# Adaptive introgression during environmental change can weaken reproductive isolation

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**Anthropogenic climate change is an urgent threat to species diversity (Thomas et al. 2004, Hoffmann and Sgro 2011). One aspect of this threat is the merging of species through increased hybridization (Todesco et al. 2016). The primary mechanism for this collapse is thought to be the weakening of ecologically-mediated reproductive barriers, as demonstrated in many cases of “reverse speciation” (Chunco 2014). Here, we expand on this idea and show that adaptive introgression between species adapting to a shared, moving climatic optimum can readily weaken *any* reproductive barrier, including those that are completely independent of climate. Using genetically explicit forward-time simulations, we show that genetic linkage between alleles conferring adaptation to a changing climate and alleles conferring reproductive isolation (intrinsic and/or non-climatic extrinsic) can lead to adaptive introgression facilitating the homogenization of reproductive isolation alleles. This effect causes the decay of species boundaries across a broad and biologically-realistic parameter space. We explore how the magnitude of this effect depends upon the rate of climate change, the genetic architecture of adaptation, the initial degree of reproductive isolation, the degree to which reproductive isolation is intrinsic vs. extrinsic, and the mutation rate. These results highlight a previously unexplored effect of rapid climate change on species diversity.**

One potential effect of global climate change (GCC) is increased interspecies hybridization by, for example, bringing together species ranges or disrupting mating timing (Chunco 2014). Such hybridization can cause a common species to subsume a rare species (Oliveira et al. 2008; Beatty et al. 2014; Vallender et al. 2007) or the collapse of multiple species into a single hybrid swarm (Taylor et al. 2006). In both cases, species diversity is lost as has been seen in smaller localized environmental shifts (Taylor et al. 2006; Vonlanthen et al. 2012).

There is a rich theoretical literature dedicated to the study of the dynamics of interspecific hybridization (reviewed in e.g. Abbot 2013, Barton 2013, Seehausen 2013). However there has thus far been poor integration between models of reproductive isolation and models of adaptation to climate change. The fact that introgression can transfer alleles between species has led to the idea that hybridization could facilitate adaptation to GCC through the transfer of adaptive alleles between species, i.e. adaptive introgression. This has traditionally been studied in the context of species/populations with pre-existing differential adaptation to the changing climate variable; for example a warm adapted species transfering alleles to a cold adapted species (e.g. Gómez et al. 2015). In this example, one species acts as a pool of alleles preadapted to a future climatic optimum. Importantly, in these types of models, introgression is being driven by selection and not demographic processes or perturbations of prezygotic isolation, as seen in other models where climate change drives hybridization.

What has not been appreciated in previous models of adaptation to a changing climate is that during a rapid environmental shift, segregating variation within two reproductively isolated species could theoretically undergo adaptive introgression even if neither species is particularly preadapted to the environmental shift. We propose that climate-induced adaptive introgression could readily occur in most species because (1) the identity of the particular alleles involved in climatic adaptation are likely idiosyncratic in each species/population, and (2) these alleles could, in principle, be globally adaptive under a GCC scenario. Indeed, segregating climate adaptation alleles (or linked blocks of alleles) could easily be strong enough to outweigh the fitness costs of any linked reproductive isolation (RI) alleles. As a side effect, RI alleles could readily be homogenized between species, reducing RI and precipitating the collapse of species boundaries. This scenario dramatically increases the likelihood of GCC-induced introgression from populations differing in altitude or latitude, to nearly any parapatric pair capable of hybridization, even if RI is initially high.

Here, we directly test the role of climate-induced adaptive introgression in degrading reproductive barriers using state-of-the-art forward time population genetic computer simulations (Supplemetary Figure 1, Online Methods). We consider the scenario of two parapatric species inhabiting demes in two different habitats. These species exchange migrants at a low level, but RI via local adaptation (i.e. extrinsic postzygotic isolation and immigrant inviability) is strong enough to prevent substantial introgression. We imagine that these two species must also cope with constant adaptation to a shared oscillating “climate” optimum. This climatic optimum does not not directly affect the degree of local adaptation and/or RI, i.e. RI is completely independent of the direct effects of climate. The climate oscillation continues for a long initial burn-in period, during which alleles conferring adaptation to climate (i.e. climate QTL) accumulate in each species. After this period, the oscillation ends and the climatic optimum begins rapidly increasing at a constant rate, as is expected under projections of anthropogenic climate change. We then measure the amount of RI lost at the end of the climate change period, in comparison to a control period of the same length. With our simulations we ask three questions; (1) Can climate change drive RI collapse and what factors control its severity? (2) Does introgression help adaptation to climate change? (3) Are the rates of evolution simulated realistic?

When climate change is rapid, we find that adaptive introgression of climate QTL alleles rapidly drives the homogenization of allele frequencies at linked RI loci between species. Figure 1 visualizes one example simulation where after 100 generations of climate change, RI is degraded to nearly half its original strength (Figure 1a) and introgressed climate QTL alleles are common (Figure 1b). As climate QTL alleles move between populations, RI and neutral alleles hitchhike along with them resulting in substantial genome-wide introgression (Figure 1a & 1c). In contrast, in the control scenario without climate change, RI remains intact and introgression is minimal (Figure 1 e-h).

For a wide range of parameters we find decreased RI and increased introgressed ancestry under the climate change scenario (Figures 2 and Supplementary Figure 2). When adaptive variation is limited, RI is initially weak, or environmental change is rapid, complete genetic homogenization is likely. In these cases, RI is completely degraded and would clearly represent speciation reversal in a natural system. In more moderate parts of parameter space, introgression is increased during environmental change, but populations do not completely homogenize (Supplementary Figure 2). In these cases, RI is still eroded between populations (Figure 2). Importantly, we believe our estimates of RI loss are likely somewhat conservative, because we do not include any additional factors that would contribute to species collapse (e.g. cases where RI is directly affected by a change in climate).

We found that in the absence of divergent selection intrinsic epistatic isolation (BDM incompatibilities) were unable to maintain RI during the burn-in period. This result is consistent with previous modelling of parapatric speciation (Barton & Bengtsson 1986, Bank et al. 2012, Lindtke & Buerkle 2015). Consistent with their effect in the burn-in period, during climate change, introgression and RI loss is enhanced when intrinsic RI is present. Other models of intrinsic isolation are possible, such as the pathway model of Lindtke and Buerkle, that are more resistant to introgression. In all cases, intrinsic isolation will get weaker with increased introgression, while extrinsic isolation has a consistent strength, so we don’t expect any form of intrinsic isolation to be more resistant to the adaptive introgression than the extrinsic isolation modelled here, assuming similar genomic architecture. Thus, although we have focused on extrinsic RI, intrinsic RI is also susceptible to adaptive introgression.

The ultimate question of which species are in danger of reverse speciation is dependent on a multitude of interacting factors and is beyond the scope of this paper, but we can highlight several risk factors.

1. For hybridization to be an issue, a potential hybridizing species must be at least in parapatry. Surveys have estimated the percent of species that hybridize with at least one other congener to be around 10-25%, although if climate change disrupts species ranges or premating isolation, that number may increase (Mallet 2005).
2. The rate of environment change and the steepness of the changing fitness landscape. Species with broader climate niches will be less susceptible because they will be under weaker selection.
3. The genetic architecture of climate adaptation in the species. Species with numerous large effect climate adaptation alleles segregating within their gene pool will be more able to adapt to the changing climate *without* introgressed alleles. Low diversity species will be more susceptible and reliant on adaptive introgression.
4. The genetic architecture of reproductive isolation between species. Species with few large effect RI loci will be more resistant to RI decay than species with a more diffuse and polygenic RI architecture. See the Supplementary Discussion for further exploration on the role of recombination.
5. The demographic and life history of the species. Unbalanced population sizes may result in one population harboring more adaptive alleles and lead to unbalanced introgression. Small populations will also be more susceptible to extinction due to the fitness costs of introgressed RI alleles. Features that reduce effective population size, e.g. high variance in reproductive success, are also likely to have reduced diversity of climate adapting alleles.

Our simulations suggest that rapidly changing environments can cause the collapse of species barriers in the *absence* of any direct effect on the underlying strength of reproductive isolation. By design, we modelled a scenario in which the strength of RI (modelled as divergent selection) is (a) invariant throughout (i.e. not reduced by environmental change itself) and (b) totally orthogonal to the strength of climate-mediated selection (i.e. extrinsic RI alleles do not affect the climate phenotype). This is an important departure from previous work, in which the collapse of reproductive isolation or “reverse speciation” occurs because RI is itself dependent on the environment (e.g. trophic or sensory niche).

This difference has several important implications. For one, the mechanism we outline here can occur in any population where adaptive introgression is possible (i.e. RI is not absolute and the climate-mediated selective optimum is to some degree shared). This greatly expands both the number of populations that may be susceptible to introgressive collapse and the potential severity of such collapses. For example, adaptive introgression could act in concert with the collapse of climate-mediated reproductive barriers, accelerating collapse.

Although we have framed our discussion in the context of climate change, our results are applicable to any strong, consistent, and shared selective event. These events include any environmental or ecological disturbance that alters the shared selective landscape of the two populations such that both populations are sufficiently displaced from their selective optima (thereby increasing the average size of selection differentials between genotypes, i.e. the strength of selection). One such event that has been studied in natural systems is eutrophication, which has been suggested to have caused speciation reversal in European lake whitefish (Vonlanthen et al. 2012). Thus far, this reversal has been attributed to changes in RI as a direct result of ecological and/or behavioural changes. However, if eutrophication exerts a common selective pressure on a group of parapatric species (e.g. mediated through changes in water chemistry) introgression could become adaptive and contribute to the collapse of species boundaries. Similarly, ocean acidification could be a strong source of shared selection and may induce introgression between previously well isolated species (Pespeni et al. 2013).

While we focus our discussion on how introgression can lead to species merging together, it is likely that the adaptive introgression of climate QTL increases the chances that a species can adapt to a changing environment instead of going extinct. We can’t directly address this question in our model (see Supplementary Discussion) but we do see that when all introgression is prevented the lag between the current phenotype and the current optimum increases (Figure 3). This is consistent with the larger total gene pool of adaptive variants available when gene flow is possible. We see this effect most strongly when climate change is fastest, suggesting the benefits of introgression mainly occur when adaptation is most challenging.

A strong shared selection pressure is ultimately the key mediator of the collapse of RI we observed. Was the magnitude of simulated selection necessary to cause this collapse realistic? One way to assess this is to measure the magnitude of the phenotypic response to selection in our simulations and compare it to estimates from natural systems. In our case, the phenotypic response to selection ranged from 0.01-0.06 Haldanes (standard deviations per generation) (Supplementary Figure 3). This is in line with the magnitude of phenotypic response observed in both natural and anthropogenically-induced selection (e.g. Hendry et al. 2008). Further, this is below the theoretical threshold of 0.1 Haldanes thought to result in an unsustainable long-term response to selection (for Ne = 500; Lynch & Lande, 1993; Bürger & Lynch, 1995).

Another way of assessing the realism of our scenarios is comparing the selection coefficients of climate QTL in our simulations with values measured in empirical studies. We measured selection coefficients in our example simulation by comparing relative fitness values for samples with and without each mutation (Supplementary Methods), and therefore are capturing not just the effect of the climate QTL mutation, but also all linked loci. Only 0.7% of introgressed climate QTL loci had selection coefficients > 1, within the range of empirical values, therefore adaptive introgression is occurring without abnormally high selection coefficients (Kingsolver et al. 2001).

Thus, the strength of selection we modelled was not particularly extreme nor would it necessarily lead to the extinction of the modelled populations. It is also worth noting that the estimated rate of phenotypic change in wild populations due to future GCC is thought to be at least as large as the rates we described here, and are projected to likely exceed 0.1 Haldanes in many cases (Gienapp, Leimu, & Merilä, 2007; Merilä & Hoffman 2016). In sum, the global strength of phenotypic selection simulated here was not unrealistically high, and if anything represents a conservative adaptive scenario.

Hybridization is a double-edged sword under rapid environmental change. It can allow species access to a larger pool of adaptive alleles but linkage with RI alleles will weaken overall RI and may lead to speciation reversal. Importantly, our work highlights the dangers of hybridization for a much wider pool of species, not just those on range margins or with existing porous species boundaries. In the longer term, we predict that specific cases of speciation reversal should be linked to climate change but we also predict effects before full speciation reversal. If our model is correct, we predict that alleles conferring adaptation to present and future climate (e.g. heat or drought) will be more likely to introgress between species. Although identifying all the loci underlying climate adaptation is challenging, recent work by Exposito-Alonso et al. (2019) highlights that it can be done. Such an approach can be combined with sequencing data in related species to identify where introgression is occuring. Our results also suggest that hybrid zones should become increasingly porous as climate adaptation alleles move between species and that this effect would be stronger in regions with more dramatic climate change (e.g. the arctic). This could be done by resampling previously studied hybrid zones or by comparing contemporary samples to museum and herbarium samples. Confirmation of these predictions would show that climate adaptation is occurring through a larger multi-species gene pool and be a warning sign for the future homogenization of these species.

*Author contributions*

G.O and K.S designed the study, created the model, analysed the results and wrote the paper.

*Acknowledgements*  
This work was supported by an NSERC Banting Postdoctoral Fellowship to GLO and an NSERC Postdoctoral Fellowship to KS. GO was also supported by postdoctoral funding from Rasmus Nielsen at UC Berkeley, while KS was further supported by postdoctoral funding and good vibes from Mohamed Noor at Duke University. Rasmus Nielsen, Matthew Osmond, Kate Ostevik and Loren Rieseberg provided helpful feedback and discussions on earlier versions of the manuscript. We thank Philip Messer and Ben Haller for assistance with the SLiM 3.X software.

*Competing Interests*

The authors declare no competing interests.

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## Figure & Table Captions

**Figure 1**

A single example simulation with Δ = 1.5, illustrating the climate driven adaptive introgression. Panels A-D present the test climate change scenario, while E-H are the control scenario. (A & E) The upper half is the average introgressed ancestry for each population (purple and green) and the average reproductive isolation between populations (black). The lower half is the ancestry for neutral loci during the post-burn in period at 20 generation intervals. The top and bottom parts of this portion represent population 1 and 2 respectively. (B & F) The allele frequency trajectory for introgressed climate QTL color coded by QTL strength. Color codes QTL effect; -ve phenotypic effect (blue), +ve effects (light red) or large +ve effect (>2, dark red). (C & G) The allele frequency trajectory for introgressed RI alleles (D & H) The distribution of selection coefficients on QTL loci per population per generation. Color groups represent QTL with -ve phenotypic effect (blue), +ve effects (light red) or large +ve effect (>2, dark red). Plot is filtered to only include loci with allele frequency < 0.9 and > 0.1.

**Figure 2**

The average reproductive isolation at generation 10,100 for climate change (red) and control simulations (blue), while varying individual parameters. RI is defined as the home fitness advantage which is the fold fitness advantage for the average sample in its home environment compared to the alternate environment based on divergent selection and BDM loci. A value of 1 means equal fitness in both environments and there is no RI. The black dot is the initial and maximum level of RI for each simulation. Individual parameters were varied to show the effect of (A) climate QTL effect size standard deviation, (B) optimum shift per generation (delta), (C) migration rate, (D) climate QTL mutation rate, (E) proportion of RI loci that are BDM instead of extrinsic, (F) the recombination rate, (G) the fitness effect of each RI loci and (H) the number of RI loci.

**Figure 3**

The adaptational lag at the final generation for simulations with (m=0.01) and without migration (m=0). Adaptational lag is defined as the phenotypic optimum minus the phenotypic mean divided by the rate of change in optimum, and represents how many generations behind the changing optimum that the population is.