COMMENTARY

Conditions when hybridization might predispose populations for adaptive radiation

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The role of hybridization in evolution is a theme that has been intensively and sometimes controversially debated, particularly amongst zoologists. Long time considered an evolutionary dead end, interspecific hybridization is now known to have left imprints in the genomes of many plant and animal lineages (Grant et al., 2003; Mallet, 2005; Arnold, 2006). While it is clear that hybridization has often times been no dead end, questions that remain contentious are whether and how hybridization affects rate and direction of evolution, and how it affects speciation. Classically, hybridization was thought to put a brake on speciation (Mayr, 1942; Dobzhansky, 1951), but this view is also beginning to change. Hybrid speciation has been quite well documented (Buerkle & Rieseberg, 2008; Abbott et al., 2013), and hybridization appears to be particularly common in the most species-rich and rapidly diversifying groups of organisms (Schwarzer et al., 2012), perhaps just as a consequence of many young species in geographical proximity. Either way it is clearly not preventing speciation in these groups (Salazar et al., 2010; Joyce et al., 2011; Genner & Turner, 2012). Whether these species radiations happen *despite* hybridization are *facilitated* or even *catalysed by* hybridization awaits strong tests.

Abbott et al. (2013) discuss effects of hybridization in secondary contact in terms of reinforcement, speciation reversal and hybrid speciation. There is yet another possible and mechanistically distinct effect of hybridization on speciation, which Abbott et al. (2013) touch in passing: genetic admixture between distinct populations or species may genetically predispose hybrid populations for repeated speciation and adaptive radiation in the future (Seehausen, 2004).

There are several mechanisms that may predispose hybrid populations to repeated speciation, and they fall into two broad categories. One is release from evolutionary constraints to adaptation. Through enrichment in standing genetic variation, hybridization can boost heritability in adaptive traits and increase realized rates of adaptive evolution. This mechanism is instantaneously effective. The generation of extreme or novel phenotypes, so-called transgressive segregation, can be considered a special case of this (Rieseberg et al., 1999; Stelkens & Seehausen, 2009). It may bring some genotypes in a hybrid population instantaneously into the attraction zone of an adaptive peak that neither parental population could tap into because of lack of suitable variation (Mallet, 2007). Additionally, recombination of the parental species genomes following hybridization may facilitate breaking of genetic correlations. Such correlations that may constrain selection response (Gomulkiewicz & Houle, 2009) may arise in the first place if selective sweeps drive adaptive gene variants to fixation that are physically linked or have pleiotropic effects on several different traits under selection.

Besides affecting adaptive potential, hybridization may also affect genomic predispositions for the evolution of reproductive isolation, and this has received far less attention. I will develop this idea here as a verbal model which might be followed up by theoretical modelling.

Ecological divergent selection often leads to only incomplete reproductive isolation, and locally adapted populations or partially isolated ecotypes may be maintained for quite a long time by selection that balances gene flow. However, without progressing further towards stronger reproductive isolation, such populations are vulnerable to changes in ecological selection regimes and genetic differentiation may eventually collapse again. Indeed this is likely to happen to most locally adapted populations. More robust reproductive isolation might evolve if genes under extrinsic (ecological) underdominant selection or independent pairs of genes under extrinsic (ecological) disruptive selection became coupled to endogenous incompatibility factors (again single locus underdominant factors or pairs of interacting incompatibility loci). However, this opportunity may rarely arise during ecological divergence in panmictic populations because incompatibility-inducing mutations will tend to get purged before they reach appreciable frequencies (Gavrilets, 2004). Herein comes the importance of hybridization. Classical Bateson–Dobzhansky–Muller incompatibilities (BDMIs) arise due to incompatibility between derived alleles at two (or more) loci that diverged unopposed by compatibility selection between populations in geographical isolation, and they only become expressed upon secondary contact with hybridization (Gavrilets, 2004). Underdominant mutations may also fix more readily between geographically isolated populations owing to drift that can overcome selection in small populations (Wright, 1931; Altrock et al., 2011).

Hybrid populations will then often suffer some fitness loss from carrying such incompatibility alleles at high frequencies (Dobzhansky, 1951), but may at the same time benefit from elevated variability at ecologically relevant loci allowing them to tap into new resources and

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undergo niche expansion. Additionally they will often have elevated variability at loci that affect mating assortment, such as at mate or habitat preference genes or genes that affect breeding seasonality. All such genes are potential reproductive barrier loci. I suggest that in the presence of disruptive ecological selection affecting some of the loci directly, perhaps as a result of reaching carrying capacity after niche expansion, individual incompatibility loci or independent pairs of interacting loci might then become coupled together by selection. Analogous to conditions modelled by Barton & de Cara (2009), it seems plausible that such coupling between extrinsic ecological barrier loci on the one hand and endogenous barrier loci on the other hand would be positively selected because, in the case of multiplicative incompatibility effects, coupling would reduce the fraction of low fitness genotypes produced in the population. Coupling effectively masks the effects of separate loci or separate pairs of interacting loci. In other words, coupling increases the variance in overall compatibility, which in turn increases mean fitness in the population (Barton & de Cara, 2009).

A difference between this scenario and the Barton & De Cara models lies in that only one element in the coupling pairs may have to be under negative frequency-dependent disruptive or divergent ecological selection. It seems likely that once some coupling happened between the first two barrier loci or independent pairs of interacting loci, additional barrier loci or pairs could be recruited into this coupling with increasing ease. Even newly arising or low frequency assortment alleles that would otherwise suffer from Allee effects could then perhaps invade through associations with other components of reproductive isolation. Moreover, Barton & de Cara (2009) showed that invasion of assortment alleles could trigger the evolution of coupling between pairs of selected loci even if their effects were additive.

The outcome of such coupling between incompatibilities is fundamentally different from reinforcement because it does not require strong initial deviations from linkage disequilibrium and it does not 'complete the unfinished process of geographical speciation'(Mayr, 1942). Instead it could probably lead to the emergence of multiple reproductively isolated species from a fully admixed hybrid swarm.

During panmixia or near-panmixia within the hybrid swarm, endogenous incompatibility alleles though will experience strong negative selection, and without coupling to polymorphisms maintained by negative frequency-dependent or divergent ecological selection, they will eventually become purged from the hybrid population. And herein lies a difference from the existing models where all incompatibility alleles are maintained by frequency dependence (Barton & de Cara, 2009). While the latter is a possibility for some incompatibility alleles, it is unlikely to apply to most of them. It then seems likely that many endogenous incompati-

bility loci in hybrid populations experience a race between purging and the evolution of coupling to loci that are under divergent ecological selection as two alternative evolutionary paths to increased mean fitness. Exploring the conditions under which coupling or purging prevails requires modelling, but I expect that weak genetic population structure, due to spatial heterogeneity in the direction of selection and in carrying capacities, would facilitate speciation through barrier coupling.

Importantly, selection for coupling of endogenous and ecological barrier loci or pairs of loci is likely a much stronger engine for speciation than is strong ecological selection alone. While local adaptation and early incipient stages of ecological speciation with very incomplete reproductive isolation may be driven by divergent natural selection alone, the intensification of reproductive isolation – hence the continuation of the speciation process beyond local adaptation – might then often depend on historical contingencies that bring an abundance of endogenous incompatibilities and adaptive variation together into the same population. That many young adaptive radiations occur in regions of secondary contact and admixture between previously allopatric lineages (Seehausen, 2004; Arnold *et al.*, 2012) is consistent with this idea but is of course no direct evidence. The coupling mechanism would perhaps also contribute to explaining the highly variable progression towards ecological speciation that is often observed within and between taxa under similar ecological conditions and remains currently often unexplained (Nosil, 2012).

The model makes predictions that can be tested empirically: (i) when crossed in the laboratory, ecologically divergent sister species in adaptive radiations should often reveal more or stronger endogenous incompatibilities than expected under drift, given their (recent) divergence time. Their discovery may not be trivial though, may often require two hybrid generations to be bred and either direct phenotypic detection followed by a screen for allelic variants genome-wide or at candidate genes, or testing for segregation distortion across a large number of genomic loci in juveniles reaching adulthood. (ii) When the incompatibility loci can be identified, divergently fixed alleles at incompatibility loci should coalesce deeper in time than alleles at average genomic loci. (iii) The same endogenous incompatibilities may contribute to coupled reproductive barriers in several species pairs, but be coupled to different extrinsic barrier loci in different species pairs or be coupled to similar extrinsic barrier loci with the direction of allele coupling different in different species pairs and different from the ancestral species that gave rise to the hybrid swarm (contrary to expectations from reinforcement).

Abbott *et al.* (2013) ask the question whether ecology should still be thought of as the initial catalytic agent of speciation when reproductive isolation depends on endogenous incompatibilities. For the coupling mecha-

nism that I outlined above for speciation from a hybrid population, the answer would have to be Yes. This is because selection for coupling under this model requires disruptive ecological selection on at least one of the incompatibility loci or pairs of loci, that is, speciation is initiated by disruptive selection between ecological niches, but requires coupling between extrinsic and endogenous barriers to go to completion.

As diverse as the different possible outcomes of hybridization appear to be, it is helpful to recognize that the collapse of reproductive barriers, reinforcement, homoploid hybrid speciation and adaptive radiation from a hybrid swarm really can be placed along a single continuum of process and mechanism. The distinction between them lies mainly in the variable inclusiveness of the mating population that results from hybridization:

1 If the resulting mating population is inclusive of the complete parental species populations, these will either collapse into a single hybrid population (a single species) or experience reinforcement of reproductive isolation

2 If the resulting mating population is inclusive of only a fraction of each parental species' populations (where inclusiveness is spatially or ecologically bounded), either reproductive isolation will be locally reinforced, or species will locally collapse in which case conditions for hybrid speciation are fulfilled (Buerkle *et al.*, 2000)

3 Finally, adaptive radiation from a hybrid swarm would ensue from either of the first two scenarios when reinforcement fails, but new reproductive isolation barriers evolve between subpopulations within the hybrid swarm

Which one of these scenarios happens will depend on the interplay between ecological opportunity (divergent selection between niches), geographical context and historical contingency (initial level of reproductive isolation and segregation of incompatibilities and their genetic architectures) and may become predictable to some extent when these factors are jointly taken into account. Speciation is a complex phenomenon and the effects of hybridization on it may be more highly dimensional than previously thought.

Acknowledgment

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