Opinion

Hybridization and genome evolution I: The role of contingency during hybrid speciation

Fabrice EROUKHMANOFF*, Richard I. BAILEY, Glenn-PETER SæTRE
Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, Norway

Abstract Homoploid hybrid speciation (HHS) involves the recombination of two differentiated genomes into a novel, functional one without a change in chromosome number. Theoretically, there are numerous ways for two parental genomes to recombine. Hence, chance may play a large role in the formation of a hybrid species. If these genome combinations can evolve rapidly following hybridization and sympatric situations are numerous, recurrent homoploid hybrid speciation is a possibility. We argue that three different, but not mutually exclusive, types of contingencies could influence this process. First, many of these “hopeful monsters” of recombinant parent genotypes would likely have low fitness. Only specific combinations of parental genomic contributions may produce viable, intra-fertile hybrid species able to accommodate potential constraints arising from intragenomic conflict. Second, ecological conditions (competition, geography of the contact zones or the initial frequency of both parent species) might favor different outcomes ranging from sympatric coexistence to the formation of hybrid swarms and ultimately hybrid speciation. Finally, history may also play an important role in promoting or constraining recurrent HHS if multiple hybridization events occur sequentially and parental divergence or isolation differs along this continuum. We discuss under which conditions HHS may occur multiple times in parallel and to what extent recombination and selection may fuse the parent genomes in the same or different ways. We conclude by examining different approaches that might help to solve this intriguing evolutionary puzzle [Current Zoology 59 (5): 667–674, 2013].

Keywords Evolvability, Constraints, Contingency, Hybrid, Adaptation

1 Introduction

The role of hybridization in the evolutionary process is still not well understood. The on-going genetic and genomic revolution has taught us that hybridization between genetically differentiated populations or species is much more widespread and common than we used to think (Mallet, 2007; Abbott et al., 2013; Sætre, 2013). Hybridization may retard phenotypic divergence and cause speciation reversals (Seehausen et al., 2007), yet under other circumstances it can play an integral part in the diversification process. Hybridization may remodel the genomic architecture of an admixed organism into a complex mosaic of blocks derived from either of the parents, which can have additional positive effects for adaptation and diversification (Gompert et al., 2006; Eroukhmanoff et al., 2013; Trier et al., unpublished data). Hybridization may also lead to the formation of new species, for instance through homoploid hybrid speciation (HHS), which has been documented in a variety of animal taxa (Rieseberg, 1997; Gross and Rieseberg, 2005; Mavárez et al., 2006; Mallet, 2007; Jiggins et al., 2008; Hermansen et al., 2011). HHS involves the recombination of two differentiated genomes into a novel, functional one without a change in chromosome number. An important question in understanding HHS is to what extent genome evolution following hybridization events depends on historical contingency and chance events, or on deterministic and predictable evolution. Indeed, we still know very little about the mechanisms favouring this apparently unusual mode of speciation, despite its potential implications in processes such as adaptive evolution and diversification (Bailey et al., 2013). Theoretically, there are numerous ways in which two parental genomes could possibly be recombined. However, only specific combinations of parental genomic contributions may produce a viable, intra-fertile hybrid species. If one or several viable genomic combinations can more readily evolve following multiple isolated hybridization events, recurrent HHS is a possibility. But once a hybrid genome has stabilized, the complexity of
the mosaic of parental genomes may still strongly influence the evolutionary trajectory of a hybrid species, a pattern we define here as genomic contingency. A second type of contingency linked to ecological conditions could influence the likelihood of recurrent HHS, such as variation in natural selection and effective population sizes during the multiple hybridization events, or the extent of habitat-related isolation of the admixed populations (e.g. Harrison and Rand, 1989). Finally, a third type of contingency linked to evolutionary history may occur if hybridization events leading to HHS occurred at different time intervals. The extent of divergence between parents may influence the outcome of hybridization and the evolution of different hybrid lineages.

These contingencies have been extensively studied in the context of classic bifurcating speciation and adaptive divergence (e.g. Langerhans and De Witt, 2004; Eroukhmanoff et al., 2009), but relatively little in hybrid species. Here, we review and discuss different cases of recurrent hybrid speciation and discuss the roles that genomic, ecological and historical contingencies may play in this process. We examine under what circumstances we would expect recurrent HHS and to what extent genotypes and phenotypes of multiple hybrid species may be convergent. Finally, we present a framework that could be used to study the evolvability of mosaic genome in hybrid species, a crucial aspect to the study of recurrent hybrid speciation.

2 Recurrent Hybrid Speciation vs. Single Origin of Hybrid Lineages

Although evidence for multiple cases of HHS across various taxa has accumulated over the last decade, relatively little is known about this mode of speciation. Several studies have investigated the possibility of recurrent origin of hybrid species, but with variable success (Table 1). The main issue resides in dissecting genetic variation due to multiple hybridization events from genetic variation arising after hybrid speciation (Nice et al., 2013). Recurrent hybrid species might evolve from multiple spatially/temporally distinct or even simply independent instances of secondary contact and admixture between the same parental species, or a single instance of admixture followed by geographic isolation of the incipient hybrid species before genome stabilization begins. However, here we restrict our investigation to cases of recurrent HHS through multiple, independent hybridization events. The potential for independence and the possible effects of historical contingency will differ between different scenarios. For instance, in the *Helianthus* genus of annual sunflowers, three homoploid hybrid species, *H. anomalus*, *H. deserticola*, and *H. paradoxus*, appear to be derived from the same two parent species, *H. annuus* and *H. petiolaris*. The three hybrid species are morphologically, ecologically, and chromosomally divergent from each other and from their parental species (Welch and Rieseberg, 2002). It also appears that across these species, ecological selection linked to different habitats has played a strong role, and the rise of the three species could thus be considered to be deterministic. In addition, genomic constraints may also have influenced their emergence, as three experimentally synthetic hybrid sunflower lineages were found to converge on a similar set of parental chromosomal blocks to their naturally occurring counterparts after only a few generations (Rieseberg et al., 1996). However, within these three hybrid species, one of them appears to have arisen only once and then expanded into regions harboring one specific environment (*H. paradoxus*; Welch and Rieseberg, 2002) while the other two species, *H. anomalus* and *H. deserticola* seem to have emerged multiple times (Schwarzbach and Rieseberg, 2002; Gross et al., 2007). The case of *H. paradoxus* is peculiar because this species occurs only in saline desert wetlands, a type of habitat that is rare on the American continent, and this is suggested to be one

Table 1 Different cases of hybrid speciation where recurrent origin has been tested, alongside with the evolution of hybrid lineages post HHS (“Evolution of admixture”) and other relevant parameters such as ecological differences with parental species and genomic variation within hybrid species

| Genus       | Ecological Differences | Genomic Variation | Recurrent Origin | Evolution of GM | Reference                      |
|-------------|------------------------|-------------------|------------------|-----------------|--------------------------------|
| *Lycaides*  | Moderate               | Moderate          | Possible         | Divergence      | Nice et al., 2013.              |
| *Helianthus*| Strong                 | Strong            | No (paradoxus)   | Divergence      | Welch and Rieseberg, 2002;      |
|             |                        |                   | Yes (deserticola, anomalous) |               | Schwarzbach and Rieseberg 2002.|
| *Argyranthemum* | Strong               | Strong            | Yes              | Convergence     | Brochmann et al., 2000.        |
| *Pinus*     | Weak                   | Strong            | Yes              | Divergence      | Wang et al., 2001.             |

GM: Genomic Mosaicism
of the constraining reasons why this hybrid species has not arisen multiple times (Welch and Rieseberg, 2002). Other factors may also have played a role, such as genetic constraints associated with adaptation to salt marsh environments (Lexer et al., 2003) and the history of the eastward expansion of this species, which might have led to differences in depletion of genetic variation among the various hybrid populations (Welch and Rieseberg, 2002).

3 Circumstances which may Favor or Prevent Recurrent Hybrid Speciation

Some hybrid species are widely geographically distributed and occur alongside their parent species (e.g. the Italian sparrow, Hermansen et al., 2011) whereas others are restricted to extreme and isolated habitats (e.g. Helianthus sunflowers (Rieseberg et al., 1996) or Lycaceides butterflies (Nice et al., 2013)). During the onset of hybrid speciation, it is largely unknown whether stabilisation of the hybrid genome may lead to multiple alternative evolutionary outcomes, as selection and genomic constraints may interact in unpredictable ways (Nolte and Tauz, 2010; but see Rieseberg et al., 1996). At a later stage, both intrinsic (Pritchard and Edmands, 20102; Trier et al., unpublished data) and extrinsic (Rieseberg et al., 2003) barriers may contribute to reproductive isolation between a hybrid species and its parents, but ecological barriers should impact this process in a more deterministic way, as genetic incompatibilities, especially if they are situated on different chromosomes, may easily be recombined, purged or coupled in different ways (Barton and de Cara, 2009; Seehausen, 2013).

A number of factors may contribute to a context favorable for HHS (Buerkle et al., 2000). One of the most important is the faculty for genomes to fuse and stabilize quickly after hybridization, and in a way that isolates the hybrid taxa from their parents. Intrinsic incompatibilities isolating the parent species may thus act as a factor strongly reducing contingency in the HHS process itself, and accordingly, in recurrent HHS. If incompatibilities are too strong and numerous, hybrid breakdown may be too much of a constraint, but if they are not too detrimental, they should influence the repeatability of both the likelihood of HHS and the structure of the resultant mosaic genomes; indeed, incompatibilities should increase repeatability since they reduce the number of pathways towards a fit mosaic genome, and provide an efficient evolutionary route towards reproductive isolation of the hybrid species from its parental species (Trier et al., unpublished data). Experimentally replicated hybrid swarms of the copepod Tigriopus californicus exhibited congruent patterns of cyto-nuclear associations, ultimately leading to parallel genomic trajectories across hybrid swarms (Pritchard and Edmands, 20102). An important role of cyto-nuclear incompatibilities, as well as of sex-linked genes, has also recently been shown in a hybrid species, the Italian sparrow Passer italicae (Trier et al., unpublished data). The hybrid Italian sparrow is almost fixed for mitochondria and sex-linked genes with mitochondrial function from one of the parent species, the house sparrow P. domesticus, and the level of introgression of alleles from the other parent species, the Spanish sparrow P. hispaniolensis is extremely low in parapatry at these genes, suggesting strong purging. Tigriopus and Passer together therefore highlight that intrinsic postzygotic barriers, such as mito-nuclear and sex-linked mismatches, may strongly influence the repeatability of the outcome of independent hybridization events.

Considering the role of evolutionary history as being a possible contingency, the case of the Italian sparrow is of particular interest since it is one of the very few examples in which the hybrid lives sympatrically or parapatrically with both its parent species (Fig. 1). In addition, the parent species themselves have large, overlapping distributions and hybrid Italian sparrow populations occur both on the Italian peninsula and on several more or less distant Mediterranean islands, e.g. Corsica, Crete and Malta (Summers-Smith, 1988). It is unlikely that ecological contingency has been favouring the possible recurrent hybrid origin of these distant populations in the same way as Helianthus sunflowers, where HHS has been strongly influenced by ecological contingencies in the form of new habitats to be colonized (see above). Historical contingency may therefore play a prominent role in sparrow HHS. As a bird commensal to humans, the Italian sparrow shares a very similar ecological niche to one of its parents, the house sparrow (Summers-Smith, 1988). Despite being phenotypically variable in response to environmental variation (Eroukhmanoff et al., 2013), there seems to be very little variation in its association with humans across its breeding range. But the influence of commensalism on recurrent HHS may have been indirect in this case. House and Spanish sparrows were until recently locally adapted and isolated seed-eating birds (Summers-Smith, 1988, Sætre et al., 2012). As agriculture spread throughout the Old World, house sparrows moved along in great numbers and eventually, the house and Spanish sparrow that had been geographically isolated for per-
haps as much as 2 million years (Ericson et al., 1997; Elgvin et al., 2011) experienced secondary contact (Fig. 1). But this process is very recent in evolutionary terms (approximately 3000 years ago) and it is unlikely that the house sparrow had fully evolved into a commensal state in the early stages of this expansion. Spatio-temporal variation in the occurrence of sympathy and the course of self-domestication itself may have then influenced the likelihood of HHS. The potential role for historical contingency in HHS needs to be investigated further in this system.

An interesting comparison of the influence of commensalism on evolution and speciation in animals can be made with experiments conducted on *Drosophila melanogaster* (Alipaz et al., 2005). These authors showed in replicated multi-generational laboratory selection experiments that hybrid populations between an ancestral Zimbabwean race and cosmopolitan races having dispersed and evolved in response to human commensalism rapidly converged towards similar, cosmopolitan race-like, reproductive behaviour. But despite this evolution towards the commensal behavioural phenotype these hybrid populations also exhibited extensive variation in genomic mosaicism, with genomic regions associated with behavioural divergence hosting alleles from both parental races. This confirms how the influence of ecology and history can favour similar evolutionary outcomes of hybridization despite strong differences in genomic trajectories (Rieseberg et al., 1996; Chapman and Burke, 2007).

Another important issue is whether different types of contingencies may interact with each other during HHS. Varying ecological conditions in different sympatric zones may interact with different genomic constraints to lead to unique and independent HHS events. Recent findings suggest a strong geographic and historical component in addition to ecology in driving multiple and complex independent HHS events in *Pinus densata* (Wang et al., 2011), although the interactions between these different contingent factors still need to be fully investigated to elucidate different geographic and historical scenarios with respect to ecological adaptations of different hybrid populations. Furthermore, selection and recombination can act in a concerted way to produce shared patterns of genomic mosaicism (Rieseberg et al., 1996), but little is known about what might cause differing patterns of mosaicism. Even if genomic constraints can be altered by selection, it is still possible that different recombination events may lead to similar genomic outcomes. For instance, it has been suggested

Fig. 1  Breeding distribution of the hybrid Italian sparrow (yellow) and its parent species, the house sparrow (grey) and Spanish sparrow (red)
The hatched area indicates regions where the parent species occur sympatrically. The darker grey area in Central Asia indicates the distribution of the non-commensal house sparrow *P. d. bactrianus*. Bird drawings indicate diagnostic male plumage characteristics of the three sparrow species. Black dots indicate locations where levels of genetic admixture have been investigated in Hermansen et al. (2011) and Sætre et al. (2012).
that synthetic hybrid yeasts can experience recurrent chromosomal rearrangements under similar selective conditions, but without any backcrossing with their parental forms (Dunn et al., 2013). Large scale genomic data in combination with other approaches such as field based selection experiments or ecological niche modelling could shed light on this crucial aspect.

4 The Evolvability of Hybrid Species and the Dimensionality of Genomic Mosaicism

Hybrids possess increased additive genetic variation relative to their parent species, and in many cases hybrid genomes produce extreme, transgressive phenotypes beyond the range of both parent species. Both of these factors may allow novel adaptation in the hybrid lineage, as exemplified by Helianthus sunflowers (Rieseberg et al., 1997). However, strong genetic correlations may occur in hybrids and have both positive and negative influences on adaptation. Physical linkage and epistatic fitness effects between loci contributing to phenotypic variation lead to genetic correlations, and hence constrain the independent evolution of traits (Chenoweth et al., 2010). In the context of hybrid speciation, genomes often consist of a mosaic of parental alleles, evolving in linkage blocks of different sizes, and these linkage blocks may be much larger than those present in the parent taxa (Buerkle and Rieseberg, 2008). Epistatic interactions are also likely to influence genetic correlations and the evolution of mosaicism (Rieseberg et al., 1996; Lindtke et al., 2012), including through the purging of incompatibilities (Barton and de Cara, 2009). The presence of pre-existing incompatibilities, strong linkage, strong epistatic fitness effects and increased additive genetic variation in ecological and sexual traits may increase the likelihood of future diversification within a hybrid relative to a non-hybrid species. Should clines or polymorphisms in both intrinsic and extrinsic isolating mechanisms come to align in positive linkage disequilibrium (Barton, 1995) through for example cline movement of incompatibilities towards sharp ecotones causing divergent selection, these multiple aligned isolating mechanisms will reinforce each other (Barton and de Cara, 2009; Seehausen, 2013). The effect would be particularly strong due to extensive divergence hitchhiking (Via and West 2008) in hybrids (Trier et al., unpublished data). This could further fuel ecological divergence (Seehausen, 2013, Trier et al., unpublished data), and potentially lead to independently evolving hybrid lineages derived from a single HHS event hardly distinguishable from independent recurrent hybrid speciation events (Nice et al., 2013). In fact, these hybrid clusters could even evolve during the onset of HHS, where a form of “parapatric recurrent hybrid speciation” could favor the emergence of multiple stabilized hybrid species from a hybrid swarm. This may be particularly likely if the hybridization events occur over a large geographic range, limiting gene flow due to isolation by distance. In such a scenario, different geographic regions may evolve partially independently towards different stabilized hybrid genomes. This scenario is consistent with patterns observed within the hybrid Italian sparrow, of discordant cline movements and the maintenance of incompatibilities within the hybrid species (Trier et al., unpublished data) combined with evidence for reduced gene flow among locally adapted hybrid populations (Eroukhmanoff et al., 2013). This process would further be favored if genomic mosaicism is evolvable in “quantitative genetic terms”, i.e. if several evolutionary dimensions representing different stable and fit genomic mosaics are available for hybrid populations, rather than populations restricted to evolving only one mosaic pattern. Whether genomic mosaicism is constrained in a hybrid species or not, the estimation of the number of dimensions where genomic variation is confined in combination with a phylogeographic analysis on parental haplotype distributions should be sufficient to test for recurrence, for example by sequencing of variable neutral genomic regions adjacent to species diagnostic markers and identification of these haplotypes among putative cases of HHS. It is therefore interesting to assess whether variation in genomic mosaicism follows different patterns across different hybrid populations in geographically widespread hybrid taxa. It is theoretically possible to use a framework derived from the field of quantitative genetics and apply it to genes or even genomic regions instead of traits to investigate this question, as described below.

This framework relies on the use of factor analysis to characterize the dimensionality of genomic mosaicism across diverging hybrid populations, which would require identification of genomic markers that were fixed or nearly so in the two parent species, in order to examine covariances in their patterns of admixture (Fig. 2). This is comparable to the issue of the dimensionality of genetic variation for phenotypic traits, in which genetic correlations constrain phenotypic divergence even when each trait alone possesses significant amounts of additive genetic variation (Chenoweth et al., 2010). Factor
analysis estimates the number of underlying variables causing variation in the data, by estimating multivariate dimension axes and condensing dimensionality by factoring in several traits into different components in a hierarchical fashion. In the context of genomic mosaicism, we define each dimension as a specific combination of parental genomic regions that hybrid populations have evolved towards. It is of course entirely possible that hybrid populations may only evolve along one dimension i.e. one pattern of mosaicism (Fig. 2A), but if several of them are available, selection and/or drift will then be influenced by the amount of variation in mosaicism present after HHS as occurred. By estimating the variance-covariance matrix of parental allele frequencies at the population level (i.e. similar to a divergence matrix sensu Chenoweth et al., 2010), one can assess the dimensionality of genomic mosaicism and how genomic constraints can thus influence the evolutionary trajectory of hybrid populations. This approach has been successfully used in other contexts such as the dimensionality of mate choice (Hohenlohe and Arnold, 2010), selection (Nosil et al., 2008) or gene expression (Innocenti and Chenoweth, 2013) across species. However, this approach entails both extensive sampling of hybrid populations and genotyping of a relatively large amount of genetic markers. Other issues may also arise due to the effect of admixture linkage disequilibrium if the HHS event is recent, or the degree of independence between hybrid populations in terms of their recurrence during speciation and their current level of gene flow. Additionally, mosaicism dimensionality could be studied in synthetic hybrid and backcrossing experiments, this time at the individual level, by estimating the genomic variance-covariance matrix of parental alleles in early generation hybrids. This could then be used to predict the evolutionary trajectory of genomic mosaicism in a similar way as the G-matrix has been used to predict the evolution and dimensionality of phenotypic traits (Hansen and Houle, 2008; Chenoweth et al., 2010). But given the expected high levels of linkage disequilibrium in these synthetic early generations hybrids, such experimental work would tend to underestimate the full evolutionary potential of genomic mosaicism.

5 Conclusions

Given the numerous recent studies, HHS may be a
more common mode of speciation than previously thought; it is therefore time to tackle the variety of evolutionary questions associated with it. The deterministic or stochastic nature of this mode of speciation should be compared to cases of bifurcating speciation, and the role of genomic, ecological and historical contingencies needs to be investigated in the recently described examples of HHS, as has been done for ecological speciation (reviewed by Langerhans and Riech, 2013). In particular, both extrinsic and intrinsic barriers between a hybrid species and its parents might favor recurrent HHS, and the role of ecology (Welch and Riech, 2002) should be assessed relative to other factors such as genomic and historical contingency in order to reach a better understanding of the underpinnings of HHS.

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**Corrigendum**

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