

Ecology and the origin of species

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The ecological hypothesis of speciation is that reproductive isolation evolves ultimately as a consequence of divergent natural selection on traits between environments. Ecological speciation is general and might occur in allopatry or sympatry, involve many agents of natural selection, and result from a combination of adaptive processes. The main difficulty of the ecological hypothesis has been the scarcity of examples from nature, but several potential cases have recently emerged. I review the mechanisms that give rise to new species by divergent selection, compare ecological speciation with its alternatives, summarize recent tests in nature, and highlight areas requiring research.

ECOLOGICAL SPECIATION (see Glossary) occurs when DIVERGENT SELECTION on traits between populations or subpopulations in contrasting environments leads directly or indirectly to the evolution of REPRODUCTIVE ISOLATION. The concept of ecological speciation dates back to the 1940s, from the time the BIOLOGICAL SPECIES CONCEPT was developed. Dobzhansky¹ believed that 'SPECIATION in *Drosophila* proceeds mainly through evolving physiological complexes which are successful each in its environment'. Mayr² recognized that many of the accumulated genetic differences between populations 'particularly those affecting physiological and ecological characters, are potential isolating mechanisms'. Acceptance of this perspective by many evolutionists in the mid-20th century resulted from the inherent appeal and simple plausibility of ecological speciation. However, until recently, neither was there evidence to support ecological speciation, nor had tests been devised and applied to distinguish ecological speciation from other mechanisms that might also cause speciation in the wild, such as GENETIC DRIFT (BOX 1).

Mechanisms of ecological speciation

'Ecological speciation' is a concept that unites speciation processes in which reproductive isolation evolves ultimately as a consequence of divergent (including DISRUPTIVE) selection on traits between environments. 'Environment' refers to biotic and abiotic elements of habitat (e.g. climate, resources and physical structure) as well as to interactions with other species (e.g. resource competition, predation, mutualism and various forms of interspecific interference). A diversity of evolutionary processes might be involved. Ecological speciation might occur in ALLOPATRY or in SYMPATRY. It might lead to mainly premating isolation, mainly postmating isolation, or a combination of both. It includes several (but not all) modes of speciation involving SEXUAL SELECTION. Ecological speciation might come about indirectly as a consequence of natural selection on morphological, physiological or behavioral traits, or it might include

direct selection on premating isolation (REINFORCEMENT). Distinguishing the ways in which divergent selection has led to reproductive isolation is among the greatest challenges of the empirical study of ecological speciation.

In what is perhaps the classic scenario for ecological speciation (Fig. 1), reproductive isolation between two populations starts to build in allopatry as populations accumulate adaptations to unique aspects of their environments. Premating isolation then evolves to completion by reinforcement after sympatry is secondarily established. The timing of SECONDARY CONTACT is flexible, however, and the extremes of possibility lead to departures from this classic model. At one extreme is pure ALLOPATRIC SPECIATION, in which the sympatric phase is entirely absent. New species might eventually become sympatric, but this occurs after reproductive isolation is complete. The other extreme is full-blown SYMPATRIC SPECIATION, which completely lacks the allopatric stage. Although debate about the plausibility of these extremes has long polarized research on speciation, from an ecological perspective, the more fundamental issue concerns the mechanisms that drive the evolution of reproductive isolation, which is the focus of this article.

By-product mechanisms

In the simplest models of ecological speciation, reproductive isolation builds between populations incidentally as a by-product of adaptation to alternative selection regimes^{2,3}. Reproductive isolation is not directly favored by selection, but is a secondary consequence of genetic differentiation driven by selection on other traits. This BY-PRODUCT MECHANISM could lead to premating isolation and to various forms of postmating isolation.

Several laboratory experiments with *Drosophila* have simulated the early stages of by-product speciation (reviewed in Ref. 4), and these hint at how the process might work in nature. Kiliyas *et al.*⁵ raised different lines of *Drosophila melanogaster* for five years in either a cold-dry-dark or a warm-damp-light environment. Dodd⁶ examined mating preferences in replicate lines of *Drosophila pseudoobscura* raised for one year on either starch-based or maltose-based larval medium. In both studies, some premating reproductive isolation evolved between lines that had experienced contrasting environments, but no premating isolation evolved between independent lines raised in the same environment (Fig. 2). The populations in these experiments were fully allopatric, as in the first part of the classic scenario (Fig. 1).

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Box 1. The major modes of speciation, according to initial causes

Speciation modes have been classified historically by the geographical arrangement of populations undergoing the process (allopatric, sympatric or parapatric), a classification that focuses on the inhibitory effects of gene flow on the evolution of reproductive isolation. Some have argued that an alternative classification centering on mechanisms that drive the evolution of reproductive isolation would be more productive^{a-c} (Via^d, this issue). Table I breaks modes of speciation events into four categories according to initial cause, and compares some other principal features of those categories.

Natural selection is involved at an early stage of two different modes of speciation. Under ecological speciation, populations in different environments, or populations exploiting different resources, experience contrasting natural selection pressures on traits that directly or indirectly bring about the evolution of reproductive isolation. However, divergence might also occur under uniform selection, for example, if different advantageous (but incompatible)

mutations arise in separate populations occupying similar environments (Turelli *et al.*^e, this issue). Reproductive isolation between populations brought about by conflict and coevolution between the sexes within populations^{f-h} is an example of this second mode.

If populations are in contact before the evolution of reproductive isolation is completed, natural selection might be involved at a late stage of all four modes of speciation, during reinforcement of premating isolation (Turelli *et al.*^e this issue)ⁱ. Similarly, sexual selection might be involved in every speciation mode, depending on the cause of divergence in mate preferences. For this reason, the presence of natural or sexual selection *per se* is probably not a good basis for classifying speciation events. Nevertheless, the classification in Table I is coarse, and finer subdivisions are necessary to highlight differences in the roles of natural and sexual selection within each mode, as well as different roles for genetic drift in speciation initiated by that mechanism.

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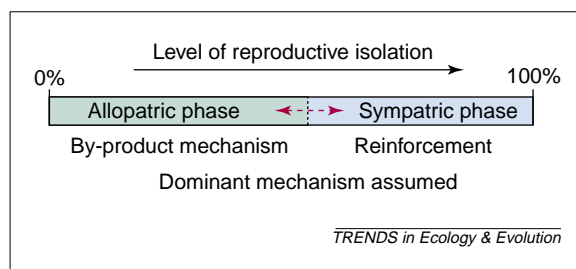
Table I. Modes of speciation

Mode of speciation	Mechanism of initial divergence	Initial form of reproductive isolation	Proximate basis of reduced hybrid fitness	Examples of the roles of natural selection	Example roles of sexual selection
Ecological speciation	Divergent natural selection	Prezygotic or postzygotic	Ecological selection, genetic incompatibility and sexual incompatibility	Initial: Drive divergence in phenotypic traits Final: Reinforcement	Amplify divergence of mate preferences initiated by natural selection Reinforcement
Speciation by divergence under uniform selection	Different advantageous mutations occur in separate populations experiencing similar selection pressures	Prezygotic or postzygotic	Genetic incompatibility and sexual incompatibility	Initial: Drive fixation of incompatible mutations in different populations Final: Reinforcement	Drive fixation of alternative incompatible mutations in different populations Reinforcement
Speciation by genetic drift	Genetic drift	Prezygotic or postzygotic	Genetic incompatibility and sexual incompatibility	Initial: None; or opposes divergence Final: Reinforcement caused by drift	Amplify differences in mate preferences Reinforcement
Polyploid speciation	Hybridization and polyploidy	Postzygotic	Genetic incompatibility	Initial: None; or promotes further genetic divergence Final: Reinforcement	Reinforcement

However, complete allopatry is not crucial for the by-product mechanism, an idea that extends the classic scenario in two ways⁴. First, selection can continue to strengthen reproductive isolation via the by-product

mechanism even when the allopatric phase is over and the sympatric phase is in progress. Reinforcement is not the only way to complete the evolution of reproductive isolation after secondary contact. Second,

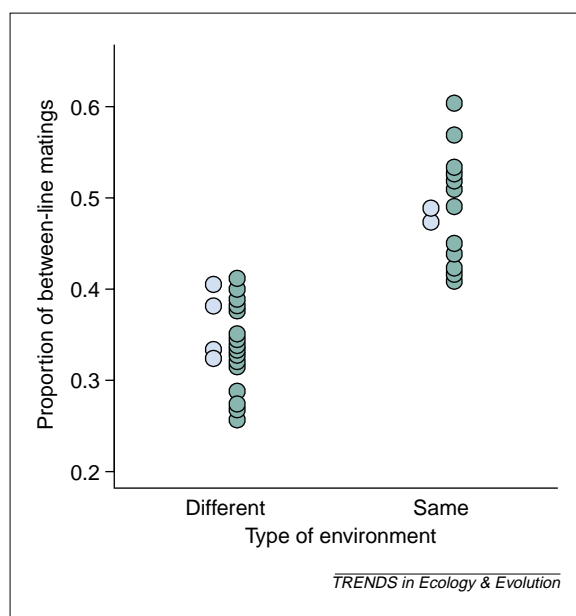
Fig. 1. The classic scenario of an ecological speciation event, from beginning to end. Reproductive isolation builds in allopatry (green) as an incidental by-product of adaptation to alternative environments (by-product mechanism). Reinforcement of premating isolation, driven by reduced hybrid fitness, completes the speciation process during the sympatric phase (blue). The timing of secondary contact is flexible (indicated by arrows at the boundary between the allopatric and sympatric phases).



an initial allopatric phase is not always essential for the by-product mechanism to work, and can be dispensed with if selection is strong enough or if gene flow between subpopulations is not too high (see Turelli *et al.*⁷, this issue, and Via⁸, this issue).

Many different environmental agents of divergent selection could lead to the evolution of reproductive isolation as a by-product, and identifying these alternatives is of major interest. During the allopatric phase, such agents might include contrasting resources, predators, competitors, cytoplasmic symbionts, structural habitat features affecting locomotion or transmission of communication signals, and other biotic and abiotic factors. Allopatric populations might also confront distinct constellations of other closely related species, which could lead to divergence of mating and social signals if these signals evolve partly in response to interspecific interference. The last mechanism extends the by-product concept to divergence in a wider set of traits, such as color and song, than those immediately related to resource acquisition. For example, divergence of color in response to interspecific reproductive or aggressive interference with other species could explain the rapid divergence of sexual signals and mate preferences between spatially separated populations of African cichlid fish that are otherwise similar in food and habitat requirements^{9,10} (see Barraclough and Nee¹¹, this issue).

Fig. 2. Mating compatibility of independent experimental lines of *Drosophila* raised separately over multiple generations in similar or in different environments. Circles represent the proportion of mating events that occurred between individuals from different lines relative to intra-line matings. Data are from *D. pseudoobscura*⁶ (green symbols) and *D. melanogaster*⁵ (blue symbols). Modified from a figure to be published by Cambridge University Press (Ref. 64).



Many agents of divergent selection that drive the evolution of reproductive isolation between two allopatric populations would continue to strengthen isolation following secondary contact. However, other agents of selection that arise from interactions between the two nascent species are added during the sympatric phase, and these too might drive reproductive isolation to completion. For example, competition for resources between sympatric populations could lead to exaggerated divergence in phenotype, and further enhance reproductive isolation as a by-product. Alternatively, divergent selection could generate body size differences that result in predation on the smaller species by individuals of the larger. Any evolution of behavioral defenses in the smaller species would probably reduce the frequency of crossbreeding as a by-product. This last mechanism was raised as a possible explanation for enhanced premating isolation between a pair of threespine stickleback *Gasterosteus* spp. in which females of the larger species prey upon eggs guarded by males of the smaller species¹². The influence of such interactions on the evolution of reproductive isolation during the sympatric phase of speciation has received very little attention.

Reinforcement and sympatric speciation

Divergent natural selection in the allopatric phase might build up differences leading to reduced hybrid fitness after secondary contact that subsequently favor reinforcement^{3,13}. Reinforcement is distinct from the by-product mechanism because selection directly favors enhanced premating isolation as a consequence of the inferiority of hybrid offspring. Dobzhansky³ viewed reinforcement as dominating the completion of ecological speciation after secondary contact (Fig. 1), a claim that remains to be proven. Of course, reinforcement might occur even in non-ecological speciation (Box 1). Consequently, testing ecological speciation requires the examination of processes acting at an earlier stage (e.g. during the allopatric phase).

Most conceptions of sympatric speciation invoke a process similar to that of reinforcement, except that there is no previous build up of phenotypic and genetic differences leading to lowered hybrid fitness. Instead, the fitness of intermediates of a single population is reduced from the start by direct ecological selection pressures. For example, intermediate phenotypes (including hybrids) might exploit available resources less effectively than do extreme phenotypes^{14,15}, or intermediate phenotypes might suffer greater overall resource competition¹⁶. Doebeli and Dieckmann¹⁷ have argued that selection against intermediate phenotypes is the expected outcome of many types of ecological interactions, including competition, shared predation and shared mutualism (see also Ref. 18) and, under certain conditions, these might favor the evolution of premating reproductive isolation in sympatry (see Via⁸, this issue).

Table 1. Tests of ecological speciation in nature

Test	Taxon ^a	Result and implication: consistent (c) or inconsistent (i) with ecological speciation	Refs
Rate of evolution of reproductive isolation is correlated with strength of divergent selection	Hawaiian versus mainland <i>Drosophila</i> spp. pairs	Evolution of reproductive isolation is not faster in Hawaiian <i>Drosophila</i> than in mainland <i>Drosophila</i> (i)	34
	Lake whitefish in different postglacial lakes	Gene flow is inversely correlated with level of morphological divergence (c)	35
Ecological selection reduces hybrid fitness	Threespine sticklebacks in postglacial lakes	F1 hybrid growth rate is lower in the wild than in the lab; rank order of growth rates of backcross hybrids reverses between parental habitats (c)	15, ^b
	Darwin's ground finches ¹	F1 hybrid survival fluctuates with resource distribution (c)	45,46
	Butterfly races	F1, F2 and backcross hybrids have higher viability in the lab than in the wild, and predation is major agent of selection (c)	39
Trait under divergent selection influences reproductive compatibility	Threespine sticklebacks in postglacial lakes	Mating compatibility is influenced by body size and by nuptial coloration (c)	49,58
	Monkey flowers ¹ on different soils	Postzygotic isolation is a pleiotropic effect of a gene encoding tolerance of copper-contaminated soil (c)	47
	Monkey flowers ²	Divergent selection by pollinators is detected on floral traits and underlying quantitative trait loci (c)	48
	Darwin's ground finches ²	Beak and body size, under divergent selection, influence vocal signals and are used as cues in interspecific mate discrimination (c)	50,51
	Pea aphids on different host plants	Divergent selection occurs on host-plant choice, which determines premating isolation (c)	41
	Host races of apple maggot fly on different host plants	Divergent selection on diapause influences timing of emergence (c)	40,61
Parallel evolution of mating incompatibilities over similar environmental gradients	Threespine sticklebacks in postglacial lakes	Independently evolved populations of the same ecotype show strong premating isolation, whereas populations of different ecotypes show little or no premating isolation (c)	55
	Freshwater amphipod from two types of environment	Mating compatibility between populations is high when body size and environment type are similar, but is low when they are different (c)	59
	Leaf beetles on different host plants	Premating isolation is high between populations from same host plants, but is low between those on different host plants (c)	60

^aLatin names: Apple maggot fly, *Rhagoletis pomonella*; Butterfly, *Heliconius erato*; Darwin's ground finches, *Geospiza fuliginosa*¹ and *G. fortis*¹, and *Geospiza* spp.²; Freshwater amphipod, *Hyalella azteca*; Fruit flies, *Drosophila* spp.; Lake whitefish, *Coregonus* spp.; Leaf beetles, *Neochlamisus bebbianae*; Monkey flowers¹, *Mimulus guttatus*; Monkey flowers², *Mimulus cardinalis* and *M. lewisii*; Pea aphids, *Acyrtosiphon pisum*; Threespine sticklebacks, *Gasterosteus* spp.

^bH.D. Rundle, unpublished.

Ecology and sexual selection

Sexual selection is regarded as a potent force driving the evolution of premating and/or postmating isolation between populations (see Panhuis *et al.*¹⁹, this issue). From an ecological perspective, the key question is how divergent mate preferences become established in the first place. In most theoretical models of speciation by sexual selection, divergent natural selection plays a dominant role, as spatial variation in selection on SECONDARY SEXUAL TRAITS²⁰, as divergent selection on sensory systems²¹, or as differences between environments in the most effective modes of mating signal transmission^{22,23}. By contrast, genetic drift²⁴ or unique mutations favored by intersexual conflict^{25,26} play the dominant role in the evolution of reproductive isolation in non-ecological models of speciation by sexual selection. Therefore, a demonstration that sexual selection is involved in the speciation process does not, by itself, restrict the range of speciation models under investigation (Box 1). The mechanisms ultimately driving divergence of mate preference, in particular the role of divergent natural selection, must still be identified.

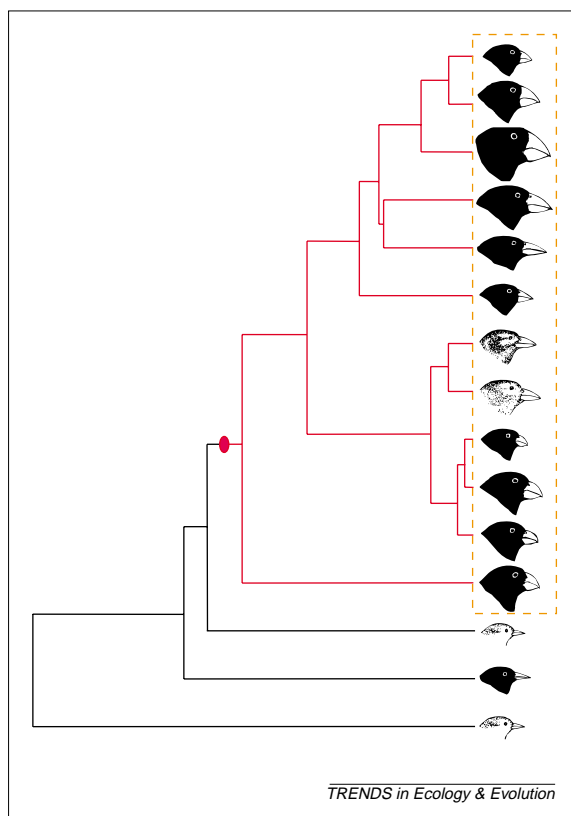
Tests of ecological speciation

Tests of ecological speciation must consider the alternatives that need to be distinguished (Box 1):

speciation by ordinary genetic drift or genetic drift during population BOTTLENECKS^{27,28}; speciation by fixation of alternative advantageous genes in populations experiencing similar selection pressures²⁹; and speciation by polyploidy^{30,31}. Speciation by polyploidy can be readily diagnosed genetically, but although it is more common in plants than animals, polyploidy accounts for only 2–4% of plant speciation events³². Even in plants, the cause of most speciation events remains to be identified.

Several tests have been carried out in recent years that indicate a role for divergent selection in the origin of species in nature (Table 1). Demonstrating a role for divergent selection in speciation, however, is only the first step to detecting an ecological speciation event. The next step is to understand the process by which divergent selection has led to the evolution of reproductive isolation (e.g. by-product alone or with reinforcement, mechanisms of hybrid fitness, etc.), a step in which less progress has been made. I have not reviewed evidence from molecular studies that infer natural selection from an unusually high rate of sequence divergence between sister species³³ because that method does not distinguish divergent from uniform selection (Box 1).

Fig. 3. A phylogenetic tree showing the possible correlation between ecological diversification and speciation rate in the Darwin's finches (*Geospiza* spp.). The high diversity of beak traits among species within the CLADE of tree and ground finches (outlined in red) contrasts with the lower diversity of beak traits among species of the three older LINEAGES. Speciation rates are also highly uneven, being significantly greater in the tree and ground finch clade than in the rest of the tree ($P = 0.011$, calculated using the Nee *et al.*⁶² equal-rates test for multiple lineages). Data are taken from Ref. 63. Bird images are reproduced, with permission, from Ref. 65.



Divergent selection and the rate of evolution of reproductive isolation

The study of ADAPTIVE RADIATION suggests that speciation rates are often elevated during periods of ecological and phenotypic differentiation³⁴ (see Barraclough and Nee¹⁹, this issue). Darwin's finches appear to exemplify this pattern (Fig. 3): one explanation is that if the level of phenotypic differentiation is indicative of strength of divergent selection, then reproductive isolation evolves most quickly when divergent selection is strongest. A correlation between strength of divergent selection and rate of evolution of reproductive isolation is a prediction of ecological speciation (Table 1).

The correlation between strength of divergent selection and rate of evolution of reproductive isolation has not been measured, probably because divergent selection is difficult to quantify. Instead, researchers have used indirect measures (Fig. 3). Lu and Bernatchez³⁵ compared gene flow with the level of morphological differentiation between INCIPIENT SPECIES of dwarf and normal lake whitefish *Coregonus* in several postglacial lakes of eastern Canada and northern Maine (USA). Estimated levels of gene flow between sympatric dwarf and normal populations were lowest where morphological differences between the forms were greatest. This is consistent with the prediction of ecological speciation if the degree of morphological differentiation is a good index of strength of divergent selection. Alternatively, the strength of divergent selection is not different between lakes, and variation in morphological

differentiation results instead from variation in gene flow. Preliminary measurements of the resources available in the lakes suggest that the strength of divergent selection is different between lakes³⁵.

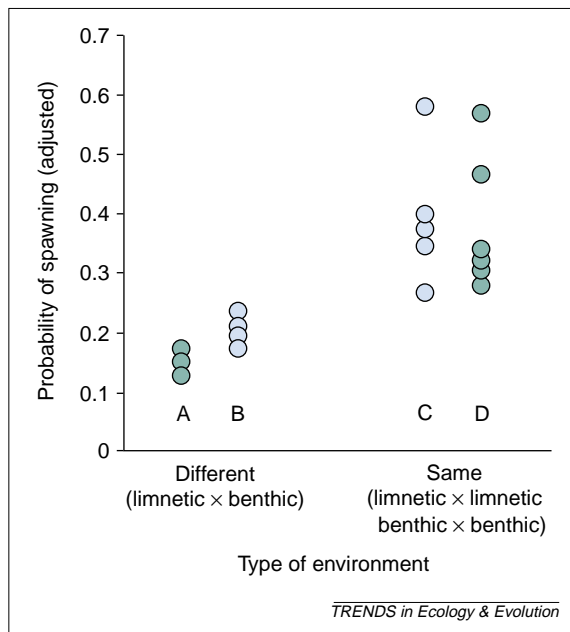
In a second test of the prediction, I used Coyne and Orr's^{36,37} survey of *Drosophila* to compare the strength of reproductive isolation in pairs of Hawaiian picture-winged *Drosophila* with the strength of isolation in pairs of populations and species of continental *Drosophila* of similar age³⁴. The Hawaiian *Drosophila* are a diverse group having a high speciation rate and possibly a higher overall rate of phenotypic and ecological differentiation. However, no difference was detected between Hawaiian and continental *Drosophila* in the average strength of premating or postmating isolation between similar-aged populations, a result that does not support the prediction of ecological speciation. The reliability of the test is uncertain, however, because nothing is known about the strength of divergent selection in either Hawaiian or continental *Drosophila*.

Ecological selection against hybrids

Stronger evidence for ecological speciation is that divergent selection arising from features of the environment directly reduces fitness of hybrids (and other individuals of intermediate phenotype) between coexisting species (ECOLOGICAL MECHANISM OF REDUCED HYBRID FITNESS). Such postmating isolation can arise because an intermediate phenotype is less efficient at capturing prey in the wild, or because intermediate defenses leave the hybrid susceptible to predation and parasitism. This type of isolation is environment dependent and should vanish in a common laboratory setting^{4,38}. By contrast, genetic mechanisms of reduced hybrid fitness arise from INTRINSIC INCOMPATIBILITIES between genes inherited from the parent species, and should be manifested in every environment. Whereas genetic mechanisms of reduced hybrid fitness could arise during ecological and non-ecological speciation, direct reduction of hybrid fitness by ecological selection pressures are a unique prediction of ecological speciation (Box 1).

Demonstrations of ecological selection against hybrids are still few (Table 1 lists only the strongest tests). F1 hybrids between the limnetic and benthic species of threespine sticklebacks have a high fitness in the laboratory but an intermediate phenotype that compromises their ability to acquire food from the two main habitats in their native lakes. The result is slower growth of F1 hybrids relative to either parent species when transplanted to the habitat of that parent¹⁵. Furthermore, relative growth rates of limnetic and benthic backcrosses are reversed between habitats, as would be expected if hybrid fitness is directly reduced by ecological selection pressures (H.D. Rundle, unpublished). A similar pattern of high viability of hybrid crosses in the laboratory, coupled with reduced viability in the wild, is seen in crosses between two PARAPATRIC RACES of the

Fig. 4. Parallel evolution of premating isolation between benthic and limnetic threespine sticklebacks (*Gasterosteus* spp.) from three lakes. Each circle indicates frequency of matings between males and females from a pair of populations, measured in no-choice laboratory mating trials. Pairs of populations from the same lake are indicated in green; values in column D are mating frequencies between males and females from the same population. Pairs of populations from different lakes are indicated in blue. Pairs of populations occurring in the same type of environment (C and D) mate with higher frequency than do pairs of populations from different types of environments (A and B). Modified, with permission, from Ref. 55.



butterfly *Heliconius erato* in Peru³⁹. Selection against rare warning color phenotypes in nature by avian predators appears to be the cause.

Differences in timing and duration of diapause of host races of the apple maggot fly *Rhagoletis pomonella* represent adaptations to the timing of fruit production of different host plants in relation to the timing of winter⁴⁰. Hybrid offspring of individuals that switch hosts should be heavily disadvantaged as a consequence, although this has not been demonstrated directly. Selection against F1 hybrids between host races of pea aphids *Acyrtosiphon pisum* on host plants of both parent species probably has an ecological basis, but this has not yet been confirmed⁴¹. Craig *et al.*⁴² showed that F1 and F2 hybrids between two host races of the fly *Eurosta solidaginis* survived poorly on the host plants of their parents, although the pattern of fitnesses was complex. An extended season of leaf production by hybrids between poplar *Populus* spp. might explain the much higher levels of insect herbivory that they experience compared with those on the parent species⁴³. Reciprocal transplants along an elevation gradient of two subspecies of sagebrush *Artemisia tridentata* and their hybrids indicated that each of the three populations has highest fitness in its own environment, with the hybrids being most fit at an intermediate elevation⁴⁴. Hybrids in the last two studies were neither F1 nor F2 hybrids, but were individuals from populations of hybrid origin.

Ecologically based postmating isolation is expected to change as environments change. For example, Grant and Grant^{45,46} recorded the fates of individual hybrids made of crosses between two species of ground finch (*Geospiza fuliginosa* and *G. fortis*) over 20 years on a Galápagos island. Hybrid survival was typically poor, owing to the low abundance of seeds that the hybrids could handle

efficiently. However, seed abundances were changed significantly in the years following a dramatic El Niño event in which rainfall increased by an order of magnitude. Remarkably, the greater relative abundance of small seeds eliminated the difference in survival between hybrids and the dominant parent species, *G. fortis*.

Ecological traits underlying reproductive isolation

Evidence for ecological speciation is gained when specific genes or phenotypic traits known to be under divergent selection between environments are found to be the basis of reproductive isolation (or are genetically correlated with traits that are the basis of reproductive isolation) (Table 1). For example, in the monkey flower *Mimulus guttatus*, alleles conferring tolerance to soils contaminated with copper are lethal when combined in the offspring of crosses with plants from uncontaminated soils⁴⁷. Reproductive isolation between two other monkey flowers (*M. cardinalis* and *M. lewisii*) is associated with differences in floral traits that attract different pollinators and therefore contribute to premating isolation. *Mimulus lewisii* has broad, flat, pink petals with yellow nectar guides, small nectar volume, and is pollinated primarily by bumblebees, whereas *M. cardinalis* has a narrow tubular corolla and large nectar rewards and is pollinated primarily by hummingbirds. These divergent adaptations to contrasting pollinators contribute to premating isolation, and pollinators are attracted to artificial F2 hybrids in proportion to the mixture of genes from the preferred parent⁴⁸.

Body size is strongly divergent between sympatric stickleback species, and several lines of evidence suggest that this difference is the result of contrasting natural selection between the main habitats that they exploit⁴⁹. Body size was also found to affect strongly the probability of interspecific hybridization in no-choice laboratory trials: crossbreeding occurred only between the largest individuals of the smallest species and the smallest individuals of the largest species⁴⁹. Similarly, in Darwin's finches, size and shape of the beak and body, which are strongly selected for efficient exploitation of different foods, are also used as cues in interspecific mate discrimination⁵⁰. Some divergence in song, albeit incomplete, might accompany divergence of size and shape of the beak in Darwin's finches, and this could also influence premating isolation⁵¹.

Adaptive life-history differentiation might lead to reproductive isolation in many insects⁵². For example, different timing of emergence between the apple and hawthorn races of the apple maggot fly is linked to changes in the timing and duration of diapause⁴⁰. Development time in populations of *Drosophila mojavensis* has diverged between populations on different cactus hosts, and this trait is genetically correlated with behavioral traits that influence reproductive isolation⁵³.

Parallel speciation

Evidence for ecological speciation is gained when traits determining mating compatibility evolve in parallel in different populations experiencing similar environments ('PARALLEL SPECIATION'^{54,55}). Threespine sticklebacks provide the clearest case (Fig. 4). Sympatric limnetic and benthic species of threespine sticklebacks have arisen independently as many as four times in separate lakes^{56,57}. The two species within a lake rarely (if ever) hybridize in the wild. Frequency of hybrid mating is raised to 10–15% in no-choice laboratory mating trials (Fig. 4, column A), which is significantly below the value for males and females from the same population (Fig. 4, column D). Remarkably, limnetics and benthics from different lakes also hybridize at low frequency in the laboratory (Fig. 4, column B), whereas populations of the same ECOTYPE from different lakes (i.e. both limnetic or both benthic) mate at high frequency (Fig. 4, column C). This pattern implies that traits influencing mating compatibility have evolved in parallel under similar environmental conditions, strongly implicating divergent natural selection in the origin of stickleback species⁵⁵. Some nonecological processes of speciation might also yield parallel evolution of mating compatibility (e.g. polyploid speciation), but no consistent association between mating compatibility and environment is expected. The traits determining mating compatibility in sticklebacks are not known, but body size⁴⁹ and nuptial coloration⁵⁸ probably each play a role.

Freshwater amphipods *Hyaella azteca* occur in two types of lakes. Lakes with predatory sunfish contain a small-bodied ecotype, whereas lakes lacking fish predators contain a large-bodied ecotype. Body size differences between amphipod populations are genetically based and are not closely correlated with electrophoretic distance⁵⁹, suggesting that multiple transitions in size have occurred. Individuals from populations of the same ecotype (i.e. both large or both small) readily interbreed, whereas individuals from different ecotypes do not⁵⁹. Again, environment and phenotype predict mating compatibility better than do genetic relationships.

Funk⁶⁰ examined levels of premating isolation between populations of the leaf beetle *Neochlamisus bebbianae*, a species that exploits different host plants in different parts of its range. Mating trials were carried out with two populations adapted to maple *Acer rubrum*, one adapted to birch *Betula nigra*, and one from willow *Salix bebbiana*. Leaves from the host plants were present in half the trials and absent from the other half, but this made no difference to the results. Reproductive isolation was strong between the birch population and both maple populations, and between the willow population and both maple populations (isolation between willow and birch populations was not tested), but was absent between the two maple populations. However, genetic divergence (based on mitochondrial DNA) was

greater between the two maple populations than between one of the maple populations and the willow population, suggesting that reproductive isolation is better predicted by environment than by PHYLOGENY.

Discussion

Speciation is one of the least understood major features of evolution. The main obstacle to progress is the variety of mechanisms that might lead to the evolution of reproductive isolation (Box 1), any one of which can be difficult to rule out in a specific case. The upshot is that it is still difficult to point to even two species in nature and state with confidence the mechanism that produced them. The exceptions are speciation events resulting from polyploidy, because polyploidy leaves a clear genetic signature for a substantial period of time. However, speciation by polyploidy is relatively common only in plants, and, even in that taxon, probably accounts for only a minority of speciation events³². The vast majority of speciation events in nature must therefore be explained by other processes.

One of these other processes is ecological speciation, driven by divergent natural selection on traits and resulting from features of the environment. Ecological speciation is probably more easily tested than is speciation by genetic drift or speciation resulting from the accumulation of alternative incompatible mutations under uniform selection. This is because, similar to speciation by polyploidy, divergent natural selection often leaves a signature in the pattern of reproductive isolation, at least for a time (further genetic divergence after speciation is complete might eliminate the signature). For example, whereas genetic mechanisms of reproductive isolation are the expected outcome of every speciation process (Box 1), ecologically based selection against hybrid phenotypes is a unique prediction of ecological speciation¹⁵ (H.D. Rundle, unpublished).

Similarly, parallel speciation is compelling evidence that divergent natural selection has ultimately brought about the evolution of reproductive isolation, as is the finding that traits under divergent natural selection are the basis of reproductive isolation (or are genetically correlated with traits that form the basis of reproductive isolation). A correlation between strength of divergent selection and the rate of evolution of reproductive isolation would be further evidence of ecological speciation, but strength of divergent selection is not easily measured. Finally, persistence of ecologically differentiated populations in the face of gene flow, and evidence of sympatric speciation coupled with strong ecological differentiation, also point to ecological speciation (Via⁸, this issue), but alternative mechanisms can produce such patterns and must be tested.

Recent progress has been made in testing ecological speciation in nature (Table 1). Although few

in number, candidate examples already indicate the multiple ways that divergent selection might lead to reproductive isolation. For example, at least one candidate for sympatric speciation is represented (*Rhagoletis*), although most species pairs appear to have histories that include an allopatric phase (e.g. threespine sticklebacks, Darwin's ground finches and *Coregonus*). The cases of ecological speciation include populations and species whose hybrids fail partly because of intrinsic genetic incompatibilities (e.g. *Mimulus guttatus* and *Coregonus*), and hybrids of other populations and species whose fitness depends on features of environment (e.g. threespine sticklebacks; Darwin's ground finches and *Heliconius erato*). Evidence for reinforcement is seen in one case (threespine sticklebacks) but even in this example, as in others (Table 1), considerable reproductive isolation appears to have evolved purely as a by-product of divergent selection. Our understanding of the range of processes involved in ecological speciation will increase as more examples accumulate.

Nevertheless, the evidence for ecological speciation is incomplete. More tests from nature are badly needed, not only on the systems already identified as good candidates (Table 1) but also in other systems. The generality of ecological speciation is a long way from being decided, but at least there are both tools available with which to address the problem, and some promising indications from a few studies of species in the wild.

The mechanisms driving ecological speciation also need to be more fully understood. What are the ecological agents of divergent selection? How important are species interactions to strengthening of reproductive isolation during the sympatric phase? Is the by-product mechanism effective by itself, and responsible for the bulk of the evolution of reproductive isolation in allopatry and sympatry, or does reinforcement in sympatry play a vital role in the

final production of two coexisting species from a single ancestor? Is divergent sexual selection often the outcome of divergent natural selection, or does it arise independently from other processes?

The link between ecological speciation and adaptive radiation also needs to be assessed³⁴. Divergent natural selection is an important process in phenotypic differentiation in adaptive radiation and, for this reason, it might be expected to contribute also to speciation, but this is less well understood. Is speciation in adaptive radiation chiefly ecological speciation? How do the agents of divergent selection, the traits that are its targets, and the consequences for reproductive isolation, change as an adaptive radiation proceeds and the numbers of species in the environment builds? How durable are 'ecological species' (the products of ecological speciation): given the importance of ecological context in determining hybrid fitness, at least when the species are young, are ecological species particularly prone to extinction when environments change? If so, how do the mechanisms of species origin affect the build up of species during adaptive radiation?

These questions emphasize the substantial challenges for research posed by Dobzhansky's³ claim, one of the clearest early statements of the hypothesis of ecological speciation, that 'the genotype of a species is an integrated system adapted to the ecological niche in which the species lives. Gene recombination in the offspring of species hybrids may lead to formation of discordant gene patterns'. Here, Dobzhansky was referring to the build up of genetic mechanisms of postmating isolation, but the hypothesis is general and applies equally well to traits causing premating isolation – these too might be the product of adaptation to environments. Happily, we are unlikely to have to wait another 50 years before the challenge is taken up, and the hypothesis receives the full evaluation that it deserves.

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