Hybridization, Organismal

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Glossary

Allopatry Occurrence of two species or populations in different areas so that their ranges do not come into contact.

Biological species concept According to Ernst Mayr, species are groups of interbreeding natural populations that are reproductively isolated from other such groups.

Haldane's rule According to this principle, if the offspring of two different populations or taxa suffer greater viability or fertility, it is the heterogametic sex.

Hybridogenesis A form of clonal reproduction in species hybrids whose gametes carry only the nuclear genome derived from one of the parental species. For example, the edible frog (*Rana esculenta*) is formed by crosses between the pool frog (*Rana lessonae*) and the marsh frog (*Rana ridibunda*) but possesses only *ridibunda* chromosomes and *lessonae* mitochondria in Western Europe (and vice versa in Eastern Europe).

Hybrid swarm A population of hybrids of higher filial and backcross generations produced after a breakdown of reproductive barriers between two species.

Hybrid zone A naturally occurring area where two genetically differentiated populations meet, mate, and produce hybrid offspring.

Introgression Invasion of foreign genetic material into a genome. A gene flow from the gene pool of one species into the gene pool of the other through repeated backcrossing of hybrids with one of the parental species.

Polyploidy A cell or an organism is called polyploid if it carries multiple sets of chromosomes. The multiplied chromosome sets can come from the same species (autopolyploidy) or two different species (allopolyploidy).

Speciation The evolutionary process of formation of a new species.

Tension zone The type of hybrid zone maintained by the balance between dispersal of individuals and selection against hybrids.

Introduction

Hybridization is usually defined as successful mating between individuals from genetically distinguishable populations (here the term refers only to hybridization in the wild). With accumulation of DNA sequence data, it is becoming apparent that limited gene flow between species or other taxa due to hybridization is more widespread than previously thought, with potentially important implications for speciation studies, biodiversity research, and conservation strategies.

It is usually asserted that hybridization is more frequent in plants than in animals. Indeed, until recently, zoologists considered it an unnatural or aberrant breakdown of reproductive barriers, often caused by habitat disturbance. This view prevails in most species concepts. By contrast, botanists usually acknowledge that hybridization is commonplace in nature and many of them consider introgression to be an important agent of adaptation. However, with the accumulation of DNA sequence data, it is becoming obvious that exchange of genetic material is widespread also in animals.

Hybridization Rates

Current estimates show that hybridization occurs in at least 25% of vascular plant species and 10% of animal species. However, these figures are likely to be underestimated since many backcross hybrids are morphologically almost indistinguishable from one of the parental species and hence remain undetected. Thus, it might be argued that the estimates of the hybridization rate are biased because this phenomenon is recorded predominantly in conspicuous species with easily detectable hybrids. This can hold for ducks, birds of paradise, or heliconid butterflies, but similar rates have also been ascertained for larger groups such as all world's bird species or European species of butterflies and mammals. Conversely, in inconspicuous and/or morphologically uniform groups such as warblers or small mammals, hybridization can remain undetected.

It is widely thought that natural hybridization is often facilitated by human introductions and/or environmental degradation caused by human disturbance. This is true for many cases of hybridization, such as between the ruddy duck (*Oxyura jamaicensis*), introduced from the Americas to Europe, and the Spanish white-headed duck (*Oxyura leucocephala*). Widely known is hybridization in the Galapagos caused by an El Niño event. Before this event, hybrids between three Darwin finches (*Geospiza fuliginosa*, *G. fortis*, and *G. scandens*) were rare and nonreproducing. After the climatic disturbance, two classes of hybrids and two classes of backcrosses demonstrated higher survival, recruitment, and rate of breeding than any of the parental taxa. It is expected that progressing deterioration of the environment and fragmentation of natural habitats will increase the frequency of hybridization events between previously reproductively isolated taxa. On the other hand, there is growing evidence of natural hybridization independent of environmental changes. For instance, many hybrid specimens of neotropical butterflies were identified long before the modern forest fragmentation that brought species from different habitats into contact.

The time since divergence of taxa is one of the factors potentially affecting the frequency of hybridization. Both

laboratory experiments and data from natural populations show that the strength of prezygotic and postzygotic isolation is strongly correlated with the genetic distance between pairs of taxa and hence with the time since their split. In other words, the longer the two taxa are separated, the stronger will be the barrier between them. However, even if we take into account different times of divergence between pairs of taxa, it appears that some groups hybridize much more readily than others. One possible explanation of these differences may be ascertainment bias. As mentioned above, hybrids of brightly colored or otherwise conspicuous species, such as ducks, birds of paradise, game birds, or many butterfly groups, are more easily identified and hence are more often recorded than hybrids between morphologically uniform species. The ascertainment bias is likely to be reduced with advancing molecular studies applied on a wide range of free-living organisms. Notwithstanding potential artifacts due to unequal proportion of various groups of organisms in hybridization studies, some intrinsic factors must exist that affect the per species rate of hybridization. For example, more integrative morphogenesis or higher rate of developmental change and regulatory gene evolution has been suggested as the factors impeding gene flow between some species. However, both explanations are unlikely to encompass the whole diversity of organisms. Another hypothesis suggests that higher hybrid incompatibilities of the heterogametic sex (Haldane's rule) exist in species with larger X or Z chromosomes.

The rate of hybridization can also be affected by behavioral influences. For example, polygynous species where males do not contribute to the care for nestlings (e.g., birds of paradise, game birds, many duck species) have been suggested to be more prone to hybridization with other taxa. In such species, a male tends to mate with any female he encounters, thus increasing the probability of interspecific crossings. However, recent molecular studies reveal that many apparently monogamous species engage in extra-pair copulations and hence can be considered effectively polygamous, suggesting that the distinction between monogamous and polygamous mating system may be blurred. Moreover, in some monogamous groups with paternal care, there are substantial differences in the per species rate of hybridization, for example, between the New World Warblers (Parulidae) with a high rate and their relatives and the Old World Warblers (Sylviidae) with a low rate of hybridization.

It was shown that the rate of introgression is highly heterogeneous across the genome: introgression of loci under divergent selection in the two hybridizing taxa (along with neighboring genomic regions) is strongly impeded, while other loci spread across the contact zone relatively freely. The most extensive introgression can be expected in loci, rendering an advantage on the foreign genetic background at the individual or gene level.

Hybridization and Hybrid Zones

Hybridization between organisms can range from an occasional and highly localized event to large-scale processes resulting in extensive areas harboring hybrids of multiple filial and backcross generations. These areas, usually called hybrid swarms (Figure 1(a)), include genotypes and phenotypes
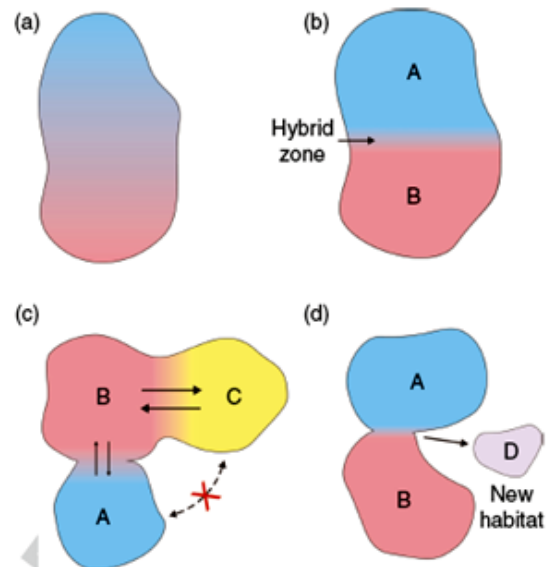

Figure 1 Various outcomes of hybridization: (a) hybrid swarm; (b) a narrow hybrid zone maintained by higher fitness of hybrids relative to parental populations at the boundary between two habitats (bounded hybrid superiority): extrinsic (exogenous) selection against alleles adapted to the opposite habitats, or intrinsic (endogenous) selection against hybrids; (c) two species are reproductively isolated (A, C) but can exchange alleles through a third species (B); (d) hybridization between species A and B results in formation of a hybrid taxon; novel combination of alleles allows colonization of a new, previously uninhabited, habitat and the origin of a new species (hybrid speciation).

ranging widely between the two parental types, thus blurring boundaries between hybridizing taxa. In extreme cases, the parental genotypes may even be completely missing. More often, hybridization is confined to spatially localized hybrid zones (Figure 1(b)). Hybrid zones are usually defined as areas where genetically distinct groups of individuals meet, mate, and leave offspring of mixed ancestry. Position and structure of a hybrid zone can be determined by environmental conditions, for example, when parental taxa are adapted to different habitats. Then the zone is localized in an area of contact between the habitats (e.g., forest–meadow), or ecotones, and its shape can vary from place to place. In addition, transitions in allele frequencies or clines are expected to be different for genes with different functions. Alleles adapted to one habitat are selected against when appearing in the other habitat and hybrid individuals are confined to the transition area, maintained by a balance between influx of parental genotypes and extrinsic selection against ill-adapted genotypes. Alternatively, fitnesses of hybrids may be higher than those of either parental population. In this case of 'bounded hybrid superiority', the zone is maintained by balancing selection favoring hybrids within a narrow region of intermediate habitat, and is thus independent of dispersal.

Sometimes, the environment is rather patchy, forming a mosaic of various habitats. If there is a close association between genotypes and different habitats, the structure of the hybrid zone may be quite complex (Figure 2). For example, two species of crickets, *Gryllus firmus* and *G. pennsylvanicus*, form a mosaic hybrid zone in northeastern United States brought about by intermingled patches of sand and loam soil. Likewise,
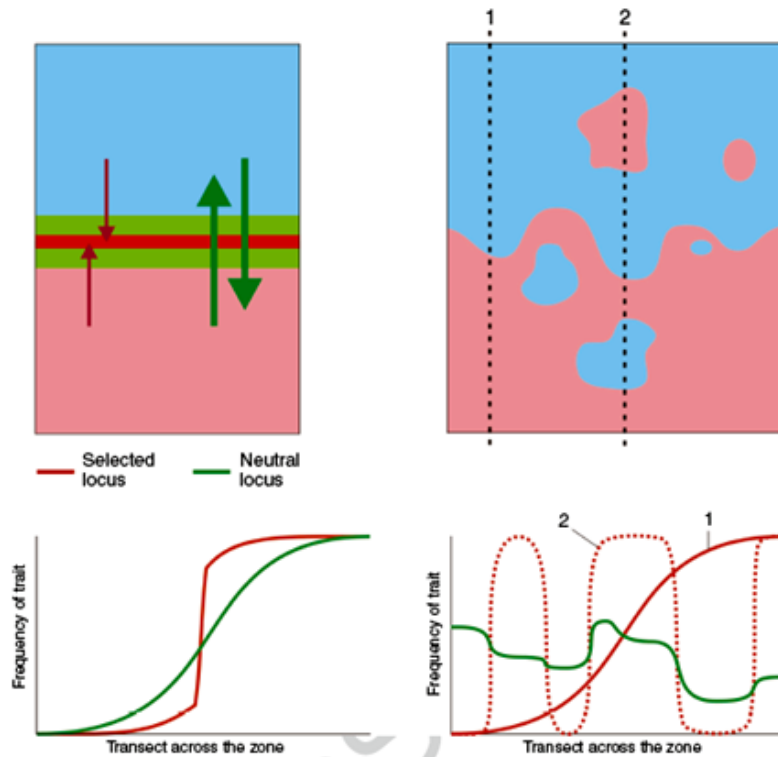
Figure 2 Left panel: smooth hybrid zone maintained by extrinsic or intrinsic selection. Whereas movement of alleles selected against across the zone is impeded so that the cline for such locus is steep, neutral alleles introgress rather freely, resulting in wide clines. Right panel: mosaic hybrid zone; although transition of an allele across this zone can be smooth (transect 1) more often, the pattern is very complex, formed by a series of local hybrid zones brought about by a complex mixture of different habitat patches (transect 2). If an allele is selectively neutral with respect to the habitats, its frequency varies randomly across the zone.

in the hybrid zone between Louisiana irises *Iris fulva* and *I. brevicaulis*, *I. fulva* individuals are restricted to more forested places.

However, clines are usually much narrower than potential environmental gradients. Moreover, most hybrid zones consist of a set of clines clustered at the same place, even for characters with no obvious functional relation and with similar width and shape across different portions of the zone. These patterns are unlikely for clines maintained directly by the external environment. The zones are maintained by a balance between dispersal and intrinsic selection, so that alleles are selected against when appearing on a foreign genetic background. These hybrid zones are called 'tension zones' because they tend to move so as to minimize their length, due to differential dispersal (Figure 3(b)). Since selection is not dependent on a particular habitat, a tension zone can move from place to place and will usually stop at a
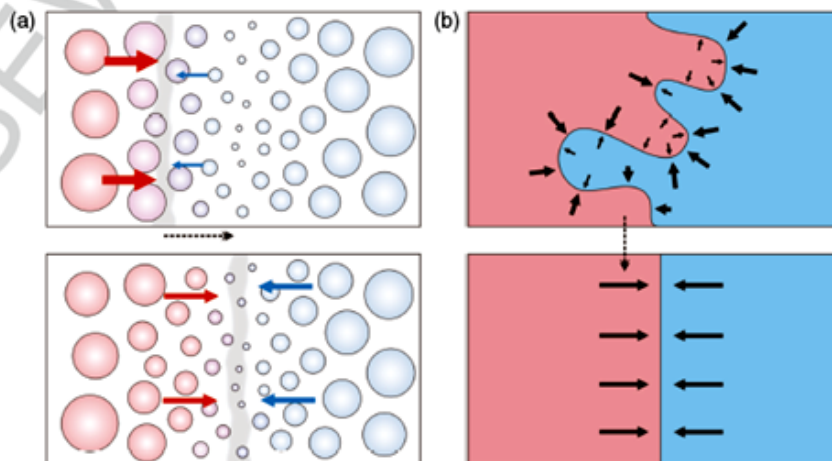

Figure 3 (a) A tension zone will move across geographical space from areas of high population densities (large bubbles) to areas of low densities (small bubbles) and eventually stop at a 'population trough' where habitat is the least suitable for both hybridizing taxa. (b) Local differences in migration due to different population sizes make the tension zone to move so as to minimize its length. In both panels, differences in migration rate are depicted with arrows of varying thickness.

geographic barrier or in an area of the lowest population density ('density trough', Figure 3(a)). Among the best studied tension zones are those between the fire-bellied toad (*Bombina bombina*) and yellow-bellied toad (*B. variegata*), grasshoppers *Chorthippus parallelus parallelus* and *C. p. erythropus*, and house mice *Mus musculus musculus* and *M. m. domesticus*. In many cases, however, exogenous and endogenous selection both may affect the same hybrid zone, or the zone structure may vary among different areas. For example, *B. bombina* and *B. variegata* form a tension zone in Central Europe, yet both species are adapted to different habitats. In Croatia, where the habitats are patchily intermingled, the zone is mosaic.

Hybridization as an Active Evolutionary Force

Some authors suggest that hybridization between species can play a more active role in species evolution than previously acknowledged. For example, many species of bacteria benefit from gene exchange with distantly related taxa, often gaining new adaptive traits such as resistance to antibiotics. Likewise, insecticide resistance is thought to be transferred via interspecific gene flow in mosquitoes and blackflies. Similar positive effects of hybridization on fitness has been recorded in Darwin's finches, *Heliconius* and *Papilio* butterflies as well as in other organisms. Introgression can increase variation but new combinations of genes that arise can allow colonization of a new habitat (Figure 1(d)) and, eventually, lead to the origin of a new species (e.g., *Helianthus* sunflowers, *Lycaeides* and *Heliconius* butterflies). Hybrid speciation is usually associated with allopolyploidization (i.e., doubling of the chromosome set via fusion of two different genomes). Polyploidy is frequent in plants, whereas in animals it can only be found in some groups with undifferentiated sex chromosomes and/or parthenogenetic reproduction (fish, amphibians).

The origin and evolution of a new species may not be restricted to a unique hybridization event. Rather it can be dependent on a specific form of long-persisting interspecific hybridization called hybridogenesis. For example, the edible frog (*Rana esculenta*) is formed through crosses between the marsh frog (*Rana ridibunda*) and the pool frog (*Rana lessonae*). Whereas both genomes participate in formation of somatic tissues, *lessonae* chromosomes are eliminated from the germ line in Western European populations (conversely, chromosomes derived from *ridibunda* are not passed on to gametes in frogs from Eastern Europe). Thus, from the pool frog's view (in Western populations), its gametes are 'stolen' by *R. esculenta* and so the latter species is sometimes called klepton (from Greek *kleptein* means 'to steal') and the whole group of the three forms is called synklepton.

See also: Hybrid Zone, Mouse (00755); Species (01454).

Further Reading

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Relevant Websites

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http://en.wikipedia.org/wiki/Hybrid_speciation – Hybrid speciation.

http://en.wikipedia.org/wiki/Hybrid_zone – Hybrid zone.

http://en.wikipedia.org/wiki/Polyploid – Polyploidy.

http://en.wikipedia.org/wiki/Species – Species concepts.