Q&A

EVOLUTIONARY BIOLOGY

Speciation

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Darwin200

On the Origin of Species ... the title of Charles Darwin's great work of 1859 seemed to promise a solution to this "mystery of mysteries". Although we now know vastly more about speciation than we did 150 years ago, the one mystery has become many — and the possible solutions have multiplied.

Are species real?

The entities we call species — definable biological groups of distinct lineage and with potentially independent futures — are certainly real. But the term 'species' as a level of biological classification is more ambiguous and amorphous; for example, the species identified by criteria typically applied to one branch of life (or by one set of biologists) would not always be similarly identified by criteria typically applied to other branches of life (or by another set of biologists). In this sense, the classification level 'species' is partly a construct developed for the convenience of biologists in organizing and simplifying the natural world. Darwin himself, in *On the Origin of Species*, was of this opinion: "In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be free from the vain search for the undiscovered and undiscoverable essence of the term species." Although Darwin has been criticized for this ambivalence, modern research has, in many respects, returned us to his original interpretation.

What taxonomic groups are we talking about?

All of them. The diversity of life around us is the product of evolution that has generated different life forms embarking on different evolutionary trajectories. This statement applies all the way from the big (polar bears versus grizzly bears) to the very small (different strains of bacteria or viruses), and across the entire tree of life. The hitch is that difficulties arise in deciding how to define species within and across these vastly different groups.

How are species delineated by biologists?

A universal 'species concept' has long been sought. The hope has been for a basic set of rules that can be broadly applied across many branches of life so as to clearly, objectively and comparably delineate separate species. Proposing species concepts has proven appealing, and has become almost a cottage industry — more than two dozen have been developed. Although none is universally accepted, one of the most popular is the 'biological species concept'.

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Figure 1 | Beetle mania: one estimate is that some 350,000 species have been described.

What is the 'biological species concept' (BSC)?

The BSC holds that species are groups of actually or potentially interbreeding individuals that are reproductively isolated from other such groups (that is, they exchange few genes). The BSC is sometimes interpreted to imply the extreme situation where two groups are separate species only when successful hybrids cannot ever be produced — and any two such groups certainly are separate species. But many other groups that are widely accepted to represent separate species frequently violate this strict criterion; for example, some estimates hold that 25% of all plant species and 10% of all animal species hybridize successfully with at least one other species. Partly for this reason, the BSC is often relaxed to the point that different groups are considered separate species if they can maintain their genetic integrity in nature. This more useful, albeit more ambiguous, criterion allows for some genetic exchange (gene flow) between species as long as they do not become homogenized.

What are the challenges to the BSC (and the alternatives)?

One is that it is very difficult to apply the BSC to groups that are geographically separated ('allopatric'), because it is hard to know if these groups would collapse into a single species if they did somehow come into contact (become 'sympatric'). This ambiguity is one reason for the qualifier 'potentially' in the BSC definition given above. For example, squirrels in New York's Central Park do not interbreed with those in nearby New Jersey, but perhaps only because of the impassable expanse of water and concrete between them. A common route around this problem is to bring allopatric groups into artificial contact, such as in the laboratory. Ambiguity still persists here, however, because the observed mating patterns may not reflect those that would occur in nature.
A second challenge is that the BSC cannot be applied to *most* organisms, including those without sexual reproduction, such as viruses and some microbes, and those that are now extinct. For these reasons, and others, an alternative set of species concepts revolves around the magnitude of morphological or genetic differences between groups. The difficulty for

these concepts is in deciding just how big a difference is sufficient to elevate two groups to the status of separate species.

At what point do groups become species?

Speciation is best thought of not as a specific endpoint (the above answers highlight the difficulty of establishing an appropriate threshold), but rather as an accumulation of reproductive isolation and of morphological/genetic differences through time. This emphasis on speciation as a *process* has helped to refocus research towards the factors that promote and constrain 'progress' towards (or from) speciation. This focus also avoids the philosophical awkwardness that the consideration of speciation as an endpoint requires that offspring are one day born who are not the same species as their parents. (Although I will describe below how this can sometimes happen.)

How many species are out there?

Approximately 1.5 million species are currently recognized by taxonomists to the point of having been awarded a Linnean binomial, such as us — *Homo sapiens*. Associated with each official species description is a 'type' specimen, considered representative of the species (curiously, humans have never had a designated type specimen, despite attempts by American palaeontologist Edward Drinker Cope to have himself so designated). One and a half million sounds like a lot, but many other species have yet to be described, or even discovered; and so the total that might warrant taxonomic designation could be upwards of 10 million. And, of course, vastly more species have gone extinct than exist today. Within animals, the most speciose group is insects. And within insects, the most speciose groups are those that feed on plants. It's said that the evolutionary biologist J. B. S. Haldane, on being asked by theologians what he had learned about the Creator, stated that He must have had "an inordinate fondness for beetles" (Fig. 1).

How quickly do species arise?

Starting with Darwin, and continuing until very recently, speciation has been considered to be usually a very slow process — perhaps requiring millions of years. But this cannot always be true given, for example, the many hundreds of cichlid fish species in Lake Victoria, Africa, that apparently arose in less than 15,000 years. On a similar time frame, numerous fish and bird species have arisen in the Northern Hemisphere since the end of the last glaciation. It has also been argued — although not without controversy — that noteworthy levels of reproductive isolation can begin to accumulate within only a few dozen generations; however, the attainment of unassailable and irreversible reproductive barriers will almost always take much longer. An exception is the almost instantaneous speciation that occurs when genomes multiply (polyploidy) and individuals with different ploidy levels cannot successfully interbreed. An example is the common cordgrass plant *Spartina anglica* in Britain, a product of chromosome doubling associated with hybridization between native (*S. maritima*) and introduced (*S. alterniflora*) species.

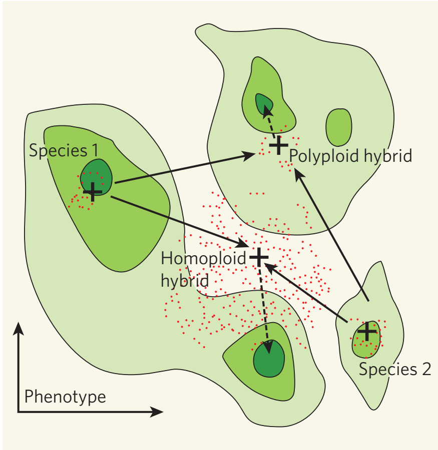

Figure 2 | Hybrid speciation. This example of hybrid speciation, depicted on an 'adaptive landscape', shows evolutionary fitness (contours, with darker green representing higher fitness) as a function of two different phenotypic traits (horizontal and vertical dimensions). Several high-fitness peaks are possible, but initially only two are occupied: by species 1 and species 2, with their average values shown as crosses and the range of individuals as dots. Species 1 and 2 then hybridize, either with (polyploid) or without (homoploid) changes in chromosome number, and the resulting combinations of traits can come into the range of attraction of a new adaptive peak. Adaptation of the hybrids to that peak can then generate a new species. (Modified from J. Mallet *Nature* 446, 279–283; 2007.)

What is the engine of speciation?

For most of the twentieth century, the dominant view of speciation was that random genetic differences accrue gradually between allopatric populations, eventually causing genetic incompatibilities that prevent successful interbreeding. More recently has come the realization that most of these differences evolve by selection. Moreover, selection can cause reproductive barriers other than strict genetic incompatibilities, and this can occur in sympatry or allopatry (more about this later). Of particular recent interest is how adaptation to different environments drives reproductive isolation, a process now called 'ecological speciation'.

... and ecological speciation works how?

One of Darwin's insights, supported by countless subsequent studies, is that populations in different environments show adaptive differences in traits that thereby improve survival and reproductive success. In some cases, this adaptive divergence can lead to reproductive isolation. For example, traits undergoing adaptive divergence might influence mating preferences, such that individuals adapted to different environments now reject each other as mates. Moreover, any hybrid offspring that are produced might die because they aren't well adapted to either environment. Although Darwin wasn't explicit about such a process, it is clear that he too considered adaptive divergence to be the engine of speciation. At present, ecological speciation is thought to have been a major player in the diversity of life. Some well-known examples for vertebrates include Darwin's finches of the Galapagos Islands, threespine stickleback fishes in the Northern Hemisphere and the hyperdiverse cichlids of Africa.

Does speciation require geographical isolation (allopatry)?

Yes. Wait, I mean no. Or perhaps maybe. Allopatric versus sympatric speciation remains one of the greatest controversies in evolutionary biology. Until recently, it was widely considered almost impossible for speciation to proceed entirely in sympatry. (Definitions of sympatry vary widely, but generally accepted contexts would include insects in a field or small forest, fishes in a small lake, or birds or plants on a small island.) And any suggestions to the contrary were quashed by the reigning authorities, particularly Ernst Mayr. Over the past ten years, however, a flurry of mathematical models has demonstrated that ecological speciation is possible in sympatry, and several putative examples have emerged. These include insects adapted to different host plants, fishes adapted to different lake habitats, birds adapted to different food types, and plants adapted to different soil types or pollinators. Most biologists, however, continue to argue that sympatric speciation is relatively rare.

Why is the anti-sympatry sentiment so strong?

Part of the reason may be different standards of proof. Allopatric speciation is usually taken to be the parsimonious default — an appeal to the simplicity of Occam's Razor. Sympatric speciation is thus accepted only when allopatric speciation can be completely ruled out. But this is virtually impossible to do, given that the distributions of organisms at present will rarely reflect their distribution at the time of speciation. And, of course, nature is probably not parsimonious, thus dulling Occam's Razor.

Can competition contribute to sympatric speciation?

Yes, at least under some conditions. Competition for shared resources in sympatry can favour a population splitting into two groups so as to reduce competition, a process some authors have called 'adaptive speciation' or 'competitive speciation'. This process is certainly known to accelerate divergence when formerly allopatric groups come into secondary contact. What remains uncertain is the extent to which competition might

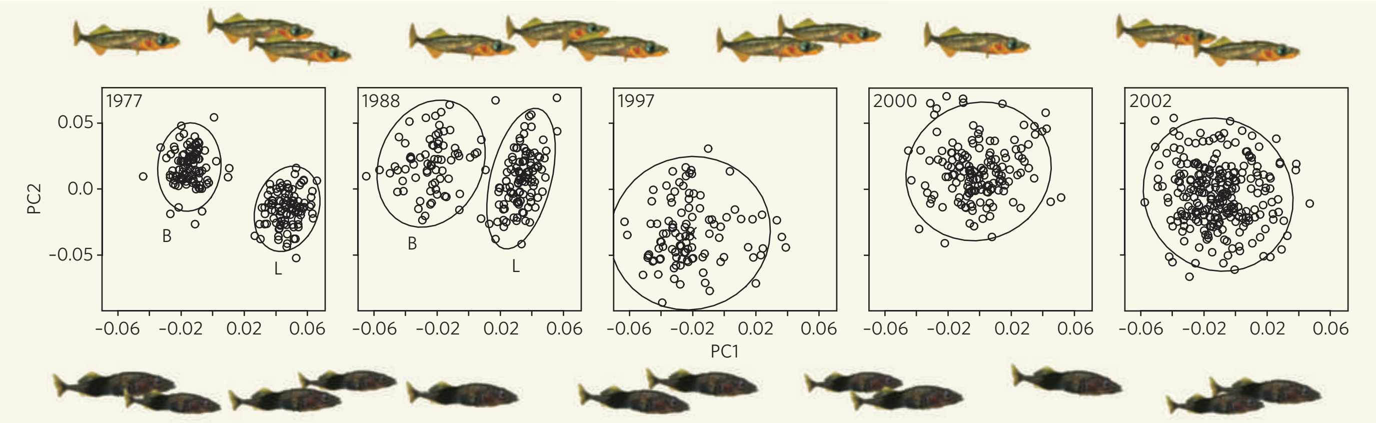

Figure 3 | Reverse speciation. **Threespine stickleback fishes in Enos Lake, British Columbia, Canada, historically existed as two distinct groups, one adapted to bottom feeding (benthic, B) and the other to open-water feeding (limnetic, L). The figure shows individuals (small open circles) of each group in morphological space as defined by two orthogonal axes (PC1 and PC2). Historically, very few intermediate (hybrid) individuals were present, despite the two forms — shown here above (L) and below (B) the plots — occurring side-by-side in the same small lake. More recently, however, the two forms have merged into a single group that shows a high degree of morphological and genetic variation. This species fusion may have been the result of human influences. (Modified from E. B. Taylor *et al. Mol. Ecol.* 15, 343–355; 2006. Fish images courtesy E. Cooper, WWF.)**

drive sympatric speciation in the absence of an earlier period of allopatry.

… and can hybridization likewise contribute?

Yes. As described above, speciation is usually considered to be the accumulation of morphological/genetic differences and of reproductive isolation — that is, the fission of a single ancestral group into multiple descendant groups. But new species can also arise through fusion, such that hybrids between existing species sometimes embark on separate evolutionary trajectories from their ancestors (Fig. 2). This 'hybrid speciation' is certainly important in plants, where more than 10% of species, perhaps many more, may have a hybrid origin. Hybridization is also increasingly implicated in the origin of some animal species. Many cases of hybrid speciation involve differences in ploidy (as mentioned above), but others do not. For example, researchers have been able to recreate many features of existing hybrid species of sunflowers and butterflies through artificial crosses between existing species, without any differences in ploidy.

Are there 'speciation genes'?

As with most of biology, the study of speciation has gone genomic. One question centres on the number and type of genes that cause reproductive isolation. Some studies have obligingly found genes that differ between species and cause strong reproductive barriers. Speciation may here involve very few genes, although it is often unclear which differences drove speciation and which simply accumulated after the fact. Ecological speciation, in contrast, proposes that reproductive isolation is the result of adaptive divergence, a process that is often caused by many genes. In these cases, 'speciation genes' may be so numerous as to complicate their accurate detection and interpretation. Studies of the genetic basis of reproductive barriers are nonetheless greatly enriching our understanding of speciation.

Can humans promote speciation?

Yes. Humans sometimes sunder the range of a formerly continuous population, which may then promote independent evolutionary trajectories. Humans can also provide new and distinct habitats that initiate ecological speciation. One example is the introduction of plants to sites where they are not native, followed by the evolution of new insect 'host races' that specialize on those plants. These host races can show considerable, although not complete, reproductive isolation from each other in less than 100 years. An example is the recent origin of a host race of tephritid fruitfly (*Rhagoletis*) on brushy honeysuckle (*Lonicera* spp.), the latter having been introduced from Asia to North America. This same fly also answers the above questions regarding how quickly speciation can commence (within a few decades) and how hybridization can form new species (the new host race was initially a hybrid between two other *Rhagoletis* species).

Can humans constrain speciation?

Again, yes. Humans can bring together partially divergent groups that haven't yet accumulated enough differences to prevent their fusion. Humans can also hamper ecological speciation by reducing the distinctiveness of formerly separate resources (habitats or food types), such as by introducing an intermediate and overlapping resource. And human activities can degrade the transmission of mating signals that keep species separate, for instance by reducing water clarity for fishes that choose mates based on colour. So far, human influences have been implicated in 'reverse speciation' or 'de-speciation' in each of these contexts, one example being stickleback fishes in British Columbia, Canada (Fig. 3).

What's next?

Sympatric speciation remains one of the most conspicuous current battlegrounds, and that debate might not wrap up soon. For me, however, the most refreshing voices are those arguing for less concern over the geography of speciation and for more emphasis on its specific drivers. Here, future work will increasingly examine the role of natural selection, including that driven by competition, and also sexual selection (selection to improve the chances of mating). Sexual selection clearly contributes to speciation, but the question is how often it does so without the collaboration of natural selection (or vice versa). Finally, genome studies are sure to increase our understanding of how natural selection acts on regions of the genome that contribute to speciation. In speciation, as in other fields of study, it seems that the more we know, the more we know we don't. Thus, although we now know vastly more than Darwin thought he *didn't* know 150 years ago, the remaining uncertainties are no less glaring. I wonder if we will say the same 150 years from now, or if the questions of speciation will finally have been answered — or perhaps supplanted by new interests. ■

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