



Risk and efficacy of human-enabled interspecific hybridization for climate-change adaptation: response to Hamilton and Miller (2016)

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Introduction

Hamilton and Miller (2016) provide an interesting and provocative discussion of how hybridization and introgression can promote evolutionary potential in the face of climate change. They argue that hybridization—mating between individuals from genetically distinct populations—can alleviate inbreeding depression and promote adaptive introgression and evolutionary rescue. We agree that deliberate intraspecific hybridization (mating between individuals of the same species) is an underused management tool for increasing fitness in inbred populations (i.e., genetic rescue; Frankham 2015; Whiteley et al. 2015). The potential risks and benefits of assisted gene flow have been discussed in the literature, and an emerging consensus suggests that mating between populations isolated for approximately 50–100 generations can benefit fitness, often with a minor risk of outbreeding depression (Frankham et al. 2011; Aitken & Whitlock 2013; Allendorf et al. 2013).

However, the notion that conservationists and managers welcome or enable interspecific hybridization (mating between individuals from different species) for the purposes of fostering climate-change adaptation is one that should be approached carefully. We question whether interspecific hybridization is generally necessary for, or likely to promote, climate-change adaptation. We further outline reasons why using interspecific hybridization as a management strategy may be problematic for conservation and often challenging to im-

plement as an effective measure against future climatic change.

Interspecific Hybridization and Climate-Change Adaptation

Major premises of Hamilton and Miller are that standing genetic variation may be insufficient for adaptive evolutionary responses to climate change and that interspecific hybridization could bolster evolutionary potential. Despite long-standing interest in whether interspecific hybridization stimulates rapid adaptive evolution (e.g., Anderson & Stebbins 1954), empirical examples are rare, especially in vertebrates (Hedrick 2013). This is particularly true in the context of climate change; we are unaware of any example where evolutionary adaptation to anthropogenic climate change was enabled by interspecific hybridization (but see Grant and Grant 1993 for an example involving adaptive hybridization following an anomalous climatic event). A lack of empirical evidence for this phenomenon is underscored by the case studies described in Hamilton and Miller, none of which specifically address adaptation to climate change in natural populations. Although evolutionary responses to climate change via natural selection operating on standing genetic variation are also limited, they have been documented across a broad range of taxa (e.g., $n = 20$ in Merilä & Hendry 2014) and far outnumber existing examples, or lack thereof, of adaptive evolutionary changes to contemporary climate change following interspecific hybridization.

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Hamilton and Miller also argue that phenotypic plasticity is insufficient for climate-change adaptation, but most adaptive responses to climate change have been plastic in nature (Merilä & Hendry 2014). Although plasticity clearly has limits, those limits are rarely well resolved. Additionally, reaction norms can respond to natural selection, and extreme environments can lead to the expression of cryptic genetic diversity for phenotypic plasticity that exceeds normal phenotypic variation, much like transgressive hybridization (Ghalambor et al. 2007). In light of this, we argue that promoting interspecific hybridization for climate adaptation is unnecessarily risky before describing existing limits to intrinsic adaptive capacity.

Consequences of Hybridization

Hamilton and Miller largely dismiss the negative impacts of hybridization, including outbreeding depression and loss of biodiversity (Allendorf et al. 2013). However, natural selection acts against hybrids in most hybrid zones (Barton & Hewitt 1985), and examples of outbreeding depression are widespread (Edmands 2007), including cases involving sympatric and parapatric sister species (e.g., Muhlfeld et al. 2009; Stelkens et al. 2015). Importantly, outbreeding depression can persist for multiple generations, especially when dispersal, not selection, is the primary mechanism driving introgression (Kovach et al. 2015), or when complex patterns of inheritance delay the efficacy of natural selection (Johnson et al. 2010). Thus, outbreeding depression can be particularly problematic when hybridization or introgression is promoted by the rapid expansion of one taxon (Muhlfeld et al. 2014; Lowe et al. 2015), conditions that may become increasingly common as species rapidly shift—or fail to shift—their spatiotemporal distributions in response to climate change (Kelly et al. 2010). Even in instances where outbreeding depression dissipates after initial interbreeding, several generations of reduced fitness—and associated declines in population vital rates—have consequences, especially for long-lived species facing increased climatic and nonclimatic stress through time.

Another negative outcome of introgressive hybridization is its homogenizing effect on intraspecific, interspecific, and community biodiversity (Olden et al. 2004). Biotic homogenization is particularly concerning given that species persistence and ecosystem stability are maximized when there are a diversity of ecological and evolutionary responses to perturbation (Schindler et al. 2015). Therefore, it is critical that managers and conservationists carefully consider various ecological criteria (e.g., risk of altering community dynamics, reducing biocomplexity, creating invasive hybrids, disease) and evolutionary criteria (e.g., degree of local adaptation, strength of natural selection, effective population size, genetic differentiation) when debating the merits and consequences of human-mediated hybridization.

Efficacy of Hybridization as a Conservation Tool

Hamilton and Miller suggest the scientific understanding necessary to predict adaptive introgression or identify donor species or populations required to produce adaptive transgressive phenotypes exists or can be obtained. Unfortunately, the ability to predict the ecological and evolutionary impacts of transporting organisms, their genes, and their associated pathogens is notably poor (Ricciardi & Simberloff 2009). Theoretically, introgressive hybridization can lead to adaptive transgressive segregation (i.e., “hopeful monsters” [sensu Dittrich-Reed & Fitzpatrick 2013]), but given the limited understanding of adaptive introgression in nature, hopeless monsters are the more likely outcome of human-mediated hybridization events. For example, despite careful management and the best of intentions, efforts to genetically and demographically augment Pacific salmon (*Oncorhynchus* spp.) populations have resulted in significant outbreeding depression (Araki et al. 2008) and substantial reductions in intraspecific biodiversity (Griffiths et al. 2014).

Although the view that genomics will help “tease apart genetic variation underlying adaptive traits” is exciting, existing knowledge of the genomic architecture underlying phenotypic variation in natural populations suggests that genecentric approaches to policy and management are currently infeasible (Shafer et al. 2015). This infeasibility is exacerbated by the fact that many traits associated with climate adaptation are polygenic, making it challenging and often impossible to predict which alleles will be beneficial, particularly given complexities arising from epistatic gene interactions (Savolainen et al. 2013). Furthermore, background selection acting against genome-wide introgression (i.e., outbreeding depression), may prevent introgression of adaptive alleles of small effect that underlie most quantitative traits. Overall, the warning from Holt (1990) remains applicable today: “There is almost no species for which we know enough relevant ecology, physiology, and genetics to predict its evolutionary response to climate change.” The weight of this statement increases exponentially when extended to multiple hybridizing species. Although future understanding will improve, adaptive microevolution in nature is a remarkably unpredictable process (Grant & Grant 2002), underscoring the need for extreme caution when considering management strategies such as the those described in Hamilton and Miller that promote “purposeful propagation of genetic variation via human-mediated hybridization . . .”

Conclusion

Hamilton and Miller rightly suggest that climate change will necessitate proactive approaches for maximizing species resiliency and adaptive capacity. Natural hybrid zones have significant conservation and evolutionary

value and are clearly important sources of novelty and biodiversity, especially on evolutionary time scales. However, given increasingly well-documented negative impacts of human-mediated hybridization on contemporary time scales, managers should consider assisted interspecific hybridization extremely risky and more likely to produce negative rather than positive outcomes. Likewise, there exists no clear evidence that interspecific hybridization will benefit species under climate change in natural systems. Even genetic rescue is often a stopgap that can only provide temporary relief from inbreeding depression if the stressors responsible for population decline are not adequately addressed (Whiteley et al. 2015). Thus, management strategies that address limiting factors while protecting fundamental environmental processes giving rise to intra- and interspecific diversity and evolutionary potential (e.g., habitat heterogeneity, natural disturbance regimes, connectivity) will likely best combat and mitigate ongoing and future global change.

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