COMMENTARY

Hybridization and the origin of species

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The phenomenon of hybridization has fascinated scientists for many decades and in various biological contexts (e.g. Darwin, 1862; Haldane, 1922; Dobzhansky, 1937; Mayr, 1946; Anderson, 1949; Hewitt, 1996; Mallet, 2005). Despite the long history of hybridization research, many open questions remain, some of which can only now be tackled due to the rapid improvement of sequencing technology. The significance of hybridization in speciation processes has long been debated, since hybridization might also promote the fusion of taxa (Seehausen, 2004). Furthermore, interspecific hybridization has often been seen as an exception rather than the rule, but it is meanwhile evident that a large number of species hybridize regularly, even though only a small fraction of a population may be involved (Mallet, 2005).

The review by Abbott *et al.* (2013) highlights the significance and the multitude of possible impacts of hybridization on speciation processes. These vary from direct formation of new hybrid taxa to indirect effects, such as reinforcement of pre-mating barriers in hybrid zones. One important message of the review by Abbott *et al.* (2013) is that a high number of possible outcomes of hybridization exist, depending on the genetic constitution, demography, ecology and spatial distribution of the species involved – all of which are highly variable. The multidimensional framework in which hybridization takes place and the fact that hybridization relationships are usually asymmetric between the involved taxa and sexes (Wirtz, 1999; Gröning & Hochkirch, 2008) creates an extraordinary high number of possible interactions and it will remain a challenging task to disentangle the contribution of each single factor to hybridization dynamics.

Here, I want to highlight five aspects, which I consider crucial for understanding the evolutionary role of hybridization: (i) the importance to think in continua rather than in categories, (ii) the need to consider also complete reproductive isolation when discussing possible effects of hybridization, (iii) the importance to distinguish selective effects of hybridization from pure recombination, (iv) the relevance to integrate interdisciplinary information in hybridization research and (v) the potential of natural model systems for the study of hybridization and introgression processes.

Accounting for variability: the hybridization continuum

In science, definitions are essential to avoid misunderstandings. However, strict definitions of categories and simple classification systems might sometimes impede scientific progress rather than enhancing it, when categorical classification systems distract from phenomena outside these categories. Many biological phenomena are better explained by continua, including hybridization and speciation processes, which contain a variety of different scenarios and a broad range of intermediate situations. Hybridization is a process that occurs along a continuous cline of relatedness (Fig. 1), spanning a large part of the potential range of matings between inbreeding and complete reproductive isolation (and even beyond, see below). There is no clear border between hybridization and outcrossing.

The critical point in the definition of hybridization as 'reproduction between members of genetically distinct populations' (Barton & Hewitt, 1985) is thus the term 'genetically distinct populations'. As relatedness varies in space and also within populations, multiple outcomes of hybridization may be found even in close proximity (i.e. within populations). Genetic incompatibilities are known to occur also among close relatives, e.g. Rhesus incompatibility in humans (Landsteiner & Weiner, 1940) or pollen incompatibilities in plants (Ascher & Peloquin, 1968). However, it is likely that there is a strong correlation between (neutral) genetic differentiation and the accumulation of genetic incompatibilities (Fig. 1). Thus, it might be easier to think of hybridization as a variable process along a cline of increasing probability of accumulating genetic incompatibilities (including coupling of barrier loci and misregulation). Nevertheless, we might expect to find occasionally compatible genotypes even between genetically more distant taxa. Hybridization between these might be more important in speciation processes than those between closer related individuals.

Beyond hybridization: reproductive interference

The second dilemma with the definition of hybridization is caused by the word 'reproduction'. Intuitively it is obvious that hybridization cannot exist without the formation of hybrids. However, the absence of hybrid offspring might simply mean that genetic incompatibilities act already during fertilization or embryonic development (Gröning & Hochkirch, 2008). Thus, by accepting the reproduction boundary we might fail to recognize the significance of interspecific sexual interac-

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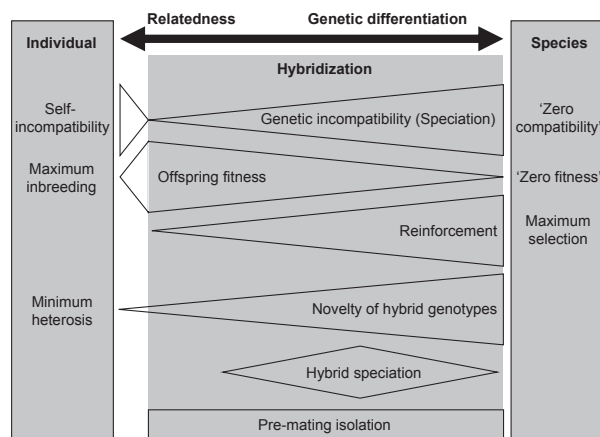Tel.: +49 651 201 4692; fax: +49 651 201 3851;
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Fig. 1 Schematic overview of the continua involved in hybridization and speciation. Genetic incompatibility (reproductive isolation), reinforcement of premating barriers and genetic novelty of hybrid genotypes increase with genetic differentiation, while hybrid fitness decreases. Hybrid speciation is affected positively by the genetic novelty of hybrid genotypes, but negatively affected by genetic incompatibility. It is most likely to occur under conditions of strong genetic differentiation. Pre-mating isolation can evolve spontaneous (independent of relatedness), but is also driven by reinforcement processes. Genetic incompatibility, reproductive isolation and reinforcement peak when speciation is completed, whereas hybrid fitness reaches its minimum ('zero fitness'). Negative effects of inbreeding on offspring fitness and genetic compatibility only occur in a small zone of highest relatedness.

tions that do not produce hybrid offspring (i.e. other types of reproductive interference). Interestingly, such 'zero fitness' situations represent the strongest conceivable selective pressure against interspecific sexual interactions as no genetic information is transferred to the next generation. Therefore, reinforcement of pre-mating barriers is much more likely to occur under such scenarios of low hybrid fitness (Spencer *et al.*, 1986), i.e. between fully reproductively isolated species. Evidently, reinforcement cannot influence a speciation event among fully isolated species. However, it may promote the evolution of pre-mating barriers within each of these species compared to populations which are not in contact with the interacting species (Noor, 1995; Gröning & Hochkirch, 2008). If we transfer this scenario to a larger geographic scale or to more complex ecological communities, we might find situations in which a species interacts with multiple other species in various parts of its geographic range (Hochkirch & Lemke, 2011). This might promote the rapid evolution of pre-mating barriers among different populations of a species, promoting bursts of rapid radiations (Hochkirch & Husemann, 2008). Due to the high variability of environmental, genetic and demographic settings across a large geographic range, we may also find multiple scenarios of hybridization dynamics, including unimodal and bi-modal hybrid zones (Jiggins & Mallet,

2000) leading to a variety of fission and fusion processes across larger hybrid zones.

Defeating species concepts: the speciation continuum

The second process which must be understand as a continuum is speciation itself. This problem is closely affiliated to the long debate on species concepts. If the biological species concept (Mayr, 1942) is applied, reproductive isolation is the main variable of interest in speciation research (Fig. 1). As explained above, reproductive isolation is highly variable among individuals within populations as well as among populations, species or other taxa. If post-mating isolation is driven by genetic incompatibilities, the process of speciation follows the same cline of relatedness as hybridization. This also means that the evolution of complete reproductive isolation gradually crosses a variety of intermediate situations, unless it is caused by near-instantaneous events (e.g. hybridization). Therefore, we might encounter numerous situations of incipient species groups, which are not fully reproductively isolated. Situations of full reproductive isolation in the sense of the biological species concept simply represent the outer edge of this continuum (Fig. 1). As a consequence, there is also no difference between species recognition systems and mate recognition systems (Mendelson & Shaw, 2012). Mate recognition systems are likely to be selected to minimize fitness loss from choosing an incompatible mate (i.e. avoiding both inbreeding and outbreeding depression). Species recognition systems can thus be considered a by-product of choosing a compatible genotype.

The hybrid species trade-off: genetic incompatibility versus evolutionary novelty

Thinking in continua helps to understand, why the accumulation of genetic incompatibilities and evolutionary novelty of hybrid genotypes represent two sides of the same coin. Both phenomena correlate with genetic differentiation: The more distantly related two individuals are, the higher is the genetic novelty of the hybrid genotype but the lower is the chance of genetic compatibility. This suggests that an 'optimal genetic distance for homoploid hybrid speciation' (Abbott *et al.*, 2013) is likely to be closer to the end of lower relatedness. On the other hand the probability to produce viable hybrids decreases along the same axis, suggesting that a trade-off between genetic novelty and incompatibility might influence hybrid speciation.

Hybridization versus selection?

Abbott *et al.* (2013) point out that it will be important to determine 'the role of hybridization *per se* versus

subsequent ecological selection' in the establishment of hybrids. Indeed, if we accept that the formation of hybrid offspring is a necessary element of hybridization, we may simply replace 'hybridization' by 'recombination', which creates variability upon which selection acts. Genetic incompatibilities may be viewed as part of this recombination process. However, if we consider the abovementioned close relationship between hybridization and 'zero fitness' situations (i.e. no hybrid offspring), it becomes clear that selection is already involved in the hybridization process itself. Selection is caused by differences in fitness. Hence, the encounter of two completely incompatible gametes (zero fitness) is equivalent to negative selection on the parental generation. Positive selection may only be found, if the hybrid reproduces. As individual development is also a continuous process, genetic incompatibilities can affect fitness at several stages, such as the formation of the zygote, embryogenesis, hybrid viability or fecundity (Fig. 2). Thus, the pair of gametes (the source of variation) passes several selection filters along this developmental continuum. This illustrates that all genetic incompatibilities are a source of negative selection, whereas the recombination part of hybridization is only determined by the idiosyncrasy of the two encountering gametes. The latter is a matter of stochastic as well as deterministic elements (e.g. dispersion, mate choice, niche overlap, demography). In order to unravel the roles of hybridization and selection, we thus need to separate factors that influence the source of variation (i.e. behavioural and ecological factors that influence the encounter of gametes) from selective elements (i.e. the compatibility of the pair of gametes).

If compatibility of gametes is strong enough to produce fertile offspring and if novel genotypes have a selective advantage, introgression is likely to occur. In this context, pre-mating isolation is a particularly interesting phenomenon, as it is more or less independent of genetic differentiation (although it can be positively selected by reinforcement processes in contact zones; Fig. 1). Pre-mating isolation is frequently found between closely related taxa (Coyne & Orr, 1989). If pre-mating isolation is strong and post-mating isolation is weak, hybridization might occur rarely, but hybrid fitness can be high as its potential to backcross is then mainly determined by the function of the pre-mating barrier. This can lead to multiple backcrosses with subsequent introgression of genetic information into the parental gene pool. Such scenarios may produce the frequently reported situations, in which the phylogenetic reconstruction of taxa (including the reconstruction of speciation events) remains difficult due to introgression of uniparentally inherited genetic information, such as mtDNA (e.g. Shaw, 2002). Introgression is an interesting evolutionary phenomenon, which probably deserves more attention.

Studying hybridization dynamics: integrating multidisciplinary information

In addition to the new possibilities from next generation sequencing, it will be important to integrate such new genetic information with data from other disciplines. As pointed out by Abbott *et al.* (2013), hybridization often occurs in 'complex spatial and temporal context'. The combination of geographic, ecological, demographic and genetic data will help to understand the mechanisms behind hybridization dynamics in a spatio-temporal context. This approach might enable us to answer questions like 'Which parental genotypes are
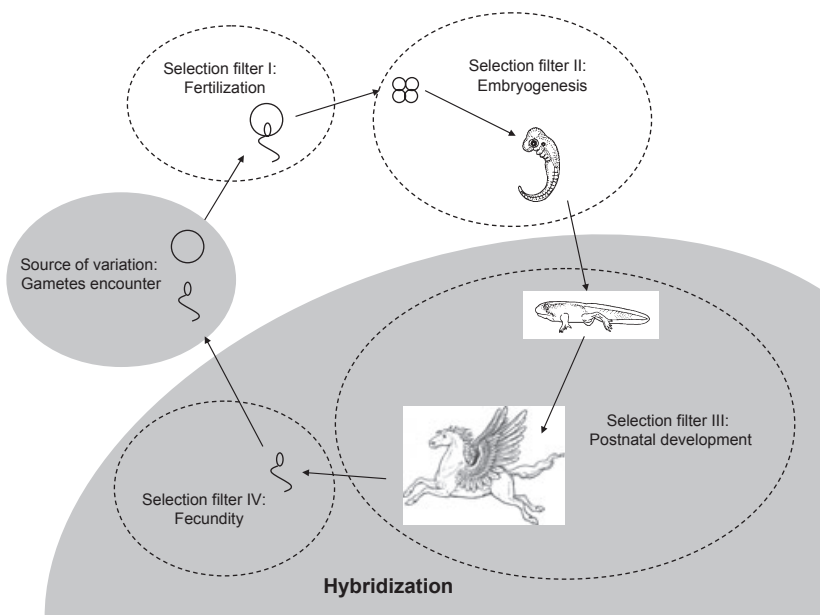

Fig. 2 Schematic overview of the developmental continuum in which hybridization takes place. The quality of the two encountering gametes represents the source of variation. The pair of gametes passes several selection filters until positive selection is reached (fertilization; embryogenesis; postnatal development; hybrid fecundity). The hybrid gametes pass these filters a second time during F1 reproduction.

compatible at which place and under which environmental or demographic conditions?', 'Which genetic conditions of hybrids are beneficial under various environmental conditions?', 'How does environmental variation influence hybridization asymmetries or equilibria?' or 'How is it possible that the gene pool of a native species is completely swamped by hybridization with an invasive species?'.

Many of these questions are probably easier explored experimentally than under natural conditions. However, the great variability of natural settings provides also some interesting opportunities for studying hybridization dynamics: (i) Hybrid zones represent the classical example for such a setting (Bigelow, 1965; Barton & Hewitt, 1985; Buggs, 2007). In some of these zones (e.g. the *Chorthippus parallelus/erythropus* hybrid zone in the Pyrenees) extensive information on the ecological and behavioural background is already available (e.g. Butlin, 1998). As individual fitness is highly variable even within populations (Rodriguez-Munoz *et al.*, 2010), it would be valuable to get information upon the individual contribution to hybridization and the role of the environment versus stochasticity. Studying the effect of directed environmental change (e.g. climate change) on hybridization dynamics and equilibria (e.g. hybrid zone stability versus movement) will also be of high interest, as it provides insight into the temporal dynamics of hybridization and might help to reconstruct past processes. In order to study spatial variation in hybridization dynamics, mosaic hybrid zones might offer an interesting variability of scenarios. (ii) Invasions of incipient species also represent ideal systems for the study of hybridization processes (Schulte *et al.*, 2013). This is particularly true if the spatio-temporal history of the invasion is well documented and if the hybridization event is rather recent. Such situations will help to unravel the processes involved in the onset of natural secondary contact zones and to determine advantageous genotypes and the introgression of alleles into the native gene pool. (iii) As outlined by Abbott *et al.* (2013), rapid radiations are likely to be strongly influenced by hybridization processes. New technologies might help to reconstruct speciation events, identify hybrid species and identify genomic regions which are positively selected and introgressed preferably. It would be particularly worthwhile to study the role of sexual interactions in the evolution of premating barriers. This might help to get answers concerning the rapid evolution of biodiversity.

Acknowledgments

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