Assisted Gene Flow to Facilitate Local Adaptation to Climate Change

Sally N. Aitken^{1,2} and Michael C. Whitlock³

¹Department of Forest and Conservation Sciences, ²Center for Forest Conservation Genetics, and ³Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada; email: Sally.Aitken@ubc.ca

Annu. Rev. Ecol. Evol. Syst. 2013. 44:367-88

First published online as a Review In Advance on September 23, 2013

The Annual Review of Ecology, Evolution, and Systematics is online at ecolsys.annualreviews.org

This article's doi: 10.1146/annurev-ecolsys-110512-135747

Copyright © 2013 by Annual Reviews. All rights reserved

Keywords

assisted migration, evolutionary rescue, genetic rescue, outbreeding depression, phenotypic plasticity, seed transfer, ecological restoration, reforestation, facilitated adaptation

Abstract

Assisted gene flow (AGF) between populations has the potential to mitigate maladaptation due to climate change. However, AGF may cause outbreeding depression (especially if source and recipient populations have been long isolated) and may disrupt local adaptation to nonclimatic factors. Selection should eliminate extrinsic outbreeding depression due to adaptive differences in large populations, and simulations suggest that, within a few generations, evolution should resolve mild intrinsic outbreeding depression due to epistasis. To weigh the risks of AGF against those of maladaptation due to climate change, we need to know the species' extent of local adaptation to climate and other environmental factors, as well as its pattern of gene flow. AGF should be a powerful tool for managing foundation and resource-producing species with large populations and broad ranges that show signs of historical adaptation to local climatic conditions.

Assisted gene flow (AGF): intentional translocation of individuals within a species range to facilitate adaptation to anticipated local conditions

Gene flow: movement of individuals or gametes (e.g., pollen) between populations that results in successful introduction of migrant alleles

INTRODUCTION

The capacity for populations to respond to climate change through rapid adaptation will directly affect the persistence of biodiversity, the provision of ecosystem services, and the production of resources by many species globally. The genotypes that are best adapted to the new climates faced by a population may occur at a higher frequency elsewhere in a species range where the historical climate better matches predicted future conditions. One potential tool for aiding the adaptation of populations to new climatic conditions is assisted gene flow (AGF), which we define as the managed movement of individuals or gametes between populations within species ranges to mitigate local maladaptation in the short and long term. Species that show local adaptation to a historical climate may benefit from AGF, but they also face potential genetic risks from this practice.

Many species show divergent local adaptation in spatially heterogeneous environments (Kawecki & Ebert 2004, Leimu & Fischer 2008, Hereford 2009b). During periods of environmental stability, natural selection maintains local adaptation, whereas gene flow diminishes it. If local environments change abruptly, populations may no longer be adapted, average fitness may decrease, and population size and productivity will likely decline. Current anthropogenic climate warming (Solomon et al. 2007) is rapidly decoupling populations from the climatic conditions to which they have adapted in the past because climates are changing faster than many populations can adapt or move. Maladaptation caused by climate change threatens to decrease species' productivity and health, as well as the ecosystem services and resources they provide. Maladaptation to climate can also exacerbate the decline of small populations for which conservation is a concern (Aitken et al. 2008, Anderson et al. 2012, O'Connor et al. 2012). Although some populations may tolerate climatic and other environmental changes through phenotypic plasticity (Crispo 2008, Chevin et al. 2010, Reed et al. 2011), achieve evolutionary rescue via adaptation to new conditions (Anderson et al. 2012, O'Connor et al. 2012, Gonzalez & Bell 2013), or migrate to track their climatic niches across the landscape (Parmesan 2006, Loarie et al. 2009), others will fail to respond through these mechanisms and will be extirpated as a result.

Historical local adaptation to climate is not universal, but it is quite common. For example, populations of many temperate and boreal tree species show local adaptation to climatic variables, particularly for phenological traits and growth rates (Savolainen et al. 2007, Aitken et al. 2008, Alberto et al. 2013). Natural populations of *Arabidopsis thaliana* show local adaptation to climate for phenotypic traits and for genomic markers (Fournier-Level et al. 2011). Many insects are locally adapted to thermal regimes (Hoffmann et al. 2002, Aardema et al. 2011). Different populations of sockeye salmon are physiologically adapted to historical water temperatures that vary with the timing of their migration to freshwater spawning grounds (Eliason et al. 2011, Martins et al. 2012).

AGF has the potential to introduce genotypes that are preadapted to new local climates or to increase the frequency of these genotypes in existing populations (Broadhurst et al. 2008, Kreyling et al. 2011, Weeks et al. 2011). In the short term, such a strategy could supply individuals of higher fitness than residents, thus increasing mean survival rate, fecundity, production of ecosystem services and resources, and local population size. For these reasons, AGF is already being implemented for some forest trees (e.g., O'Neill et al. 2008) and has been suggested for other species and applications (e.g., Broadhurst et al. 2008, Vitt et al. 2010, Riegl et al. 2011). AGF and genetic engineering have both been proposed as conservation tools for facilitated adaptation (Thomas et al. 2013). In the longer term, AGF could provide greater genetic variation for future evolutionary response, fueling evolutionary rescue as selection regimes continue to change. Unfortunately, AGF often requires movements over large geographic distances, and these movements may result in problems such as outbreeding depression, the disruption of local adaptation to other environmental factors, or the loss of original local lineages (Edmands 2007,

Byrne et al. 2011, Weeks et al. 2011). Here we review the genetic issues, risks, and benefits of AGF in relation to natural responses of populations to climate change, and we assess this potential management and conservation tool from a genetic perspective.

Assisted Gene Flow Has Lower Ecological Risks but Higher Genetic Risks than Assisted Migration Outside Species Ranges

Assisted migration (AM)—defined as the intentional anthropogenic movement of individuals and populations—has received a great deal of attention in the ecological and conservation literature in recent years (Hoegh-Guldberg et al. 2008, Ricciardi & Simberloff 2009, Schwartz et al. 2009, Vitt et al. 2009, Hewitt et al. 2011, Thomas 2011, Webber et al. 2011, Schwartz et al. 2012). AM has a broader definition than AGF; AM includes both movements within species ranges (AGF) and movements outside ranges (assisted colonization). As species may be unable to disperse, establish, or adapt quickly enough to keep up with a warming climate (Davis & Shaw 2001, Loarie et al. 2009), AM has been suggested as a potential management tool for conservation and resource-production purposes. Most discussions of AM have emphasized the movement of individuals outside of existing species ranges.

The use of AM as a tool for addressing conservation and resource productivity problems associated with climate change has been controversial, largely because the ecological effects of introducing species into new ecosystems outside their native ranges are unpredictable and potentially damaging (e.g., Ricciardi & Simberloff 2009, Webber et al. 2011, Van der Putten 2012). The ecological effects of AGF should be on average considerably less risky and somewhat more predictable than species introduction outside historical ranges. In addition, AGF is associated with much less risk than long-distance (e.g., crosscontinental or intercontinental) introductions (Mueller & Hellmann 2008) because the focal species is already present in the ecosystems to which individuals will be moved. However, managers using AGF must be concerned about the genetic effects that the introduced individuals will have on the preexisting population (e.g., through outbreeding depression or lineage swamping; see The Genetic Effects of Assisted Gene Flow, below); these effects do not occur without a preexisting local population.

In the AM debate, ecological effects have received far more attention than genetic effects, and relatively little discussion of the movement of individuals or populations within existing species ranges to promote adaptation to new climatic conditions has occurred. Few scientific papers on AM have rigorously addressed genetic issues (but see Broadhurst et al. 2008, Kreyling et al. 2011, Weeks et al. 2011), especially for AGF in large populations of ecologically important foundation species or economically important resource-production species. Although the value of translocations between populations has been well reviewed in the context of reducing extinction risks from inbreeding depression in small populations (genetic rescue), less attention has been paid to the potential of AGF for helping ecological foundation species or species used for resource production. We begin to fill this gap with this review.

Local Adaptation to Climate Indicates Potential Benefits from Assisted Gene Flow

Undertaking AGF to promote adaptation to new climatic conditions makes sense only if the source populations were previously locally adapted to the same climate conditions as those now experienced by the target population. Local adaptation results from divergent natural selection pressures among environments (Williams 1966, Kawecki & Ebert 2004). A strong response to local selection pressures promotes local adaptation, but the homogenizing influence of gene flow counters it. If dispersal between environments is too common, the differences that evolve through

Assisted migration (AM): the intentional translocation of individuals within or

translocation of individuals within or outside the natural range of a species

Local adaptation:

higher fitness of local than nonlocal populations resulting from divergent selection among environments selection can be erased. Because gene flow rates are similar for all loci in the genome but loci can have different selection strengths, we expect that genetic differentiation caused by alleles of larger selective effect is more likely to persist in the face of gene flow (Macnair 1991, Kawecki & Ebert 2004, Yeaman & Whitlock 2011). Small populations that experience high levels of genetic drift are less likely to be locally adapted than are large populations (Willi et al. 2006, Leimu & Fischer 2008, Yeaman & Otto 2011). Moreover, species with metapopulation dynamics and frequent population extirpation and recolonization are less likely to develop local adaptation before they go extinct.

An adaptive response to local selection is greatest when the population has more genetic variation. The amount of genetic variation available to local populations can be too low to allow effective adaptation if the effective population size is small (Yeaman & Whitlock 2011, Blanquart et al. 2012), so local adaptation is more often expected when the local population size is large [as was observed in the meta-analysis of Leimu & Fischer (2008)]. Because genetic variation can limit response to selection, low levels of gene flow can facilitate local adaptation by providing new genetic diversity (Gomulkiewicz et al. 1999, Kawecki & Ebert 2004, Blanquart et al. 2012). As climates change, population sizes are also likely to change, and habitat fragmentation and changes in other biotic and abiotic conditions affecting dispersal, such as wind speed and direction, may modify levels of gene flow (Kremer et al. 2012).

Moreover, a subtle difference exists between factors that can increase local adaptation and those that can increase local fitness. Alleles that are beneficial in all populations can increase local fitness, whereas local adaptation (by most definitions) requires that the local population is unusually well suited to its environment. Small populations in particular may lack such beneficial alleles, so gene flow can increase local fitness even if the population is not becoming more adapted to local conditions (Sexton et al. 2011, Blanquart et al. 2012). Increased gene flow from other sites can also improve the fitness of a target population if individuals from elsewhere in a species range are better adapted to the climate of the target site than are resident individuals. Such species may be candidates for AGF.

How common is local adaptation? Given the challenges of effectively following individual organisms for most animal species, it is not surprising that the literature on local adaptation is dominated by plant research, although some examples in animals are well known (e.g., Reznick & Endler 1982, Huey et al. 2000, Hoffmann et al. 2002, Vignieri et al. 2010, Kelly et al. 2012). Leimu & Fischer (2008) conducted a meta-analysis of 36 reciprocal transplant studies for herbaceous plant species with a total of 1,032 comparisons of local and nonlocal populations. They found that 71% of the local populations analyzed showed evidence of local adaptation, defined as the local genotypes at each site having higher fitness, on average, than the nonlocal genotypes. Plant life-history traits, geographic scale, and spatial and temporal variability in habitat had no detectable effects on local adaptation, but small populations (<1,000 flowering individuals) were much less likely to be locally adapted than were larger populations. These findings suggest that genetic drift and lack of genetic variation limit the capacity of small populations to adapt to a changing climate in situ (Willi et al. 2006). Hereford (2009b) analyzed a larger and more diverse data set that included local adaptation results from 74 studies (50 plant, 21 animal, 2 fungi, 1 protist) with a total of 777 comparisons of local and nonlocal populations, and also found that local populations had equal or greater fitness than nonlocal populations in 71% of the comparisons. He estimated that local populations had, on average, 45% greater fitness than nonlocal populations. Although the majority of studies in Hereford's analysis indicated local adaptation, many populations may have been prevented from reaching adaptive optima owing to genetic drift or gene flow.

How common is local adaptation specifically to climatic factors? This has not been studied as systematically as the occurrence of local adaptation in general. Of the 74 studies included

in Hereford's (2009b) meta-analysis, 27 included climatic factors that differed among sites, 12 considered only nonclimatic environmental factors, and 35 did not specify environmental factors. Population pairs compared within studies including climate-based factors and those specifying nonclimatic or no environmental factors did not differ in their probability of showing local adaptation (p = 0.85 based on a two-sample t-test with archived data from Hereford 2009a).

Many locally adapted populations will likely become maladapted to new climates as a result of global warming. The prevalence of local adaptation to climate, particularly for many widespread species, suggests that AGF may help mitigate this maladaptation. However, AGF may also result in maladaptation to nontargeted environmental factors, as discussed below.

Foundation species: a species that plays an important role in structuring and creating habitat within

a community

TARGET POPULATIONS AND SPECIES FOR ASSISTED GENE FLOW

Given the speed at which climates are changing, the limited resources available for mitigating negative effects of climate change in natural ecosystems, and the species-specific logistical demands and knowledge required to successfully translocate individuals, very few species can be targets for AGF. Many life-history traits will affect the relative risks and benefits of AGF. In this review, we focus on three high-priority targets for such actions: (a) foundation species that dominate ecosystems, have relatively large populations, and provide vital habitat and ecosystem services; (b) species that are already managed to produce economically important renewable resources for humans (these may also be foundation species); and (c) small populations at risk of extirpation.

Foundation Species

Foundation species are prime candidates for AGF owing to their central roles in ecosystem structure, function, and habitat. An increase in the fitness of foundation species may have positive impacts on other species in those communities. For example, many forest trees are foundation species in terrestrial ecosystems, as they play key roles in structuring forested communities and providing elements of habitat for other species (Ellison et al. 2005). A recent global survey of forests found that many tree species are showing signs of heat stress and drought-related diebacks (Allen et al. 2010). Corals are also foundation species that are currently suffering widespread mortality, and they have been proposed as candidates for AGF (Hoegh-Guldberg et al. 2008, Riegl et al. 2011). Some plant species in tallgrass prairie ecosystems and other grasslands may also be suitable (Vitt et al. 2010). Ecosystem restoration and the remediation of disturbed sites often involve reestablishing foundation species, particularly plants, and so necessitate sourcing appropriate germplasm for those environments (Broadhurst et al. 2008). The traditional approach would use source populations that are as local as possible to the restoration site (McKay et al. 2005), but because of climate change, this approach may no longer result in successful restoration.

Many foundation plant species, including trees and grassland species, also play key roles in the global carbon cycle, sequestering carbon in woody biomass, roots, or soil organic matter. These species are usually locally abundant and regionally common and are therefore not at high risk of extinction. Nevertheless, a decline in fitness could have far-reaching ecological effects and could even generate a positive feedback with climate change through increasing greenhouse gas accumulation (e.g., Kurz et al. 2008, Mooney et al. 2009). In addition to large population sizes, these species often have relatively wide distributions. Moreover, many of these species, e.g., trees, have long generation lengths and thus will be unable to disperse or adapt quickly enough given predicted rates of climate change per generation (Aitken et al. 2008, Mooney et al. 2009). AGF for foundation species should attempt to increase the frequency of climate-adapted alleles to facilitate adaptation over generations (**Figure 1**).

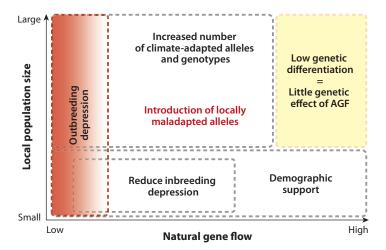


Figure 1

Positive and negative effects of assisted gene flow (AGF) vary with historical levels of gene flow between source and recipient populations and with the size of the recipient population. Each box on this graph indicates a parameter combination for which certain genetic or demographic forces are important. The red box indicates that the risk of negative effects of outbreeding depression likely outweighs the potential positive effects of increased adaptive capacity, the white boxes indicate that positive effects likely outweigh negative effects, and the yellow box indicates lower-priority situations for AGF for which high natural gene flow likely provides sufficient variation for evolutionary rescue.

Resource-Production Populations

Economically valuable native species that produce resources harvested by people or consumed by livestock may also be candidates for AGF. (These may also be foundation species.) These species include forest trees that produce timber, fiber, and fuel; woody plants that produce fruit crops; forage and grassland species used for livestock grazing; and some fish. Unlike most wild species, managed species (e.g., forest trees, native grasses, and some fish species) often have wellestablished systems for the collection or production of propagules, the cultivation of individuals, and the establishment of those individuals in ecosystems. Plant species may also have guidelines for seed transfer, usually emphasizing the use of local seed (Morgenstern 1996, McKay et al. 2005). AGF for resource-production populations should seek primarily to increase fitness and productivity in current and future generations through introducing preadapted genotypes and increasing genetic variation for climate adaptation (Figure 1).

Small and Declining Populations

Although much of this review focuses on foundation and resource-production species with large populations, we briefly consider implications of AGF for small and declining populations. Populations with small effective population sizes are expected to be less able to adapt quickly to environmental changes than large populations because of inbreeding depression (Charlesworth & Willis 2009) and a lack of standing genetic variation (Weber & Diggins 1990, Frankham 2005, Willi et al. 2006). They are also less likely to have been locally adapted prior to anthropogenic climate change (Willi et al. 2006, Leimu & Fischer 2008) and are more likely to have fragmented distributions and lower rates of contemporary gene flow (Leimu et al. 2010). AGF is equivalent to genetic rescue for small populations that are not locally adapted to climate, and these populations may benefit substantially from increased genetic diversity and decreased inbreeding depression

increase in population fitness due to alleviating inbreeding depression and increasing genetic

(Tallmon et al. 2004, Byrne et al. 2011, Miller et al. 2012). If populations are locally adapted to climate, however, AGF will also provide infusions of preadapted alleles and phenotypes for new climates, which may increase population viability. AGF and genetic rescue differ primarily in terms of source population environments: Source populations for genetic rescue are usually selected to match historical environments between source and recipient populations (Frankham et al. 2011), whereas source populations for AGF ideally have historical climates similar to the current or near-future climates of recipient populations while considering longer-term climate change dynamics. AGF for small populations will attempt to increase population size in order to increase genetic diversity and fitness, reduce inbreeding depression, and reduce risk of extirpation due to demographic stochasticity or negative population growth rates (Figure 1).

Evolutionary rescue: reversal of the demographic decline of a population through adaptation to new environmental conditions

EFFECTS OF ASSISTED GENE FLOW ON EVOLUTIONARY AND ECOLOGICAL RESPONSES TO CLIMATE CHANGE

AGF needs to be evaluated against the capacity for natural populations to respond sufficiently to ensure population persistence or productivity in future climates without intervention. In this section, we review the factors influencing whether adaptive responses will be sufficient for genetic rescue of populations, how phenotypic plasticity and gene flow affect evolutionary responses to climate change, and how AGF differs from and will interact with these evolutionary processes.

Adaptation, Evolutionary Rescue, and Assisted Gene Flow

An important environmental change may cause populations to experience reduced fitness, increased mortality, or decreased fecundity, leading to negative population growth in the new environment (Bell & Gonzalez 2009, Bell 2013, Gonzalez & Bell 2013). Population size may decline after the environmental change, leaving fewer and fewer individuals in subsequent generations to supply the genetic variation needed for adaptation to the new environment. If the population size recovers due to evolution that results in a positive growth rate in the new conditions before the population goes extinct, a phenomenon known as evolutionary rescue has occurred. Whether evolutionary rescue occurs before a population is extirpated depends on the initial population size, the amount of genetic variation, the extent of gene flow, and the degree to which new stresses reduce the absolute fitness of the population below one (i.e., how far a population's growth rate falls relative to its replacement rate) (Lynch & Lande 1993, Orr & Unckless 2008, Bell 2013, Gonzalez & Bell 2013, Martin et al. 2013).

Can we predict which populations are likely to adapt quickly to climate change and undergo evolutionary rescue without AGF? Small populations are less likely to experience evolutionary rescue than are large populations because their small size makes them more likely to be extirpated prior to adaptation and because they likely lack the genetic diversity needed to fuel adaptation (Willi et al. 2006). Large populations with high levels of genetic diversity, such as widespread foundation species or resource-production populations, may persist because they are more likely to have adequate genetic diversity and sufficient time to adapt. Despite these advantages, large populations will still suffer from a demographic decline with reduced fitness, resulting in reduced population size in the short term in the absence of AGF. Moreover, long-lived species such as forest trees will experience greater stress per generation. Thus, productivity, carbon sequestration, and levels of ecosystem services produced are likely to be lower than they would have been prior to climate change (Bonan 2008, Mooney et al. 2009). Populations in topographically variable regions may be more able to respond to climate change in comparison with those in more homogeneous landscapes because (a) they may be able to migrate relatively short distances to track climate (Loarie



et al. 2009), and (b) they may have more genetic diversity owing to gene flow from differently adapted populations (Yeaman & Jarvis 2006). For species with an abundant center distribution (those for which the highest population densities are in the center of the species range), gene flow may have very different effects on population fitness in a warming climate. Leading edge populations may benefit from gene flow from core populations, whereas gene flow from core to rear edge populations may exacerbate maladaptation and hasten extirpation (Davis & Shaw 2001) (see **Supplemental Text** and **Supplemental Figure 1** by following the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**). AGF can be designed to accelerate adaptation and to avoid worsening maladaptation through translocations in only the favorable direction (e.g., poleward translocations in a warming environment).

In recent decades, researchers have observed many phenotypic changes for some species, particularly in phenological traits such as the timing of flowering or the initiation of growth in plants and the timing of migration, reproduction, or hibernation in animals (Parmesan 2006). However, it is challenging to determine whether such changes in natural populations result from phenotypic plasticity, adaptation, or dispersal among populations (Gienapp et al. 2008, Anderson et al. 2012, Franks & Hoffmann 2012, Hansen et al. 2012). Few studies have conclusively shown that phenotypic changes associated with climate change have resulted from adaptation (Balanya et al. 2006, Gienapp et al. 2008, Visser 2008, Hansen et al. 2012). A lack of adaptive responses, if not just an artifact of low statistical power, may be attributed to several causes, including (a) countergradient variation, i.e., opposing genetic and phenotypic correlations with environment; (b) a lack of genetic variation; (c) inbreeding; (d) antagonistic genetic correlations; or (e) gene flow (Gienapp et al. 2008). If historical local adaptation to climate has occurred, AGF can help ameliorate each of these limitations.

Model species and artificial environments have been used to test the limits of adaptation to environmental changes, and studies using these species and environments have demonstrated adaptive responses. For example, scientists have tested the limits of evolutionary rescue by monitoring yeast populations after increasing the salinity of their environments (Bell & Gonzalez 2009, Gonzalez & Bell 2013). Studies showing adaptive responses to climate change in natural populations have focused on species with relatively short generation lengths and therefore more ability to adapt quickly. For example, Reale and coworkers (2003) observed that the mean date of birth in a pedigreed red squirrel population advanced by six days over a 10-year period, and approximately 10% of this shift had a genetic basis. Franks et al. (2007) conducted a resurrection study in which they collected seeds from wet and dry populations of the annual plant field mustard (Brassica rapa) before and after a 5-year drought. By growing these accessions together in a common garden, these researchers detected an advance in the flowering date in the wet population of nearly 9 days but only a slight advance in that of the dry population (~2 days). Nevo et al. (2012) also conducted a resurrection study, using seeds from wild wheat (Triticum disoccoides) and barley (Hordeum spontaneum) populations collected in Israel 28 years apart. Their study showed that flowering time advanced by an average of \sim 10 days in the two species over this period.

Atkins & Travis (2010) simulated plant populations spanning an environmental gradient across a two-dimensional landscape and investigated the effects of local adaptation on range dynamics over a period of warming. They found that extinction risk increased with shorter pollen dispersal, a longer period of climate change, and a broader landscape. Counterintuitively, perhaps, they also found that a greater extinction risk was associated with a lower probability of extrinsic mortality because colder-adapted genotypes could persist longer once established and, through prior occupancy, prevent the establishment of warmer-adapted genotypes with higher fitness. Many of the scenarios they modeled led to the fragmentation of previously continuous ranges, further decreasing gene flow across the species range. Although AGF can be used to increase dispersal and

to establish preadapted genotypes when open niches are available (e.g., after a natural disturbance or harvest), in the absence of a disturbance, the persistence of somewhat maladapted individuals may reduce available niche space.

AGF affects rates of adaptation and the probability of evolutionary rescue in two ways. First, it immediately increases the frequency of genotypes adapted to new climates in the generation when individuals are first introduced. This change in genotype frequency should increase the survival, fecundity, and productivity of individuals if climate is the primary driver of local adaptation. It should also dampen the negative demographic effects of new selection pressures and reduce the probability of population extirpation for small populations. Second, AGF introduces or increases the frequency of preadapted alleles for new climatic conditions and increases genetic variation on which selection can act. The change in allele frequency from AGF should increase the rate of adaptation to new conditions and shorten the period of negative population growth. However, if populations are already locally adapted to nontargeted environmental factors, then AGF may reduce fitness, exacerbate negative population growth, reduce productivity, and increase the probability of extirpation of small populations, as discussed below.

Phenotypic plasticity: ability of a genotype to produce different phenotypes under different environmental conditions

Assisted Gene Flow Differs from Natural Gene Flow

How will the effects of AGF on populations differ from the effects of natural gene flow? First, AGF has an unlimited potential geographic scale, which will be greater than that of natural gene flow for many species. Second, AGF is directional and involves moving alleles that are preadapted for current or future climates into targeted populations, whereas natural gene flow can occur in any direction and may either lead to adaptation or exacerbate maladaptation. Finally, natural gene flow often has a leptokurtic distribution from the source population, whereas AGF can have any distribution desired. Combined, these features imply that AGF can, when used with sufficient information, maximize the benefits of gene flow in a particular setting while minimizing its costs.

Assisted Gene Flow and Phenotypic Plasticity

Phenotypic plasticity can buffer the negative effects of climate change, and the evolution of plasticity can contribute to adaptive responses and population persistence (Chevin & Lande 2010, Chevin et al. 2010). Under what conditions will phenotypic plasticity render AGF unnecessary? Chevin & Lande (2010) showed that plasticity, especially if it is initially adaptive, can greatly increase the ability of a population to survive environmental change. In fact, a meta-analysis has shown that most responses to climate change result from phenotypic plasticity, not new adaptation (Gienapp et al. 2008). Epigenetic changes associated with parental environments can also cause intergenerational changes in plasticity (Franks & Hoffmann 2012).

The extent to which phenotypic plasticity promotes population persistence and fitness in a changing climate also depends on the reliability of the environmental cues that allow phenotypic responses to match environmental conditions and the extent of environmental stochasticity (Reed et al. 2010). In some circumstances, phenotypic plasticity will enhance the probability of population persistence. In others, however, particularly those with high environmental variation and low cue reliability, plasticity could increase extinction probability. For example, plastic responses to environmental cues that have previously evolved in one locality could be unreliable in a new environment (e.g., Soolanayakanahally et al. 2013). In addition, plasticity can also dampen genetic responses to climate change by providing rapid phenotypic responses (Crispo 2008). Some important behaviors and life-cycle events are timed in response to temperature cues, e.g., the initiation of growth or flowering in many plants in the spring requires heat-sum accumulation.

Outbreeding depression:

reduction in fitness resulting from mating individuals from different populations These traits will likely respond to climate warming primarily through phenotypic plasticity rather than through genetic adaptation. Conversely, some behavioral and physiological events are triggered by factors that remain stable despite climate change, such as photoperiod. These biological processes may require genetic changes to be adaptive (Bradshaw & Holzapfel 2007, Jackson 2009). In populations that are not locally adapted, spatial or temporal phenotypic variation in situ results from plasticity, and if all populations have equivalent plasticity, then AGF will have little effect on climate change—related outcomes in these populations.

Phenotypic plasticity itself has a genetic basis, and its extent can differ among populations. For example, the mean laying dates of great tit (*Parus major*) populations in both the Netherlands and the United Kingdom have advanced with climate warming in recent decades as a result of phenotypic plasticity. However, compared with the Netherlands population, the UK population has had a greater phenotypic response to the same amount of warming (Husby et al. 2010). As the world warms, climates are also predicted to become more variable (Solomon et al. 2007). Increased phenotypic plasticity may allow populations to tolerate wider climatic fluctuations, and preferentially assisting the movement of individuals from populations with a high degree of plasticity may be desirable in some cases. For example, some populations of lodgepole pine (*Pinus contorta*) have reaction norms that show a wider climatic tolerance than others, and these populations also tend to be among the most productive for forestry (Wang et al. 2006). Choices of source populations for AGF should consider the full spectrum of future projected environments for the target population, although doing so will be difficult given the considerable uncertainty around projections. Moreover, gene flow (whether anthropogenic or natural) introduces genetic variation not only for traits but also for plasticity, meaning that gene flow may facilitate the further evolution of adaptive phenotypic plasticity if new environmental conditions persist over a number of generations.

Effects of Assisted Gene Flow on Colonization

Assisted gene flow as described here focuses on the movement of genotypes within existing species ranges and does not include assisted colonization, i.e., the introduction of a species beyond the leading edge of migration to nucleate a range shift. However, AGF may facilitate the natural expansion of species' ranges by increasing the average fitness of individuals in leading edge populations, thereby resulting in higher fecundity and ultimately in higher dispersal into newly available, climatically suitable habitats (Hu & He 2006). Because marginal populations have less genetic variation than central populations, on average (Eckert et al. 2008), AGF should increase diversity in leading edge populations and is therefore expected to have a positive effect on colonization ability.

THE GENETIC RISKS OF ASSISTED GENE FLOW

As we have seen, AGF has many potential benefits, but it may also have negative consequences, which we outline in the following subsections. The greatest genetic risk associated with AGF is outbreeding depression, but AGF may also disrupt local adaptation to environmental factors other than those climatic factors taken into consideration when designing a strategy.

Outbreeding depression is a reduction in offspring fitness relative to parental types following hybridization between populations (Edmands 2007, Frankham et al. 2011). There are three primary causes of outbreeding depression: chromosomal incompatibilities, epistatic interactions between diverged loci, and local adaptation losses resulting from the introduction of locally maladapted alleles. These mechanisms of outbreeding depression have markedly different implications for AGF, which we discuss below. We also address the potential deleterious consequences

of lineage swamping (the loss of ancestral local genetic variation through replacement by migrant genotypes) that may result from increased gene flow.

Epistatic Incompatibilities

Outbreeding depression may result from chromosomal differences between populations that cause partial or complete sterility (Frankham et al. 2011). Choosing source populations for AGF that differ in chromosome number should be avoided; doing so is relatively straightforward. Unfortunately, more subtle chromosome differences such as inversions may also cause problems in hybrids, although such problems are sometimes caused by the epistatic genic effects discussed below (Rieseberg 2001). The effects of inversions often result from the genetic differences they capture rather than the inversion per se.

Genotypes from different populations may also be incompatible because of deleterious epistatic interactions and the breakup of coadapted gene complexes (Schiffers et al. 2013). Isolated populations can diverge genetically, and sometimes local alleles perform poorly when combined with alleles from other populations. These Dobzhansky-Muller incompatibilities (Dobzhansky 1937, Muller 1940) typically require many generations to develop and are not likely to develop when substantial natural gene flow occurs between populations (Coyne & Orr 1989, Frankham et al. 2011). This intrinsic outbreeding depression is often not seen until the F2 generation of interpopulation hybridization, as F1 individuals have a balanced complement of alleles from each parent. In some cases, the greatest extent of this breakdown can occur in later generations (Fenster & Galloway 2000).

Models can help us understand the magnitude and time frame of outbreeding depression effects. We investigated the relative costs and benefits of AGF through intrinsic outbreeding depression and enhanced local adaptation in a simple simulation model that introduced foreign individuals fixed for novel alleles not previously present in the local population (simulation details are given in the caption for **Figure 2**). We explored the temporal pattern of mean fitness after replacing 5% of the population with individuals carrying locally incompatible gene combinations (**Figure 2***a*). (We also ran similar simulations replacing 20% of the population with foreign individuals, and observed qualitatively similar patterns in all cases; see **Supplemental Figure 2**.) In each case represented here, the decline in mean fitness of F1 hybrids between local and immigrant genotypes is roughly 40%, caused by epistatic interactions within pairs of loci. There was no overdominance in our fitness model, unlike that of Edmands & Timmerman (2003).

Figure 2a shows the decline and rapid partial recovery of mean fitness when the local and immigrant populations differ only by fixed epistatic incompatibilities. Although outbreeding depression can decrease a population's mean fitness, the population recovers relatively rapidly, especially when incompatibilities are due to fewer loci of larger effect. This recovery is much stronger because of the positive linkage disequilibrium between immigrant alleles: Indirect selection on each locus in this case enhances selection against any deleterious immigrant genes. In contrast, when outbreeding depression is caused by many loci of small effect, fitness recovers rapidly while the immigrant alleles are still in linkage disequilibrium with each other, but the rate of recovery slows after the covariance dissipates. Thus, in most situations, outbreeding depression is temporary.

We also wanted to know whether locally beneficial alleles introduced through AGF could improve local mean fitness, even if the introduced individuals also had epistatic incompatibilities with the local population. Figure 2b shows the same range of deleterious epistatic loci as Figure 2a (except for the addition of a new dashed curve that shows the case with no outbreeding depression), but the immigrants in this panel also introduce alleles at five loci that mimic the alleles for climate adaptation targeted by AGF. In these cases, mean fitness drops in early generations because of

Supplemental Material

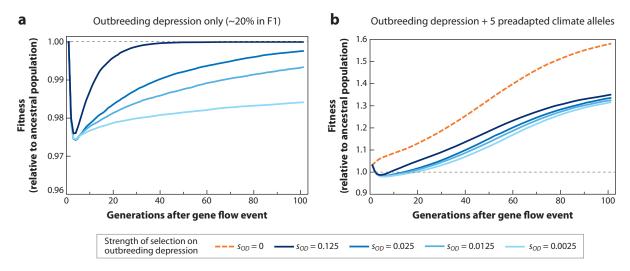


Figure 2

Outbreeding depression may reduce the fitness of a population that receives genetically distinct immigrants, but the effect is temporary. Gray dotted lines represent the initial population mean fitness before immigration. Different curves on each graph represent various numbers of genes causing outbreeding depression, each yielding in total a ~40% reduction in F1 fitness [2 pairs of loci for a strength of selection on outbreeding depression (s_{OD}) = 0.125, 10 pairs for s_{OD} = 0.025, 20 pairs for s_{OD} = 0.0125, 100 for s_{OD} = 0.0025; s_{OD} defined below]. (a) Outbreeding depression with no locally beneficial alleles. (b) Fitness change when immigrants carry locally beneficial alleles mixed with other genes causing epistatic incompatibilities (except for the case when $s_{\rm OD}=0$). Note the difference in scale between the two graphs. In each case, the relative fitness reported is standardized to the initial population mean fitness before immigration (gray dotted lines), so numbers greater than one represent an improvement in the mean fitness of the population after immigration. These simulations were run in *Mathematica* with a constant population size of N = 1,000 individuals with biallelic loci. All loci contributing to outbreeding depression interacted via purely additive-by-additive epistasis with one other locus; specifically, both local and foreign ancestral double homozygotes had relative fitness that was increased by sop, whereas the other two double homozygotes had relative fitness that was decreased by -sop. All single or double heterozygotes had a relative fitness of one, and all fitness effects were enacted in juvenile survival. Individual fitness was determined multiplicatively when combining the effects of different pairs of epistatically interacting loci. Each simulation in panel a began with an ancestral population that was fixed at all loci; 5% of the population was replaced by migrant individuals homozygous for the alternative alleles, and no gene flow occurred thereafter. The simulations in panel b are similar, but the introduced individuals are now homozygous at five loci for novel alleles that are locally beneficial with a 5% advantage under current conditions. These beneficial alleles interact multiplicatively both within and among loci. All genes were placed randomly onto a genetic map with 10 chromosomes of 1 Morgan in length. Each graph represents the means of 1,000 replicates.

outbreeding depression. However, fitness quickly recovers (within a few generations) and evolves to higher values than observed before the introduction of immigrants because the population incorporates the new beneficial alleles while selecting out the alleles that interact deleteriously. Thus, selection after introduction acts to minimize the effects of deleterious alleles and boost the effects of beneficial alleles. When AGF introduces sufficient alleles for climate adaptation, the net benefit to mean fitness can be large, even with substantial outbreeding depression. Minor outbreeding depression should not prevent effective management via AGF unless the populations are so small that immediate extinction is a risk.

Local Adaptation to Additional Environmental Factors

AGF requires that populations be genetically differentiated for alleles that affect fitness in different climates. The conditions that allow local adaptation for aspects of climate may also allow local

adaptation along other environmental axes, and the optima for these other environmental factors may not change over space in the same way as the climate optima do. As a result, individuals that are well adapted for the new climate conditions anticipated by managers may simultaneously be maladapted for other local environmental variables. For example, plant populations may be adapted to nonclimatic abiotic or biotic environmental factors, such as soil type (Wright et al. 2006), local mycorrhizal communities (Kranabetter et al. 2012), photoperiod (Jackson 2009), or the presence of certain pests or pathogens (Van der Putten 2012). Some of these environmental factors may covary with the target climate variables, but others do not. Adaptation to edaphic factors may outweigh adaptation to climate in the case of remediation and restoration of some highly disturbed environments, e.g., mine tailings. When local adaptation does not correlate with the targeted climate variables, the advantages of AGF are counterbalanced by a reduction in fitness caused by introducing genes that are maladapted to other environmental factors (Schiffers et al. 2013).

Many temperate, boreal, and Arctic species, both plant and animal, are adapted to photoperiod; day- or night-length triggers seasonal biological responses including growth cessation, dormancy, and flowering time in plants (Jackson 2009) and reproduction, migration, and hibernation in animals (Bradshaw & Holzapfel 2007). As photoperiod is stable but climatic regimes are changing, novel combinations of temperature and moisture with photoperiod may arise, and maladaptation may result. AGF over large latitudinal distances, especially at high latitudes, may confuse photoperiodic responses and be confounded by thermal responses (e.g., Soolanayakanahally et al. 2013), whereas AGF across elevational or longitudinal climatic gradients is less likely to create problems with adaptation to photoperiod.

In contrast, some environmental challenges may also shift with climate, especially cooccurring biotic factors. Many insect species show range shifts as a result of recent warming (Robinet & Roques 2010). For example, an insect herbivore may shift its range as low-temperature limitations to its life cycle decrease. Thus, the insect may occupy more of a host species range over time, and some naïve host populations could now be exposed to it [e.g., lodgepole pine populations in colder environments that have recently experienced the *Dendroctonus ponderosae* (mountain pine beetle) expansion (Cudmore et al. 2010)].

Genetic Swamping and Loss of Lineages

Another potential side effect of AGF, in addition to outbreeding depression and maladaptation to other environmental factors, is the loss of native genotypes. The introduction of nonlocal genotypes could result in the swamping of local genotypes and a loss of genetic lineages (Rhymer & Simberloff 1996, Hufford & Mazer 2003). If too many individuals are introduced or if introduced individuals have high relative fitness and reproductive success, local genotypes can be evolutionarily replaced. In most cases, the number of genotypes introduced through AGF will constitute a small fraction of the total population, so numerical swamping can be avoided in the short term by introducing only a limited number of individuals. The literature on genetic rescue provides some guidance on this topic. Hedrick (1995) recommended using 20% gene flow in the first generation and 2–4% gene flow in subsequent generations for genetic rescue of the critically endangered and highly inbred Florida panther (*Felis concolor* ssp. *coryi*) without swamping alleles unique to that subspecies. He suggested that these levels of gene flow would allow for the maintenance of Florida panther alleles in the face of Texas cougar (*Felis concolor* ssp. *stanleyana*) translocations.

If introduced genotypes have higher fitness, on average, than local genotypes in new climates, and if introduced alleles increase in frequency through selection, it will be hard to distinguish a positive outcome (successful evolutionary rescue) from a potentially negative one (loss of ancestral genetic variation in the recipient population). However, the difference between these

MANY TREE SPECIES ARE GOOD CANDIDATES FOR ASSISTED GENE FLOW

Many widespread temperate and boreal tree species fit the criteria for AGF well (Figure 2). Trees are foundation species in many ecosystems (Ellison et al. 2005); produce wood, fuel, and fiber; and are key components of the global carbon cycle (Bonan 2008). Most are wind pollinated and have relatively high levels of gene flow (Kremer et al. 2012); therefore, they are at low risk of strong outbreeding depression. Many species show moderate to strong local adaptation to climate (Savolainen et al. 2007; Alberto et al. 2013). Their long generation lengths will make it difficult for populations to adapt to climate change in situ (Aitken et al. 2008). AGF has the potential to increase mean fitness in tree populations; doing so will increase forest health, carbon sequestration, and wood productivity and will also provide economic benefits. For example, \sim 149 million cubic meters of wood were harvested in 2011 in Canada, contributing ~CA\$24 billion to Canada's gross domestic product (Can. For. Serv. 2012). If forest productivity declines by 10-35% owing to maladaptation of populations to new climates, as has been predicted for Pinus contorta (Wang et al. 2006), economic benefits and carbon sequestration will decline proportionally. Systems are well established for seed collection and seedling production for reforestation for many species, making AGF straightforward to implement. Multisite, multipopulation common garden experiments guide seed source selection. Over the past decade, over 500 million tree seedlings have been planted annually in Canada (Can. For. Serv. 2013), and the incremental costs of AGF over conventional planting of local seed sources are low. AGF is already underway in British Columbia (O'Neill et al. 2008).

outcomes may be more philosophical than biological because swamping from a limited bout of gene flow implies that the remaining population will be a better fit to its new environment than it would have been without AGF. AGF can also reduce the loss of genetic diversity and lineages by migrating individuals from divergent rear edge populations at high risk of extirpation (Hampe & Petit 2005, Alberto et al. 2013) into populations that have a higher probability of persisting.

RECOMMENDATIONS FOR ASSISTED GENE FLOW

Assessing the relative genetic risks and benefits of AGF for a species requires weighing the extent of that species' local adaptation to climate against the probabilities of outbreeding depression, maladaptation to other environmental factors, and genetic swamping (Figure 1). Species that may experience very strong outbreeding depression are poor candidates for AGF because the genetic risks outweigh the potential benefits. Species with strong historical local adaptation to climate will likely benefit from AGF. Assisting gene flow for species with high levels of historical gene flow and with no local adaptation to climate will waste resources and is unlikely to benefit these species. Importantly, our simulations suggest that the costs of outbreeding depression are unlikely to outweigh the benefits of AGF in reducing maladaptation caused by climate change, except for species in imminent danger of extinction. AGF has the potential to increase the fitness and adaptive capacity of populations of foundation and resource-production species (e.g., see sidebar, Many Tree Species Are Good Candidates for Assisted Gene Flow). It can also ameliorate inbreeding depression and provide demographic support for small populations at risk of extinction. In the following subsections, we discuss the information required and the criteria managers should consider to make informed decisions about AGF for a given species.

Detecting Local Adaptation to Climate and Other Factors

The potential risks and benefits of AGF depend on the degree of preexisting local adaptation to climate. Unfortunately, the relative importance of local adaptation to specific climate factors and

that of local adaptation to nonclimate variables are not yet known for many species. AGF should be considered only in cases for which there is cause to believe that historical adaptation to changing climate variables is strong relative to other sorts of local adaptation. The gold standard for detecting local adaptation remains the reciprocal transplant experiment, in which researchers measure the fitnesses of genotypes planted in common gardens at local and distant sites (Kawecki & Ebert 2004, Leimu & Fischer 2008, Hereford 2009b). Improved performance of warm-adapted foreign populations planted into warming environments provides strong support for the potential benefits of AGF, although measuring the costs of outbreeding depression requires at least a second generation.

Experiments in controlled environments (such as growth chambers or greenhouses) can also be used to test for genotype-by-environment interactions among temperature or moisture treatments. Differences among population responses to these experimental treatments provide evidence of local adaptation to climate. Such experiments can often be conducted on a shorter timescale than can field-based reciprocal transplant experiments, and they require fewer resources (e.g., Mimura & Aitken 2010).

Other classic approaches to look for local adaptation are less useful for this purpose. For example, Q_{ST} - F_{ST} comparisons (Spitze 1993, Whitlock 2008) may indicate local adaptation to some features of the environment, but they cannot readily be used to show adaptation to a particular environmental feature such as climate. However, if the traits with the highest Q_{ST} are associated with thermal or drought adaptation, this approach could be informative.

Historical patterns of adaptation to local climate conditions can be inferred through associations between past environment patterns and either phenotypic variation or candidate alleles. The proliferation of high-throughput DNA sequencing and associated genomic tools allows researchers to test genetic polymorphisms for statistical associations among local allele frequencies and climate or other factors (Schoville et al. 2012). Allele-environment associations can be used to detect single nucleotide or other polymorphisms associated with climatic or other environmental variables (e.g., Coop et al. 2010), much as analysis of phenotypic clines along environmental gradients can reflect local adaptation (Endler 1977). However, genome-wide scans for evidence of local adaptation are feasible for relatively few species. Candidate gene approaches to testing markers for signatures of local adaptation require fewer resources. Studies of model organisms have identified some candidate genes involved in adaptive differences among populations in multiple species (e.g., genes that mediate phenology, photoperiod detection, drought hardiness, and response to temperature extremes or other stresses) (Franks & Hoffmann 2012). Climatic clines in single nucleotide polymorphisms of candidate genes provide an indication of local adaptation but may underestimate its extent for complex genetic traits (Le Corre & Kremer 2012).

Weighing Risks of Outbreeding Depression Against Benefits of Assisted Gene Flow

Severe outbreeding depression remains a substantial genetic risk for AGF if mating individuals come from long-isolated populations (**Figure 1**). However, for many species, our simulations and the literature suggest that outbreeding depression is unlikely to outweigh maladaptation due to climate change, especially after a few generations. We agree with Frankham and colleagues (2011), who suggested that the risks of outbreeding depression have been overemphasized in the conservation biology literature. They developed a decision tree for genetic rescue and suggested that the probability of outbreeding depression is high if the combined populations: (*a*) are from different species, (*b*) have fixed chromosomal differences, (*c*) have had no gene flow for 500 years, or (*d*) occupy different environments. We agree with three of these criteria regarding AGF. AGF should be used with great caution when a recently derived sister species is present in the

new location because interspecific hybridization can be destructive (Rhymer & Simberloff 1996). Similarly, AGF should not be used between chromosomal races or long-isolated populations, although the definition of long-isolated should be based on genetic estimates of population differentiation (such as estimates used to define evolutionarily significant units; see Moritz 1999), not on an arbitrary length of time regardless of a species' generation length (Allendorf et al. 2013). Researchers can use genetic markers to reveal cryptic species, chromosomal races, or long-isolated populations between which AGF should not be used.

However, effective AGF will necessarily violate Frankham et al.'s (2011) fourth criterion for genetic rescue: that source and recipient populations occupy similar environments. This criterion was intended to prevent outbreeding depression due to adaptive differentiation between populations. Outbreeding depression due to extrinsic maladaptation to the local climate is environment dependent and is less likely to occur when the historical environment of the source population for AGF is similar to the contemporary environment of the focal population. If AGF effectively matches recent pre-Anthropocene source climates with contemporary or near-future recipient environments, then translocated individuals should be well adapted, and their hybrid offspring with local individuals should be better adapted to climate than are local individuals. However, if this genotype-environment matching does not occur, either owing to differences between projected and actual climate change trajectories or because populations are locally adapted to non-climatic factors, then natural selection should remove maladapted individuals from the recipient population.

The genetic risks of AGF are proportional to the fraction of the population replaced, but the long-term benefits of AGF depend on only the introduction of an adequate number of individuals that carry useful new variation. Therefore, we suggest caution in choosing the magnitude of the AGF effort. Introduced fractions of 5–20% may ensure suitable genetic variation, and the deleterious effects of outbreeding depression are likely to be manageable at that level (**Figure 2**, **Supplemental Figure 2**). However, a larger migration fraction may be necessary to maintain productivity if AGF is intended for short-term augmentation of resource-production populations in which individuals are harvested and replaced each generation.

Managing the Uncertainty of Future Climates

Despite strong evidence of rapid, anthropogenic climate change (Solomon et al. 2007), future climate projections are highly uncertain. The amount of climatic change over the next century relative to current model-based projections will depend on the extent and success of human efforts to reduce greenhouse gas emissions, the effects of warming on carbon storage in terrestrial and aquatic ecosystems, and the accuracy of fine-scale projections from global to regional and local effects (Solomon et al. 2007, Deser et al. 2012). Climate variability is also projected to increase with climate change (Seager et al. 2012), and novel combinations of climatic factors may develop. AGF will likely increase adaptive genetic variation within populations and should thereby increase the ability of those populations to adapt to a range of future climatic conditions. However, given the range of possible future climates, selecting a single source population for AGF may be risky. Genetic variability could be further increased by composite provenancing (Broadhurst et al. 2008, Weeks et al. 2011), i.e., sourcing translocated individuals from several populations with somewhat different climates spanning the range of future projections rather than from a single environment. The buffering effect of using multiple populations, called the portfolio effect, has been illustrated for Bristol Bay salmon in Alaska, where different populations fluctuate in productivity over years, but the overall productivity of the aquatic system remains high (Schindler et al. 2010). Potential strategies for composite provenancing include choosing the proportion of individuals from a

Supplemental Material

particular climate used for AGF on the basis of the probability of that climate occurring in a given location in the near future. Weeks et al. (2011) proposed weighting source populations on the basis of their proximity to the target population, mimicking a leptokurtic distribution typical of natural gene flow patterns. When novel climates (new combinations of climatic variables) are projected, composite provenancing could combine source populations chosen on the basis of different climatic variables. All of these strategies will benefit from the portfolio effect.

AGF has the potential to facilitate adaptation to rapidly changing climates for some key species. For it to be effective, the potential for increased fitness resulting from alleles that are adapted to future climates must be greater than the costs of outbreeding depression, other environmental drivers of local adaptation, and the management itself. We believe that this will generally be true for intraspecific moves in species that depend critically on climate. Research on the consequences of AGF is still in its early stages; to have greater confidence in management decisions, we need more knowledge. We need better information about what makes for an optimal source (provenance) of migrants to maximize benefits and minimize risks in an uncertain future. How far should individuals be moved? How many populations should be used? How far in advance should we anticipate the change in the environment when we select sources? Importantly, the appropriate solution will depend on the specifics of the species' natural history and the environments it occupies.

SUMMARY POINTS AND RECOMMENDATIONS FOR ASSISTED GENE FLOW

- 1. Because resources are limited, relatively few species can be targets for AGF. Species should be prioritized strategically for assisted migration on the basis of life-history traits, ecological roles, resource-production value, and conservation status.
- 2. The potential degree of improvement in local adaptation resulting from AGF should be weighed against the probability of outbreeding depression. The relative strength of these factors requires further study, although current work suggests that the long-term effects of outbreeding depression will be small.
- 3. Over time, selection will eliminate extrinsic outbreeding depression due to adaptive differences between populations. It should also resolve mild intrinsic outbreeding depression due to epistasis when populations have been exchanging migrants.
- 4. AGF should not be used between widely diverged, long-isolated populations, between subspecies, or between chromosomal races, as intrinsic outbreeding depression due to epistasis and breakup of coadapted gene complexes is likely (Figure 1). Assisting gene flow between populations that are connected by high levels of gene flow and that do not show local adaptation will waste resources.
- 5. In situations in which AGF is indicated (Figure 1), reducing risk and managing uncertainty can be achieved through the portfolio effect. This entails assisting gene flow of individuals from multiple provenances with climates spanning the range of climate change projections for the recipient provenance.
- 6. Individuals moved through AGF should constitute a minority fraction of the recipient population to minimize the risks of the technique while maintaining its benefits.
- 7. Field experiments should be established and monitored to validate fitness or productivity estimates for local versus nonlocal genotypes and to allow refinement of AGF strategies over time as climates warm.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Florence DéBarre, Sarah Bisbing, Carol Horvitz, Jeremy Draghi, Kimberly Gilbert, Holly Kindsvater, Katie Lotterhos, Sally Otto, Loren Rieseberg, Susannah Tysor, Elizabeth Wolkovich, Jack Woods, and Sam Yeaman for thoughtful comments, suggestions, and discussions on this manuscript. This paper resulted from the AdapTree project, funded by Genome Canada, Genome British Columbia, the Forest Genetics Council of British Columbia, and Alberta Innovates Bio Solutions (funding to S.N.A. and M.C.W.). The work was also supported by individual Natural Sciences and Engineering Research Council of Canada Discovery Grants to S.N.A. and M.C.W.

LITERATURE CITED

- Aardema ML, Scriber JM, Hellmann JJ. 2011. Considering local adaptation in issues of lepidopteran conservation—a review and recommendations. Am. Midl. Nat. 165:294–303
- Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol. Appl. 1:95–111
- Alberto FJ, Aitken SN, Alía R, González-Martínez SC, Hänninen H, et al. 2013. Potential for evolutionary responses to climate change—evidence from tree populations. *Glob. Change Biol.* 19:1645–61
- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manag. 259:660–84
- Allendorf FW, Luikart G, Aitken SN. 2013. Conservation and the Genetics of Populations. Oxford: Wiley-Blackwell
- Anderson JT, Panetta AM, Mitchell-Olds T. 2012. Evolutionary and ecological responses to anthropogenic climate change. Plant Phys. 160:1728–40
- Atkins KE, Travis JMJ. 2010. Local adaptation and the evolution of species' ranges under climate change. J. Theor. Biol. 266:449–57
- Balanya J, Oller JM, Huey RB, Gilchrist GW, Serra L. 2006. Global genetic change tracks global climate warming in *Drosophila subobscura*. Science 313:1773–75
- Bell G. 2013. Evolutionary rescue and the limits of adaptation. Philos. Trans. R. Soc. B 368:20120080
- Bell G, Gonzalez A. 2009. Evolutionary rescue can prevent extinction following environmental change. Ecol. Lett. 12:942–48
- Blanquart F, Gandon S, Nuismer SL. 2012. The effects of migration and drift on local adaptation to a heterogeneous environment. *J. Evol. Biol.* 25:1351–63
- Bonan GB. 2008. Forests and climate change: forcings, feedbacks and the climate benefits of forests. *Science* 320:1444–49
- Bradshaw WE, Holzapfel CM. 2007. Evolution of animal photoperiodism. Annu. Rev. Ecol. Evol. Syst. 38:1–25Broadhurst LM, Lowe A, Coates DJ, Cunningham SA, McDonald M, et al. 2008. Seed supply for broadscale restoration: maximizing evolutionary potential. Evol. Appl. 1:587–97
- Byrne M, Stone L, Millar MA. 2011. Assessing genetic risk in revegetation. 7. Appl. Ecol. 48:1365-73
- Can. For. Serv. 2012a. Statistical data: overview. Nat. Resour. Can., retrieved April 1, 2012. http://cfs.nrcan.gc.ca/statsprofile/overview/ca
- Can. For. Serv. 2013. National forestry database. Can. Counc. Forest. Minist., updated May 28, 2013. http://nfdp.ccfm.org/data/compendium/html/comp_68e.html
- Charlesworth D, Willis JH. 2009. Fundamental concepts in genetics: the genetics of inbreeding depression. Nat. Rev. Genet. 10:783–96

- Chevin L-M, Lande R. 2010. When do adaptive plasticity and genetic evolution prevent extinction of a density-regulated population? Evolution 64:1143–50
- Chevin L-M, Lande R, Mace GM. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. PLoS Biol. 8:e1000357
- Coop G, Witonsky D, Di Rienzo A, Pritchard JK. 2010. Using environmental correlations to identify loci underlying local adaptation. Genetics 185:1411–23
- Coyne JA, Orr HA. 1989. Patterns of speciation in Drosophila. Evolution 43:362-81
- Crispo E. 2008. Modifying effects of phenotypic plasticity on interactions among natural selection, adaptation and gene flow. J. Evol. Biol. 21:1460–69
- Cudmore TJ, Bjorklund N, Carroll AL, Lindgren BS. 2010. Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naive host tree populations. J. Appl. Ecol. 47:1036–43
- Davis MB, Shaw RG. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* 292:673–79
- Deser C, Knutti R, Solomon S, Phillips AS. 2012. Communication of the role of natural variability in future North American climate. Nat. Clim. Change 2:775–79
- Dobzhansky T. 1937. Genetics and the Origin of Species. New York: Columbia Univ. Press
- Eckert CG, Samis KE, Lougheed SC. 2008. Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. *Mol. Ecol.* 17:1170–88
- Edmands S. 2007. Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. *Mol. Ecol.* 16:463–75
- Edmands S, Timmerman CC. 2003. Modeling factors affecting the severity of outbreeding depression. *Conserv. Biol.* 17:883–92
- Eliason EJ, Clark TD, Hague MJ, Hanson LM, Gallagher ZS, et al. 2011. Differences in thermal tolerance among sockeye salmon populations. *Science* 332:109–12
- Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 3:479–86
- Endler JA. 1977. Geographic Variation, Speciation, and Clines. Princeton, NJ: Princeton Univ. Press. 246 pp.
- Fenster CB, Galloway LF. 2000. Inbreeding and outbreeding depression in natural populations of Chamaecrista fasciculata (Fabaceae). Conserv. Biol. 14:1406–12
- Fournier-Level A, Korte A, Cooper MD, Nordborg M, Schmitt J, Wilczek AM. 2011. A map of local adaptation in *Arabidopsis thaliana*. *Science* 333:86–89
- Frankham R. 2005. Genetics and extinction. Biol. Conserv. 126:131-40
- Frankham R, Ballou JD, Eldridge MDB, Lacy RC, Ralls K, et al. 2011. Predicting the probability of outbreeding depression. *Conserv. Biol.* 25:465–75
- Franks SJ, Hoffmann AA. 2012. Genetics of climate change adaptation. Annu. Rev. Genet. 46:185–208
- Franks SJ, Sim S, Weis AE. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proc. Natl. Acad. Sci. USA* 104:1278–82
- Gienapp P, Teplitsky C, Alho JS, Mills JA, Merila J. 2008. Climate change and evolution: disentangling environmental and genetic responses. Mol. Ecol. 17:167–78
- Gomulkiewicz R, Holt RD, Barfield M. 1999. The effects of density dependence and immigration on local adaptation and niche evolution in a black-hole sink environment. *Theor. Pop. Biol.* 55:283–96
- Gomulkiewicz R, Shaw RG. 2013. Evolutionary rescue beyond the models. *Philos. Trans. R. Soc. B* 368:20120093
- Gonzalez A, Bell G. 2013. Evolutionary rescue and adaptation to abrupt environmental change depends upon the history of stress. *Philos. Trans. R. Soc. B* 368:20120079
- Hampe A, Petit RJ. 2005. Conserving biodiversity under climate change: The rear edge matters. Ecol. Lett. 8:461–67
- Hansen MM, Olivieri I, Waller DM, Nielsen EE, Ge MWG. 2012. Monitoring adaptive genetic responses to environmental change. Mol. Ecol. 21:1311–29
- Hedrick PW. 1995. Gene flow and genetic restoration: the Florida panther as a case-study. *Conserv. Biol.* 9:996–1007

- Hereford J. 2009a. Data from: A quantitative survey of local adaptation and fitness trade-offs. *Dryad Digit. Repos.* http://datadryad.org/resource/doi:10.5061/dryad.315
- Hereford J. 2009b. A quantitative survey of local adaptation and fitness trade-offs. Am. Nat. 173:579-88
- Hewitt N, Klenk N, Smith AL, Bazely DR, Yan N, et al. 2011. Taking stock of the assisted migration debate. *Biol. Conserv.* 144:2560–72
- Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, et al. 2008. Assisted colonization and rapid climate change. *Science* 321:345–46
- Hoffmann AA, Anderson A, Hallas R. 2002. Opposing clines for high and low temperature resistance in Drosophila melanogaster. Ecol. Lett. 5:614–18
- Hu X-S, He F. 2006. Background selection and population differentiation. J. Theor. Biol. 235:207-19
- Huey RB, Gilchrist GW, Carlson ML, Berrigan D, Serra L. 2000. Rapid evolution of a geographic cline in size in an introduced fly. *Science* 287:308–9
- Hufford KM, Mazer SJ. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. Trends Ecol. Evol. 18:147–55
- Husby A, Nussey DH, Visser ME, Wilson AJ, Sheldon BC, Kruuk LEB. 2010. Contrasting patterns of phenotypic plasticity in reproductive traits in two great tit (*Parus major*) populations. *Evolution* 64:2221– 37
- Solomon S, Qin D, Manning M, Chen Z, Marquis M, et al., eds. 2007. Climate change 2007: the physical science basis. IPCC Fourth Assess. Rep., Work. Group I, Intergov. Panel Clim. Change, Cambridge, UK. http:// www.ipcc.ch/publications_and_data/publications_ipcc_fourth_assessment_report_wg1_report_ the_physical_science_basis.htm
- Jackson SD. 2009. Plant responses to photoperiod. New Phytol. 181:517-31
- Kawecki TJ, Ebert D. 2004. Conceptual issues in local adaptation. Ecol. Lett. 7:1225-41
- Kelly MW, Sanford E, Grosberg RK. 2012. Limited potential for adaptation to climate change in a broadly distributed marine crustacean. Proc. R. Soc. B 279:349–56
- Kranabetter JM, Stoehr MU, O'Neill GA. 2012. Divergence in ectomycorrhizal communities with foreign Douglas-fir populations and implications for assisted migration. Ecol. Appl. 22:550–60
- Kremer A, Ronce O, Robledo-Arnuncio JJ, Guillaume F, Bohrer G, et al. 2012. Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecol. Lett.* 15:378–92
- Kreyling J, Bittner T, Jaeschke A, Jentsch A, Steinbauer MJ, et al. 2011. Assisted colonization: a question of focal units and recipient localities. Restor. Ecol. 19:433–40
- Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, et al. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987–90
- Le Corre V, Kremer A. 2012. The genetic differentiation at quantitative trait loci under local adaptation. Mol. Ecol. 21:1548–66
- Leimu R, Fischer M. 2008. A meta-analysis of local adaptation in plants. PLoS ONE 3:e4010
- Leimu R, Vergeer P, Angeloni F, Ouborg NJ. 2010. Habitat fragmentation, climate change, and inbreeding in plants. Ann. N. Y. Acad. Sci. 1195:84–98
- Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD. 2009. The velocity of climate change. Nature 462:1052–55
- Lynch M, Lande R. 1993. Evolution and extinction in response to environmental change. In *Biotic Interactions and Global Change*, ed. PM Kareiva, JG Kingsolver, RB Huey, pp. 234–50. Sunderland, MA: Sinauer
- Macnair MR. 1991. Why the evolution of resistance to anthropogenic toxins normally involves major gene changes: the limits to natural selection. *Genetica* 84:213–19
- Martin G, Aguilee R, Ramsayer J, Kaltz O, Ronce O. 2013. The probability of evolutionary rescue: towards a quantitative comparison between theory and evolution experiments. *Philos. Trans. R. Soc. B* 368:20120088
- Martins EG, Hinch SG, Cooke SJ, Patterson DA. 2012. Climate effects on growth, phenology, and survival of sockeye salmon (*Oncorbynchus nerka*): a synthesis of the current state of knowledge and future research directions. *Rev. Fish Biol. Fish.* 22:887–914
- McKay JK, Christian CE, Harrison S, Rice KJ. 2005. "How local is local?"—A review of practical and conceptual issues in the genetics of restoration. *Restor. Ecol.* 13:432–40
- Miller JM, Poissant J, Hogg JT, Coltman DW. 2012. Genomic consequences of genetic rescue in an insular population of bighorn sheep (*Ovis canadensis*). *Mol. Ecol.* 21:1583–96

- Mimura M, Aitken SN. 2010. Local adaptation at the range peripheries of Sitka spruce. J. Evol. Biol. 23:249–58

 Mooney H, Larigauderie A, Cesario M, Elmquist T, Hoegh-Guldberg O, et al. 2009. Biodiversity, climate
- Mooney H, Larigauderie A, Cesario M, Elmquist T, Hoegh-Guldberg O, et al. 2009. Biodiversity, climate change, and ecosystem services. *Curr. Opin. Environ. Sustain.* 1:46–54
- Morgenstern EK. 1996. Geographic Variation in Forest Trees: Genetic Basis and Application of Knowledge in Silviculture. Vancouver, Can.: UBC Press
- Moritz C. 1999. Conservation units and translocations: strategies for conserving evolutionary processes. Hereditas 130:217–28
- Mueller JM, Hellmann JJ. 2008. An assessment of invasion risk from assisted migration. *Conserv. Biol.* 22:562–67
- Muller HJ. 1940. Bearings of the *Drosophila* work on systematics. In *The New Systematics*, ed. J Huxley, pp. 185–268. Oxford: Clarendon
- Nevo E, Fu YB, Pavlicek T, Khalifa S, Tavasi M, Beiles A. 2012. Evolution of wild cereals during 28 years of global warming in Israel. *Proc. Natl. Acad. Sci. USA* 109:3412–15
- O'Connor MI, Selig ER, Pinsky ML, Altermatt F. 2012. Toward a conceptual synthesis for climate change responses. Glob. Ecol. Biogeogr. 21:693–703
- O'Neill GA, Ukrainetz NK, Carlson MR, Cartwright CV, Jaquish BC, et al. 2008. Assisted migration to address climate change in British Columbia: recommendations for interim seed transfer standards. Tech. Rep. 48, B.C. Minist. Forest. Range, Res. Branch, Victoria, Can. http://www.for.gov.bc.ca/hfd/pubs/Docs/Tr/Tr048.pdf
- Orr HA, Unckless RL. 2008. Population extinction and the genetics of adaptation. Am. Nat. 172:160-69
- Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37:637–69
- Reale D, McAdam AG, Boutin S, Berteaux D. 2003. Genetic and plastic responses of a northern mammal to climate change. *Proc. R. Soc. B* 270:591–96
- Reed TE, Schindler DE, Waples RS. 2011. Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. *Conserv. Biol.* 25:56–63
- Reed TE, Waples RS, Schindler DE, Hard JJ, Kinnison MT. 2010. Phenotypic plasticity and population viability: the importance of environmental predictability. Proc. R. Soc. B 277:3391–400
- Reznick D, Endler JA. 1982. The impact of predation on life history evolution in Trinidadian guppies (Poecilia reticulata). Evolution 36:160–77
- Rhymer JM, Simberloff D. 1996. Extinction by hybridization and introgression. Annu. Rev. Ecol. Syst. 27:83– 109
- Ricciardi A, Simberloff D. 2009. Assisted colonization is not a viable conservation strategy. Trends Ecol. Evol. 24:248–53
- Riegl BM, Purkis SJ, Al-Cibahy AS, Abdel-Moati MA, Hoegh-Guldberg O. 2011. Present limits to heatadaptability in corals and population-level responses to climate extremes. *PLoS ONE* 6:e24802
- Rieseberg LH. 2001. Chromosomal rearrangements and speciation. Trends Ecol. Evol. 16:351-58
- Robinet C, Roques A. 2010. Direct impacts of recent climate warming on insect populations. *Integr. Zool.* 5:132–42
- Savolainen O, Pyhajarvi T, Knurr T. 2007. Gene flow and local adaptation in trees. Annu. Rev. Ecol. Evol. Syst. 38:595–619
- Schiffers K, Bourne EC, Lavergne S, Thuiller W, Travis JMJ. 2013. Limited evolutionary rescue of locally adapted populations facing climate change. *Philos. Trans. R. Soc. B* 368:20120083
- Schindler DE, Hilborn R, Chasco B, Boatright CP, Quinn TP, et al. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465:609–12
- Schoville SD, Bonin A, Francois O, Lobreaux S, Melodelima C, Manel S. 2012. Adaptive genetic variation in the landscape: methods and cases. *Annu. Rev. Ecol. Evol. Syst.* 43:23–43
- Schwartz MW, Hellmann JJ, McLachlan JM, Sax DF, Borevitz JO, et al. 2012. Managed relocation: integrating the scientific, regulatory, and ethical challenges. BioScience 62:732–43
- Schwartz MW, Hellmann JJ, McLachlan JS. 2009. The precautionary principle in managed relocation is misguided advice. Trends Ecol. Evol. 24:474
- Seager R, Naik N, Vogel L. 2012. Does global warming cause intensified interannual hydroclimate variability? 7. Clim. 25:3355–72

- Sexton JP, Strauss SY, Rice KJ. 2011. Gene flow increases fitness at the warm edge of a species' range. Proc. Natl. Acad. Sci. USA 108:11704–9
- Soolanayakanahally RY, Guy RD, Silim SN, Song M. 2013. Timing of photoperiodic competency causes phenological mismatch in balsam poplar (*Populus balsamifera* L.), *Plant Cell Environ*. 36:116–27
- Spitze K. 1993. Population structure in *Daphnia obtusa*: quantitative genetic and allozymic variation. *Genetics* 135:367–74
- Tallmon DA, Luikart G, Waples RS. 2004. The alluring simplicity and complex reality of genetic rescue. Trends Ecol. Evol. 19:489–96
- Thomas CD. 2011. Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends Ecol. Evol.* 26:216–21
- Thomas MA, Roemer GW, Donlan CJ, Dickson BG, Matocq M, et al. 2013. Gene tweaking for conservation.

 Nature 501:485–86
- Van der Putten WH. 2012. Climate change, aboveground-belowground interactions, and species' range shifts. Annu. Rev. Ecol. Evol. Syst. 43:365–83
- Vignieri SN, Larson JG, Hoekstra HE. 2010. The selective advantage of crypsis in mice. *Evolution* 64:2153–58 Visser ME. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc. R. Soc. B* 275:649–59
- Vitt P, Havens K, Hoegh-Guldberg O. 2009. Assisted migration: part of an integrated conservation strategy. Trends Ecol. Evol. 24:473–74
- Vitt P, Havens K, Kramer AT, Sollenberger D, Yates E. 2010. Assisted migration of plants: changes in latitudes, changes in attitudes. Biol. Conserv. 143:18–27
- Wang T, Hamann A, Yanchuk A, O'Neill GA, Aitken SN. 2006. Use of response functions in selecting lodgepole pine populations for future climates. *Glob. Change Biol.* 12:2404–16
- Webber BL, Scott JK, Didham RK. 2011. Translocation or bust! A new acclimatization agenda for the 21st century? *Trends Ecol. Evol.* 26:495–96
- Weber KE, Diggins LT. 1990. Increased selection response in larger populations. II. Selection for ethanol vapor resistance in *Drosopbila melanogaster* at two population sizes. *Genetics* 125:585–97
- Weeks AR, Sgro CM, Young AG, Frankham R, Mitchell NJ, et al. 2011. Assessing the benefits and risks of translocations in changing environments: a genetic perspective. *Evol. Appl.* 4:709–25
- Whitlock MC. 2008. Evolutionary inference from Q_{ST}. Mol. Ecol. 17:1885–96
- Willi Y, Van Buskirk J, Hoffmann AA. 2006. Limits to the adaptive potential of small populations. Annu. Rev. Ecol. Evol. Syst. 37:433–58
- Williams GC. 1966. Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought. Princeton, NJ: Princeton Univ. Press
- Wright JW, Stanton ML, Scherson R. 2006. Local adaptation to serpentine and non-serpentine soils in Collinsia sparsiflora. Evol. Ecol. Res. 8:1–21
- Yeaman S, Jarvis A. 2006. Regional heterogeneity and gene flow maintain variance in a quantitative trait within populations of lodgepole pine. Proc. R. Soc. B 273:1587–93
- Yeaman S, Otto SP. 2011. Establishment and maintenance of adaptive genetic divergence under migration, selection, and drift. Evolution 65:2123–29
- Yeaman S, Whitlock MC. 2011. The genetic architecture of adaptation under migration-selection balance. Evolution 65:1897–911



Annual Review of Ecology, Evolution, and Systematics

Volume 44, 2013

Contents

Genomics in Ecology, Evolution, and Systematics Theme
Introduction to Theme "Genomics in Ecology, Evolution, and Systematics" H. Bradley Shaffer and Michael D. Purugganan
Genotype-by-Environment Interaction and Plasticity: Exploring Genomic Responses of Plants to the Abiotic Environment David L. Des Marais, Kyle M. Hernandez, and Thomas E. Juenger
Patterns of Selection in Plant Genomes Josh Hough, Robert J. Williamson, and Stephen I. Wright
Genomics and the Evolution of Phenotypic Traits Gregory A. Wray
Geographic Mode of Speciation and Genomic Divergence Jeffrey L. Feder, Samuel M. Flaxman, Scott P. Egan, Aaron A. Comeault, and Patrik Nosil
High-Throughput Genomic Data in Systematics and Phylogenetics Emily Moriarty Lemmon and Alan R. Lemmon
Population Genomics of Human Adaptation Joseph Lachance and Sarah A. Tishkoff
Topical Reviews
Symbiogenesis: Mechanisms, Evolutionary Consequences, and Systematic Implications Thomas Cavalier-Smith
Cognitive Ecology of Food Hoarding: The Evolution of Spatial Memory and the Hippocampus *Vladimir V. Pravosudov and Timothy C. Roth II
Genetic Draft, Selective Interference, and Population Genetics of Rapid Adaptation *Richard A. Neher**
Nothing in Genetics Makes Sense Except in Light of Genomic Conflict William R. Rice

The Evolutionary Genomics of Birds **Hans Ellegren**	9
Community and Ecosystem Responses to Elevational Gradients: Processes, Mechanisms, and Insights for Global Change Maja K. Sundqvist, Nathan J. Sanders, and David A. Wardle	61
Cytonuclear Genomic Interactions and Hybrid Breakdown Ronald S. Burton, Ricardo J. Pereira, and Felipe S. Barreto	31
How Was the Australian Flora Assembled Over the Last 65 Million Years? A Molecular Phylogenetic Perspective Michael D. Crisp and Lyn G. Cook)3
Introgression of Crop Alleles into Wild or Weedy Populations Norman C. Ellstrand, Patrick Meirmans, Jun Rong, Detlef Bartsch, Atiyo Ghosh, Tom J. de Jong, Patsy Haccou, Bao-Rong Lu, Allison A. Snow, C. Neal Stewart Jr., Jared L. Strasburg, Peter H. van Tienderen, Klaas Vrieling, and Danny Hooftman	25
Plant Facilitation and Phylogenetics Alfonso Valiente-Banuet and Miguel Verdú	∤ 7
Assisted Gene Flow to Facilitate Local Adaptation to Climate Change Sally N. Aitken and Michael C. Whitlock	5 7
Ecological and Evolutionary Misadventures of Spartina Donald R. Strong and Debra R. Ayres	39
Evolutionary Processes of Diversification in a Model Island Archipelago Rafe M. Brown, Cameron D. Siler, Carl H. Oliveros, Jacob A. Esselstyn, Arvin C. Diesmo. Peter A. Hosner, Charles W. Linkem, Anthony J. Barley, Jamie R. Oaks, Marites B. Sanguila, Luke J. Welton, David C. Blackburn, Robert G. Moyle, A. Townsend Peterson, and Angel C. Alcala	
Perceptual Biases and Mate Choice Michael J. Ryan and Molly E. Cummings	7
Thermal Ecology, Environments, Communities, and Global Change: Energy Intake and Expenditure in Endotherms Noga Kronfeld-Schor and Tamar Dayan	61
Diversity-Dependence, Ecological Speciation, and the Role of Competition in Macroevolution Daniel L. Rabosky	
Consumer Fronts, Global Change, and Runaway Collapse in Ecosystems Brian R. Silliman, Michael W. McCoy, Christine Angelini, Robert D. Holt, John N. Griffin, and Johan van de Koppel)3

Implications of Time-Averaged Death Assemblages for Ecology and Conservation Biology Susan M. Kidwell and Adam Tomasovych	539
Population Cycles in Forest Lepidoptera Revisited *Judith H. Myers and Jenny S. Cory**	
The Structure, Distribution, and Biomass of the World's Forests Yude Pan, Richard A. Birdsey, Oliver L. Phillips, and Robert B. Jackson	593
The Epidemiology and Evolution of Symbionts with Mixed-Mode Transmission Dieter Ebert	623
Indexes	
Cumulative Index of Contributing Authors, Volumes 40–44	645
Cumulative Index of Article Titles, Volumes 40–44	649

Errata

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at http://ecolsys.annualreviews.org/errata.shtml