EVOLUTION

Sex, Sunflowers, and Speciation

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Why sex evolved and is maintained in most living organisms remains a key question in evolutionary biology (*1*). What is indisputable, however, is that sexual reproduction generates new gene combinations, some of which may render the organism better adapted to new environments. The range of different genotypes among offspring increases with the level of genetic divergence between parents. Therefore, matings between different species (that is, interspecific hybridization) could potentially generate a vast range of different offspring genotypes, provided that the resulting hybrid zygotes develop and exhibit some fertility. On page 1211 of this issue, Rieseberg *et al.* (*2*) describe how hybridization between two sunflower species generated offspring genotypes that are adapted to habitats very different from those occupied by the parents. This resulted in three diploid hybrid sunflower species that are ecologically isolated from each other and their progenitors. The Rieseberg *et al.* findings provide proof that interspecific hybridization can be adaptive.

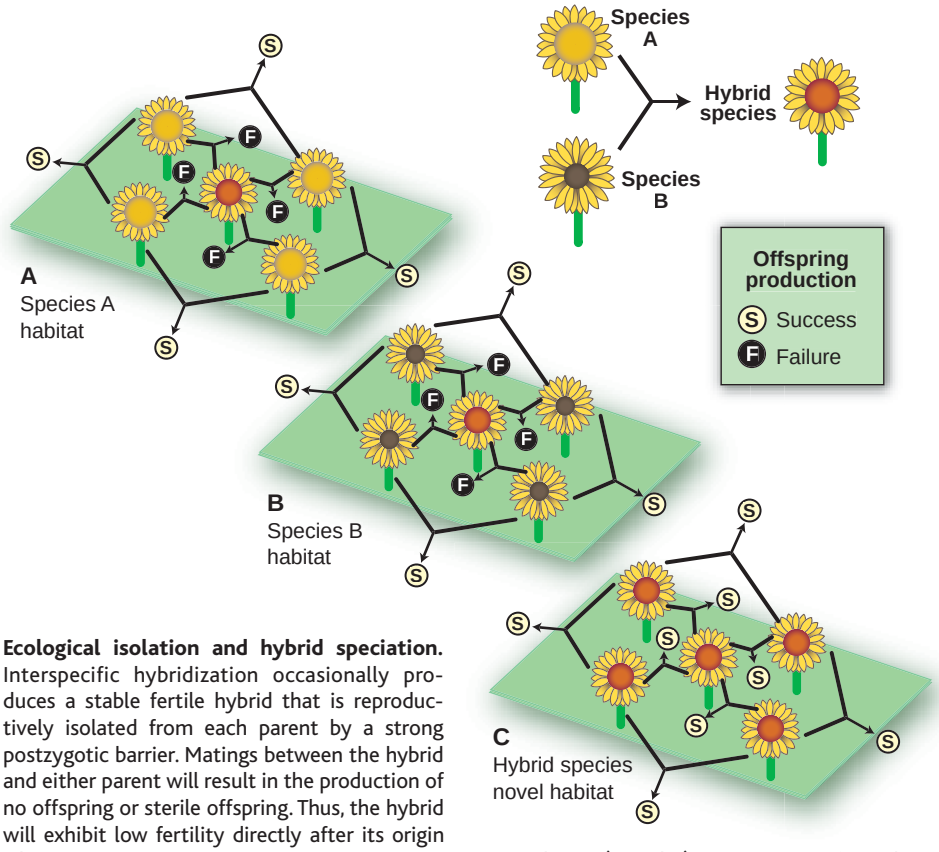
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In many plant groups, hybridization between different species is prevented by prezygotic barriers. Such barriers may arise when species have their own specific pollinator, occupy a habitat different from other species, or are spatially separate from other species. Under these conditions, postzygotic barriers manifested in the form of embryo abortion or low hybrid viability may be absent or weak. However, prezygotic barriers can be "leaky," especially when habitats are disturbed in some way, so hybrids are sometimes produced that are often sterile or exhibit reduced fertility. Such problems of low fertility can be overcome, either by chromosome doubling (allopolyploidy) or recombination (*3*), to produce a stable fertile hybrid that is reproductively isolated from its parents by a strong postzygotic barrier (*4, 5*), and which is therefore regarded as a new species.

Although postzygotic barriers are effective mechanisms of reproductive isolation, they present major obstacles to the establishment of a new hybrid species in the wild. Hybrids are born into populations comprising one or both parent species and will initially be represented as a minority component. Consequently, most matings by a fertile hybrid will be with a parent rather than another hybrid, and will result in the production of no offspring or sterile offspring. The hybrid therefore suffers from what is termed a "minority type disadvantage" (*4*). It can escape from this predicament by evolving a prezygotic barrier that prevents it from mating with its parents. This can be achieved through uniparental reproduction (asexual reproduction or selfing), by flowering earlier or later, by attracting a different pollinator, by occupying a different habitat (ecological isolation), or through spatial isolation due to geographical separation after dispersal (*3, 6*). Ecological or spatial isolation will also enable a hybrid to avoid any adverse effects of interspecific competition with a parent.

So how did the diploid hybrid sunflowers studied by Rieseberg *et al.* escape the minority type disadvantage and become established? Each species is hermaphrodite and, like its parents, reproduces by sexual outcrossing; each occupies a habitat extremely different from those of either parent or the other hybrid species. It is therefore feasible that each species became established in ecological isolation as a result of possessing a hybrid genotype adapted to a new habitat. Alternatively, hybridization may have been incidental and mutation could have created the adapted genotypes over a period of 60,000 to 200,000 years, which is the estimated age of each hybrid species.

To distinguish between these possibilities, Rieseberg *et al.* (*2*) resynthesized a hybrid population between the two sunflower species (*Helianthus annuus* and *H. petiolaris*) known to be the progenitors of the three diploid hybrid species (*H. anomalus*, *H. deserticola*, and *H. paradoxus*). Then they determined whether certain synthetic hybrids possessed the same adaptations as the hybrid species. They found that the majority of extreme phenotypes exhibited by



Ecological isolation and hybrid speciation. Interspecific hybridization occasionally produces a stable fertile hybrid that is reproductively isolated from each parent by a strong postzygotic barrier. Matings between the hybrid and either parent will result in the production of no offspring or sterile offspring. Thus, the hybrid will exhibit low fertility directly after its origin when occurring as a minority component in a parent population (**A** and **B**). It may escape from this "minority type disadvantage" if it is adapted to another habitat where it is ecologically isolated from both parents (**C**). In such habitats it will also avoid any adverse effects of interspecific competition.

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the hybrid species were produced in the synthetic hybrid population, and that synthetics possessing these phenotypes were favored by selection when planted into the natural habitats of the hybrid species. An analysis of the effects of chromosomal segments [termed quantitative trait loci (QTLs)] on each trait showed that in each parent species, at least one QTL of a set controlling a trait had an effect in the opposite direction to that of the others. Therefore, a full set of QTLs with effects in the same direction can be generated by recombination after interspecific hybridization. This produces an extreme phenotype because phenotypic expression is based on the sum of the individual effects of the QTLs (complementary gene action) plus interactive effects (epistasis).

Rieseberg and colleagues show further that QTLs in the hybrid species with effects that increase or decrease the expression of a trait have similar directional effects on other traits (or are linked to genes with such effects). These genetic correlations will have facilitated the selection of appropriate suites of adaptive traits in the formation of the diploid hybrid species and enabled speciation to have proceeded rapidly. Final proof that hybridization generates the adapted genotypes of each hybrid species was obtained when each was shown to contain the right combination of parental chromosomal segments for producing their extreme phenotype, as determined by QTL analysis of synthetic hybrids.

The findings of Rieseberg *et al.* are an important advance in our understanding of the significance of interspecific hybridization in evolution. Proof that this process can be adaptive has until now remained elusive (*7*). Diploid hybrid speciation may be a rare phenomenon (*8*), whereas allopolyploidy is a relatively common mechanism of plant speciation. Future studies of allopolyploids, particularly neoallopolyploids, also should examine whether successful establishment in the wild is dependent on adaptations to new environments generated by the initial bout of interspecific hybridization.

References

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GEOPHYSICS

Mantle Flow Revisited

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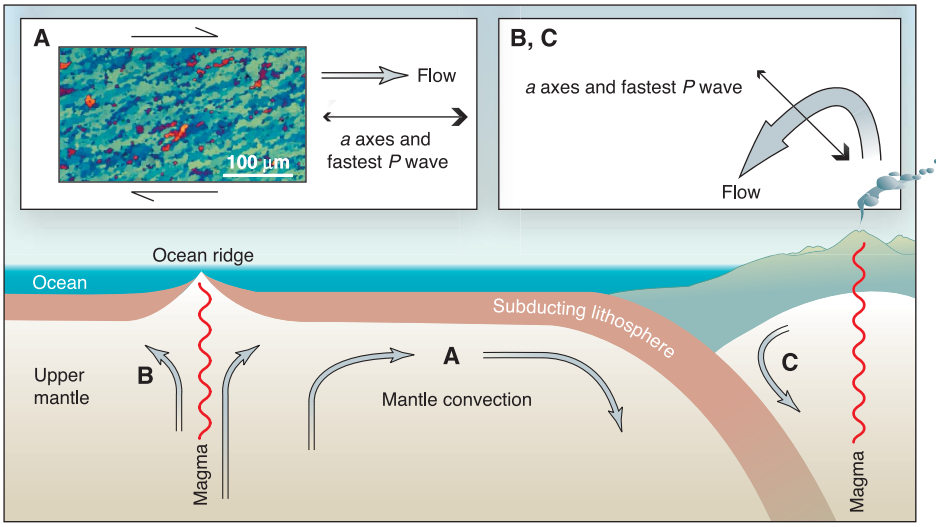
In Earth's upper mantle, high-strain deformation and recrystallization of minerals result in preferred orientations of their crystallographic axes. Because the elastic properties of the minerals vary along different crystallographic axes, the propagation of seismic waves in the upper mantle is anisotropic. Measurements of seismic anisotropy can therefore elucidate flow patterns in the mantle, if the relation between high-strain deformation and mineral orientation is known.

Analyses of naturally deformed upper mantle rocks (*1*, *2*) have provided the basis for a broad interpretation of upper mantle anisotropy and structure. However, the complex seismic anisotropy observed in some regions—for example, close to mid-ocean ridges and subduction zones—has proved difficult to model. On page 1227 of this issue, Holtzman *et al.* (*3*) report laboratory data that may help us to understand seismic data in these regions. They show that melt segregation and strain partitioning in samples of olivine and melt cause a different alignment of olivine crystals than expected. The results necessitate a reinterpretation of flow patterns in partially molten regions of the upper mantle (see the figure).

High-strain experiments have shown that during simple shear deformation of dry olivine, the most abundant mineral in the upper mantle, crystallographic *a* axes tend to align parallel to the shear direction (*4*, *5*). These preferred orientations are consistent with those typically observed in mantle rocks (*2*) and predicted by numerical simulations (*6*). Known intracrystalline deformation properties of olivine (*7*) suggest that the orientations result primarily from "*a*-slip" (the movement of crystal dislocations in the *a* direction).

In olivine, compressional waves (*P*-waves) travel fastest along the *a* axes. Hence, the direction with the fastest *P*-wave velocity is commonly assumed to indicate the flow direction in the mantle. However, Jung and Karato recently showed in laboratory experiments in approximate simple shear that wet olivine preferentially orients with the *c*-axis nearly parallel to the shear direction (*8*). In mantle regions with high water content, the seismically fast direction may thus not indicate the flow direction.

Jung and Karato proposed (*8*) that the presence of water changes the dislocation dynamics in olivine from dominant *a*-slip to



New clues to mantle flow. When dry olivine rocks are exposed to high strains, the *a* axes of the olivine crystals tend to orient nearly parallel to the flow direction (**A**). Based on these results, modeling of seismic anisotropy has provided a broad picture of flow patterns in the upper mantle during mantle convection. Laboratory studies show that in the presence of melt (*3*) or water (*8*), the *a* axes are not parallel to the flow direction. Flow patterns in mantle regions with high melt or water content—for instance, close to spreading centers (**B**) and in the mantle wedge above subduction zones (**C**)—may therefore have to be reinterpreted.

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