzpatrick 2013; Hamilton et al. 2013). 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) that allow 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 (Dittich-Reed & Fitzpatrick 2013).

However, hybridization is often dismissed in a conservation context due to multiple risks, including the potential for genetic assimilation of pure species or spread of invasive genotypes; the potential for outbreeding depression (reduction in fitness of offspring between genetically divergent lineages); and murky legal

**Table 1. Glossary of terms**

<i>Term</i>	<i>Definition</i>
Hybridization	successful mating between individuals from 2 genetically differentiated lineages
Introgression	movement of genetic material from the genome of 1 species into the genome of another through repeated interbreeding
Transgressive segregation	formation of extreme phenotypes in recombinant hybrids relative to parental species due to complementary gene action of segregating genetic variation between parent species
Genetic rescue	introduction of variation to counter the demographic and genetic consequences of small population size
Evolutionary rescue	change in the genetic composition of a population to an increased frequency of adaptive alleles following an adaptive evolutionary response
Evolutionary resilience	ability of a species to not only maintain its current state but also to undergo evolutionary adaptation in response to environmental change
Hybrid swarm	population containing multiple generations of hybrids that are actively backcrossing or mating with other hybrid genotypes
F1 hybrid	first-generation hybrid progeny resulting from mating between 2 parental species; see Fig. 2
F2 hybrid	second-generation hybrid progeny resulting from mating between 2 F1 hybrids; see Fig. 2

status of hybrids under laws such as the Endangered Species Act (Rhymer & Simberloff 1996; Muhlfeld et al. 2014). Reexamination 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 (Rhymer & Simberloff 1996; Levin 2002; Hovick & Whitney 2014), so too have there been instances in which a parental genome remained relatively intact despite long histories of association and possible interbreeding (Fitzpatrick et al. 2008; Steeves et al. 2010) and cases of stable hybrid zone formation (Harrison 1993; Arnold 1997). Furthermore, a contrasting view on the risk of genetic swamping is taken if one adopts a gene-centric rather than species-centric view (Petit 2004). In a gene-centric 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. These simulations showed that although reduced fitness was initially observed due to outbreeding depression, populations rebounded over time. Furthermore, when introduced individuals had novel alleles preadapted to the

change in conditions, the duration of the drop in mean fitness was reduced and was followed by a significant increase in fitness (i.e., evolutionary rescue occurred) (Aitken & Whitlock 2013). Long-term experimental hybrid swarms provide empirical evidence that supports these observations (Hwang et al. 2011). 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, may outweigh the costs and can be maintained beyond the first generation (Willi et al. 2007; Whitely et al. 2015).

Challenges based on the legal status of hybrids may be harder to overcome because laws effectively dealing with hybrids remain unclear (Haig & Allendorf 2006; Garnett et al. 2011). Both intercross policies and propagation policies have been suggested to provide flexibility and guidelines in dealing 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 in species distributions (Garraway et al. 2010; Pauls et al. 2012; Mortiz & Agudo 2013). 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 non-native species) (Allendorf et al. 2001; 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.



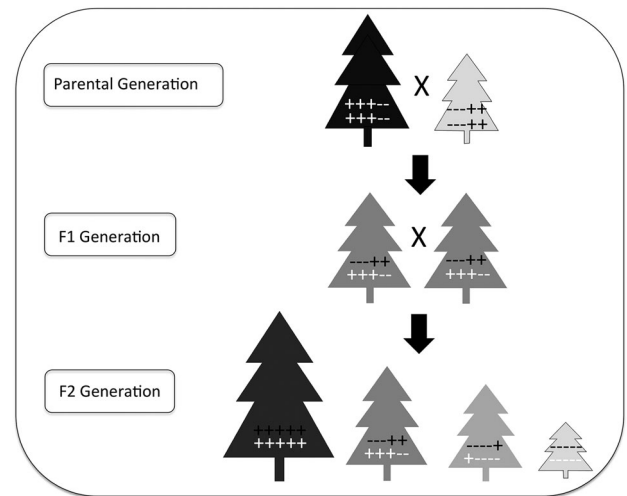
Introgression results from several generations of backcrossing and selection where segregating genetic variation is reshuffled. In the shorter term, early hybrid generations may contribute to demographic decline following hybrid breakdown (Fenster & Galloway 2000). The rate of demographic recovery and the potential for successful evolutionary rescue depend on species-specific life-history characteristics. Theoretical work of Baskett and Gomulkiewicz (2011) suggests that an adaptive evolutionary response depends on the level of assortative mating, the fitness of introgressed loci, and the mating system. While their work presents a significant step forward, it will be important to empirically validate their results. Evidence for successful evolutionary rescue over a short time frame can be seen in several cases of interpopulation genetic rescue (Madsen et al. 1999; Weeks et al. 2011; Miller et al. 2012; Pickup et al. 2013) 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

### Hybridization and Adaptive Introgression in Changing Environments

Experiments specifically testing the potential for evolutionary rescue from hybridization under changing environments are few. Stelkens et al. (2014) assessed yeast strain crosses for survival across increasingly stressful environments. They found that survival, following transfer to solutions with increasing salt concentrations, is higher for interspecific hybrids than for parental strains or intraspecific crosses. They also found that F2 hybrids perform better than F1 hybrids under increasingly severe conditions. They concluded that the likelihood of evolutionary rescue in response to rapidly changing environmental conditions is greater where interspecific recombination augments genetic diversity, even between distant relatives.

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 because 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, favors the survival and spread of hybrid mosquitoes with introgressed insecticide-resistance genes (Norris et al. 2015).



**Figure 2.** Schematic crossing design between 2 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 parent trees. The F1 represents a 50% shading of black and white tree, whereas the darker shade in the F2 generation indicates a greater proportion of segregating genetic variation inherited from the black parent tree. The pluses and minuses represent segregating allelic variation in parental populations that positively (+) or negatively (–) influences 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.

### Transgressive Segregation and New Environments

Heritable transgressive traits play an important role in increasing the niche breadth of individuals, which enables 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 recombines in hybrids at multiple loci to produce extreme phenotypes (Fig. 2). In a study of salt tolerance in the hybrid species *Helianthus paradoxus*, Welch and Rieseberg (2002) found that hybrids exhibit extreme values for traits associated with salt tolerance relative to either of the parental species (*Helianthus annuus*  $\times$  *Helianthus petiolaris*). Similarly, hybrid genotypes of spruce species display greater cold tolerance within a certain temperature range than either parental species (Hamilton et al. 2013).

While transgressive segregation is more often ascribed to plant species (Rieseberg & Carney 1998; Rieseberg et al. 1999; Stelkens & Seehausen 2009; Yakimowski &

Rieseberg 2014), it is also a key source for adaptation across 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, which is consistent with adaptive introgression as a mechanism to conserve evolutionary potential (Gompert et al. 2006). Pereira et al. (2013) developed multigeneration interspecific crosses between populations of the copepod *Tigriopus californicus* with varying levels of thermal tolerance. The authors found that crosses between ecologically and genetically similar populations lead to introgressed genotypes that exhibit 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 and thus allow admixed individuals to occupy fitness peaks on the adaptive landscape outside those used by parental taxa (Pereira et al. 2013). These examples attest to the important role introgressive hybridization and transgressive segregation play in the evolutionary trajectory and adaptive potential of populations (Yakimowski & Rieseberg 2014).

### Facilitated Admixture and 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*), indicate that human-mediated hybridization has led to increased fitness and preservation of parental genomes at risk of extinction (Benson et al. 2011; Garnett et al. 2011; Hostetler et al. 2013). 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 that 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 (Lewontin & Birch 1966; Seehausen 2013; Rius & Darling 2014). 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 provides 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 (Bell & Gonzalez 2009; Baskett & Gomulkiewicz 2011).

As the field of conservation evolves, combining conservation management with evolutionary theory is required (Eizaguirre & Baltazar-Soare 2014). We suggest that genetic variation that 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 has been observed (Becker et al. 2013). Inclusion of hybridization and introgression in conservation may require a shift in conservation to a gene-centric view (Petit 2004; Crispo et al. 2011) and inclusion of evolutionary processes contributing to the maintenance of adaptive evolutionary potential (Sgro et al. 2011; Weeks et al. 2011; Eizaguirre & Baltazar-Soare 2014). To maximize adaptive potential in response to changing environmental conditions, purposeful propagation of genetic variation via human-mediated hybridization may be necessary to conserve at-risk species (Shafer et al. 2015).

Managers first need to identify populations that may benefit from evolutionary rescue. These will likely be a combination of threatened species for which traditional management options have failed or failure is imminent (Hoffmann et al. 2015). Following this, evaluation of the potential outcomes of hybridization and introgression is required to validate theoretical models. Restoration projects provide an excellent opportunity to experimentally evaluate the role hybridization and introgression may have in conserving evolutionary potential, 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 and thus provide the opportunity to tease apart the genetic variation contributing to adaptive introgression (Hoffmann et al. 2015).

We suggest that managers consider hybrids alongside parental species when formulating conservation strategies. The benefits of adaptive introgression are multifaceted and include increased genetic diversity (through genetic rescue) and formation of new recombinant

genotypes that may have increased capacity to respond to changing selective pressures. These recombinant genotypes may enable an adaptive evolutionary response that limits demographic decline under rapidly changing conditions. This mechanism of evolutionary rescue will be particularly 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 our ideas provoke a discussion regarding the conservation value of hybridization and consideration of its potential role in adaptation to climate.

## Acknowledgments

This manuscript initially stemmed from a conservation genetics course at the University of British Columbia led by E.B. Taylor and S.N. Aitken. We especially thank D. Runcie for help with figure preparation and S. Aitken, R. Malenfant, and anonymous reviewers for providing useful comments that greatly improved the manuscript. JAH was supported by a start-up grant from the office of the North Dakota Experimental Program to Stimulate Competitive Research (ND-EPSCoR).

## Literature Cited

- Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* **1**:95–111.
- Aitken SN, Whitlock MC. 2013. Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution and Systematics* **44**:367–388.
- Alberto F, et al. 2013. Potential for evolutionary responses to climate change - evidence from tree populations. *Global Change Biology* **19**:1645–1661.
- Allendorf F, Leary R, Spruell P, Wenburg J. 2001. The problems with hybrids: setting conservation guidelines. *Trends in Ecology & Evolution* **16**:613–622.
- Anderson EC. 1949. *Introgressive hybridization*. John Wiley and Sons, Inc., New York.
- Anderson EC, Stebbins GL. 1954. Hybridization as an evolutionary stimulus. *Evolution* **8**:378–388.
- Anderson JT, Lee C, Mitchell-Olds T. 2013. Strong selection genome-wide enhances fitness trade-offs across environments and episodes of selection. *Evolution* **68**:16–31.
- Arnold ML. 1997. *Natural hybridization and evolution*. Oxford University Press, New York.
- Baskett ML, Gomulkiewicz R. 2011. Introgressive hybridization as a mechanism for species rescue. *Theoretical Ecology* **4**:223–239.
- Becker M, Gruenheit N, Steel M, Voelckel C, Deusch O, Heenan P, McLenachan PA, Kardailsky O, Leigh JW, Lockhard P. 2013. Hybridization may facilitate in situ survival of endemic species through periods of climate change. *Nature Climate Change* **3**:1039–1043.
- Bell G, Gonzalez A. 2009. Evolutionary rescue can prevent extinction following environmental change. *Ecology Letters* **12**:942–948.
- Benson J, Hostetler J, Onorato D, Johnson W, Roelke M, O'Brien S, Jansen D, Oli M. 2011. Intentional genetic introgression influences survival of adults and subadults in a small, inbred felid population. *Journal of Animal Ecology* **80**:958–967.
- Bijlsma R, Loeschcke V. 2012. Genetic erosion impedes adaptive responses to stressful environments. *Evolutionary Applications* **5**:117–129.
- Bridle JR, Vines TH. 2006. Limits to evolution at range margins: When and why does adaptation fail? *Trends in Ecology & Evolution* **22**:140–147.
- Broadhurst LM, Lowe A, Coates DJ, Cunningham SA, McDonald M, Vesk PA, Yates C. 2008. Seed supply for broadscale restoration: maximizing evolutionary potential. *Evolutionary Applications* **1**:587–597.
- Carlson SM, Cunningham CJ, Westley P. 2014. Evolutionary rescue in a changing world. *Trends in Ecology & Evolution* **29**:521–530.
- Chunco AJ, Jobe R, Pfennig KS. 2012. Why do species co-occur? A test of alternative hypotheses describing abiotic differences in sympatry versus allopatry using Spadefoot toads. *PLoS ONE* **7**(e32748). DOI: 10.1371/journal.pone.0032748.
- Crispo E, Moore J-S, Lee-Yaw J, Gray SM, Haller BC. 2011. Broken barriers: human-induced changes to gene flow and introgression in animals. *Bioessays* **33**:508–518.
- Dittrich-Reed DR, Fitzpatrick BM. 2013. Transgressive hybrids as hopeful monsters. *Journal of Evolutionary Biology* **40**:310–315.
- Dowling TE, Secor CL. 1997. The role of hybridization and introgression in the diversification of animals. *Annual Review of Ecology and Systematics* **28**:593–619.
- Eizaguirre C, Baltazar-Soare M. 2014. Evolutionary conservation - evaluating the adaptive potential of species. *Evolutionary Applications* **7**:963–967.
- Fenster CB, Galloway LF. 2000. Inbreeding and outbreeding depression in natural populations of *Chamaecrista fasciculata* (Fabaceae). *Conservation Biology* **14**:1406–1412.
- Fitzpatrick BM, Placyk JS, Niemiller ML, Casper GS, Gurchardt GM. 2008. Distinctiveness in the face of gene flow: hybridization between specialist and generalist gartersnakes. *Molecular Ecology* **17**:4107–4117.
- Frankham R. 2015. Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. *Molecular Ecology* **24**:2610–2618.
- Frankham R, Ballou J, Eldridge M, Lacy R, Ralls K, Dudash M, Fenster C. 2011. Predicting the probability of outbreeding depression. *Conservation Biology* **25**:465–475.
- Franks SJ, Hoffmann AA. 2012. Genetics of climate change adaptation. *Annual Review of Genetics* **46**:185–208.
- Franks SJ, Weber JJ, Aitken SN. 2013. Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evolutionary Applications* **7**:123–139.
- Garnett ST, Olsen P, Butchart S, Hoffmann AA. 2011. Did hybridization save the Norfolk Island boobook owl *Ninox novaeseelandiae undulata*? *Oryx* **45**:500–504.
- Garroway CJ, Bowman J, Cascaden T, Holloway G, Mahan C, Malcolm JR, Steele M, Turner G, Wilson PJ. 2010. Climate change induced hybridization in flying squirrels. *Global Change Biology* **16**:113–121.
- Gompert Z, Fordyce JA, Forister ML, Shapiro AM, Nice CC. 2006. Homoploid hybrid speciation in an extreme habitat. *Science* **314**:1923–1925.
- Gonzalez A, Ronce O, Ferrier R, Hochberg M. 2013. Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**:20120404.
- Haig SM, Allendorf FW. 2006. Hybrids and policy. Pages 150–163 in Scott JM, Goble DD, Davis FW, editors. *The Endangered Species Act at thirty. Volume 2: Conserving biodiversity in human-dominated landscapes*. Island Press, Washington, D.C.
- Hamilton JA, Lexer C, Aitken SN. 2013. Genomic and phenotypic architecture of a spruce hybrid zone (*Picea sitchensis* x *P. glauca*). *Molecular Ecology* **22**:827–841.



- Harrison RG. 1993. Hybrids and hybrid zones: historical perspective. Oxford University Press, New York.
- Hedrick PW. 2013. Adaptive introgression in animals: examples and comparison to new mutation and standing variation as sources of adaptive variation. *Molecular Ecology* **22**:2606–4618.
- Hellmann J, Pineda-Krch M. 2007. Constraints and reinforcement on adaptation under climate change: selection of genetically correlated traits. *Biological Conservation* **137**:599–609.
- Hoffmann AA, et al. 2015. A framework for incorporating evolutionary genomics into biodiversity conservation and management. *Climate Change Responses* **2**:1–23.
- Hoffmann AA, Sgro CM. 2011. Climate change and evolutionary adaptation. *Nature* **470**:479–485.
- Hostetler JA, Onorato DP, Jansen D, Oli MK. 2013. A cat's tale: the impact of genetic restoration on Florida panther population dynamics and persistence. *Journal of Animal Ecology* **82**:608–620.
- Hovick SM, Whitney KD. 2014. Hybridisation is associated with increased fecundity and size in invasive taxa: meta-analytic support for the hybridisation-invasion hypothesis. *Ecology Letters* **17**:1464–1477.
- Hwang AS, Northrup SL, Alexander JK, Vo KT, Edmands S. 2011. Long-term experimental hybrid swarms between moderately incompatible *Tigriopus californicus* populations: hybrid inferiority in early generations yields to hybrid superiority in later generations. *Conservation Genetics* **12**:895–909.
- Kremer A, et al. 2012. Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecology Letters* **15**:378–392.
- Levin DA. 2002. Hybridisation and extinction: in protecting rare species, conservationists should consider the dangers of inter-breeding, which compound the more well-known threats to wildlife. *American Scientist* **90**:254–261.
- Lewontin RC, Birch LC. 1966. Hybridization as a source of variation for adaptation to new environments. *Evolution* **20**:315–336.
- Madsen T, Shine R, Olsson M, Wittzel H. 1999. Restoration of an inbred adder population. *Nature* **402**:34–35.
- Mayr E. 1963. Animal species and evolution. Belknap Press, Cambridge.
- McCarty JP. 2001. Ecological consequences of recent climate change. *Conservation Biology* **15**:320–331.
- Millar CI, Libby WJ. 1991. Strategies for conserving clinal, ecotypic, and disjunct populations diversity in widespread species. Oxford University Press, New York.
- Miller JM, Poissant J, Hogg JT, Coltman DW. 2012. Genomic consequences of genetic rescue in an insular population of bighorn sheep (*Ovis canadensis*). *Molecular Ecology* **21**:1583–1596.
- Mortiz C, Agudo R. 2013. The future of species under climate change: resilience or decline. *Science* **504**:504–508.
- Muhlfeld C, Kovach RP, Jones LA, Al-Chokhachy R, Boyer M, Leary RF, Lowe W, Luikart G, Allendorf FW. 2014. Invasive hybridization in a threatened species is accelerated by climate change. *Nature Climate Change* **4**:620–624.
- Nice CC, Gompert Z, Fordyce JA, Forister ML, Lucas LK, Buerkle CA. 2013. Hybrid speciation and independent evolution in lineages of alpine butterflies. *Evolution* **67**:1055–1068.
- Norris LC, Main BJ, Lee Y, Collier TC, Fofana A, Cornel A, Lanzaro G. 2015. Adaptive introgression in an African malaria mosquito coincident with the increased usage of insecticide-treated bed nets. *Proceedings of the National Academy of Science USA* **112**:815–820.
- Orr HA, Unckless RL. 2014. The population genetics of evolutionary rescue. *PLoS Genetics* **10**(e1004551). DOI: 10.1371/journal.pgen.1004551.
- Pauls SU, Nowak C, Balint M, Pfenninger M. 2012. The impact of global climate on genetic diversity within populations and species. *Molecular Ecology* **22**:925–946.
- Pereira RJ, Barreto FS, Burton RS. 2013. Ecological novelty by hybridization: experimental evidence for increased thermal tolerance by transgressive segregation in *Tigriopus californicus*. *Evolution* **68**:204–215.
- Pertoldi C, Bijlsma R, Loeschcke V. 2007. Conservation genetics in a globally changing environment: present problems, paradoxes and future challenges. *Biodiversity and Conservation* **16**:4147–4163.
- Petit RJ. 2004. Biological invasions at the gene level. *Diversity and Distributions* **10**:159–165.
- Pickup M, Field DL, Rowell DM, Young A. 2013. Source population characteristics affect heterosis following genetic rescue of fragmented plant populations. *Proceedings of the Royal Society B: Biological Sciences* **280**:20122058.
- Rhymer J, Simberloff D. 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics* **27**:83–109.
- Rieseberg L. 1995. The role of hybridization in evolution: old wine in new skins. *American Journal of Botany* **82**:944–953.
- Rieseberg LH, Archer MA, Wayne RK. 1999. Transgressive segregation, adaptation and speciation. *Heredity* **83**:363–372.
- Rieseberg LH, Carney SE. 1998. Plant hybridization. *New Phytologist* **140**:599–624.
- Rieseberg LH, Ellstrand NC. 1993. What can molecular and morphological markers tell us about plant hybridization. *Critical Reviews in Plant Sciences* **12**:213–241.
- Rieseberg LH, Wendel JF. 1993. Introgression and its consequences in plants. Hybrid zones and the evolutionary process. Oxford University Press, New York.
- Rius M, Darling JA. 2014. How important is intraspecific genetic admixture to the success of colonising populations? *Trends in Ecology & Evolution* **29**:233–242.
- Rweyongeza DM, Dhir NK, Barnhardt LK, Hansen C, Yang R-C. 2007. Population differentiation of the lodgepole pine (*Pinus contorta*) and jack pine (*Pinus banksiana*) complex in Alberta: growth, survival, and responses to climate. *Canadian Journal of Botany* **85**:545–556.
- Savolainen O, Lascoux M, Merila J. 2013. Ecological genomics of local adaptation. *Nature Reviews Genetics* **14**:807–820.
- Schiffers K, Bourne EC, Laverne S, Thuiller W, Travis JM. 2014. Limited evolutionary rescue of locally adapted populations facing climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**:20120083.
- Seehausen O. 2013. Conditions when hybridization might predispose populations for adaptive radiation. *Journal of Evolutionary Biology* **26**:279–281.
- Sgro CM, Lowe AJ, Hoffmann AA. 2011. Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications* **4**:326–337.
- Shafer ABA, et al. 2015. Genomics and the challenging translation into conservation practice. *Trends in Ecology & Evolution* **30**:78–87.
- Shaw RG, Etterson JR. 2012. Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. *New Phytologist* **195**:752–765.
- Song Y, Endepols S, Klemann N, Richter D, Matuschka F, Shih C, Nachman MW, Kohn MH. 2011. Adaptive introgression of anticoagulant rodent poison resistance by hybridization between old world mice. *Current Biology* **21**:1296–1301.
- Stebbins GL. 1959. The role of hybridization in evolution. *Proceedings of the American Philosophical Society* **103**:231–251.
- Steeves T, Maloney R, Hale M, Tylaniakis J, Gemmill N. 2010. Genetic analyses reveal hybridization but no hybrid swarm in one of the world's rarest birds. *Molecular Ecology* **19**:5090–5100.
- Stelkens R, Seehausen O. 2009. Genetic distance between species predicts novel trait expression in their hybrids. *Evolution* **63**:884–897.
- Stelkens RB, Brockhurst MA, Hurst G, Greig D. 2014. Hybridization facilitates evolutionary rescue. *Evolutionary Applications* **7**:1209–1217.
- Vander Wal E, Garant D, Festa-Bianchet M, Pelletier F. 2013. Evolutionary rescue in vertebrates: evidence, applications and uncertainty.



- Philosophical Transactions of the Royal Society B: Biological Sciences **368**:20120090.
- Visser ME. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences* **275**:649–659.
- Walther G. 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**:2019–2024.
- Weeks AR, et al. 2011. Assessing the benefits and risks of translocations in changing environments: a genetic perspective. *Evolutionary Applications* **4**:709–725.
- Welch ME, Rieseberg LH. 2002. Habitat divergence between a homoploid hybrid sunflower species, *Helianthus paradoxus* and its progenitors. *American Journal of Botany* **89**:472–478.
- Wheeler NC, Guries RP. 1987. A quantitative measure of introgression between lodgepole and jack pines. *Canadian Journal of Botany* **65**:1876–1885.
- Whitely AR, Fitzpatrick SW, Funk WC, Tallmon DA. 2015. Genetic rescue to the rescue. *Trends in Ecology & Evolution* **30**:42–49.
- Wilczek AM, Cooper MD, Korves TM, Schmitt J. 2014. Lagging adaptation to warming climate in *Arabidopsis thaliana*. *Proceedings of the National Academy of Science USA* **111**:7906–7913.
- Willi Y, Kleunen M, Dietrich S, Fischer M. 2007. Genetic rescue persists beyond first-generation outbreeding in small populations of a rare plant. *Proceedings of the Royal Society B: Biological Sciences* **274**:2357–2364.
- Yakimowski SB, Rieseberg LH. 2014. The role of homoploid hybridization in evolution: a century of studies synthesizing genetics and ecology. *American Journal of Botany* **101**:1247–1258.