> It is therefore possible that subglacial lakes are not isolated … which means that the accidental contamination of one lake could spread to others

Vostok, and are located relatively close to it (Bell *et al*, 2006). "The size and origin of the two recently discovered large subglacial lakes suggest that these lakes are tectonically controlled. In contrast to the smaller and shallower lakes, tectonically controlled subglacial lakes are deep and quite old," said Studinger. "The tectonic control and longevity of these lakes suggests that they probably host a diverse ecosystem." The idea that subglacial lakes are interconnected by a hydrological network beneath the ice has existed for some time, but evidence to prove it was not available until now, Studinger added. He noted that the work by Duncan Wingham and others showed that these linkages exist, and that the flux of water beneath large continental ice sheets can be relatively fast and voluminous. "Model predictions of future sea-level rise have to take into account the lubricating effects of subglacial water on ice sheet stability and drainage, and the possible influx of large volumes of fresh water into the ocean," said Studinger.

Although the final programme of IPY scientific activities is not yet available, clearly a large part of it will be built on previous experiences. Among those is the work of a multi-disciplinary study of the microbial diversity in benthic microbial mats from freshwater and saline surface Antarctic lakes, MICROMAT (www.nerc-bas.ac.uk/mlsd/micromat). "What was 'special' to MICROMAT was the fact that bacteriologists, cyanobacteriologists, mycologists, protistologists and algologists were working for the first time on the same samples," said Annick Wilmotte, a microbiologist at the University of Liége, Belgium, and the project's coordinator. She added that MICROMAT revealed an unprecedented level of microbial diversity in Antarctic lakes, especially for bacteria and cyanobacteria, which raises questions as to how these communities have evolved and how their dispersal affects local biodiversity. As part of the project, a screening programme by pharmaceutical and academic partners indicated the presence of metabolites with significant biological activities, which has led to a renewed interest in the exploitation of Antarctic microbial diversity. Flavia Marinelli, from the University of Insubria at Varese, Italy, stated that several novel antibacterial, antifungal and antitumour compounds were isolated from bacteria, cyanobacteria and filamentous fungi, and are currently under investigation.

MICROMAT's promising results, Wilmotte hopes, will be extended during the next IPY, and will fertilize a new international project called Microbiological and Ecological Responses to Global Environmental Changes in the Polar Regions (MERGE). Briefly described as "an umbrella programme that aims to understand the responses of terrestrial, limnetic and supraglacial polar ecosystems to climate change" (IPY, 2005), MERGE will, among other tasks, study the polar microbial diversity of a large range of biotopes in both the Arctic and Antarctica, Wilmotte said.

Understandably, research at the poles is not an easy undertaking. The extreme weather conditions—howling winds and the coldest temperatures on Earth—present a major challenge to any scientific explorations, which is one of the reasons for the distinct international and collaborative spirit of polar research. No man's land thus becomes, to use a definition forged for Antarctica but also applicable to the Arctic, 'a natural reserve devoted to peace and science'. In addition to the hard science facts that the new IPY will produce, its long-lasting value will be calculated on the basis of its capacity to forge further research partnerships and to strengthen the alliance to conserve polar ecosystems.

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Defining species

The indirect impact of humans on biodiversity

For more than a century, Charles Darwin's theory of evolution has explained how new species appear on Earth. Driven by mutations, genetic recombination and selective pressures from new or changing environments, various subpopulations accumulate changes in their genomes until a new population eventually emerges that is sufficiently different—genetically and physiologically—from the original species, such that individuals from the two populations are reproductively isolated from each other. Until recently, most biologists subscribed to this linear view of evolution, succinctly expressed by the leading evolutionary biologist Ernst Mayr, who stated that "the living world is comprised of more or less distinct entities which we call species" (Mayr, 1957). However, recent work paints a more complicated picture of species differentiating, diverging, merging and reverting in response to environmental changes, which suggests that many of the species categorizations applied by taxonomists are arbitrary.

Indeed, various recent studies report cases where the process of species divergence has been halted or even reversed by ecological changes (Taylor *et al*, 2006; Hendry *et al*, 2006). These results not only shed light on the process of speciation itself, which might work much faster than anticipated, but also highlight the influence of human activities—directly or indirectly—on the evolution of new species. It is becoming clear that human activities have a more profound effect on biodiversity than was previously believed, particularly in the animal kingdom, by inhibiting the process of species divergence within certain ecosystems. As a result, our understanding of conservation might need to be revised, leading to new approaches for maintaining biodiversity.

> It is becoming clear that human activities have a more profound effect on biodiversity than was previously believed … by inhibiting the process of species divergence

In order to study species divergence, it is necessary to agree on the definition of a species. This apparently basic step can be complex, with opinions differing widely as to what constitutes a separate species. Such definitions are particularly relevant for conservation, when the protection of a particular group of animals is dependent on whether it is accorded the status of an 'endangered species'. By definition, only a distinct species should enjoy such status, but there are many grey areas. One example is the case of gorillas, which are considered to include three subspecies: two living in lowland central Africa, and one living in the mountains around the borders of Congo, Rwanda and Uganda. Although there are approximately 60,000 lowland gorillas, the mountain gorillas, which have longer and darker hair as protection against lower temperatures, are endangered: only about 600 are left in the wild. Consequently, there is the question of whether the mountain gorillas are really a separate species worthy of protection. If they merely represent a subspecies, there is an argument against wasting resources in an effort to save them; instead, their numbers could be boosted by moving some lowland gorillas into the highland areas.

In contrast to the prevailing view that species are distinct entities, there is growing momentum behind a new notion that organisms are divided into clusters of varying distinctiveness, without any single cluster necessarily having more evolutionary or genetic significance than others (Hendry *et al*, 2000). This view has implications for interpreting the process of divergence and might be more realistic, as many groups of animals and plants are diverging yet are still able to mate and produce viable offspring.

It is true that populations can, and often do, diverge to a point of no return, beyond which hybridization and subsequent convergence is impossible. However, the ability of species to diverge—often relatively quickly and even when there are no obvious reproductive barriers such as geographical separation—is better explained by a model based on the idea that organisms converge in clusters around favourable points in a rugged ecological landscape. Such a point might correspond to a particular type or source of food, or traits that allow an individual to evade a particular predator or give a distinct advantage over competitors. In a world where this landscape was constant, organisms would eventually separate into species or subspecies, converging around the points to which they were particularly adapted.

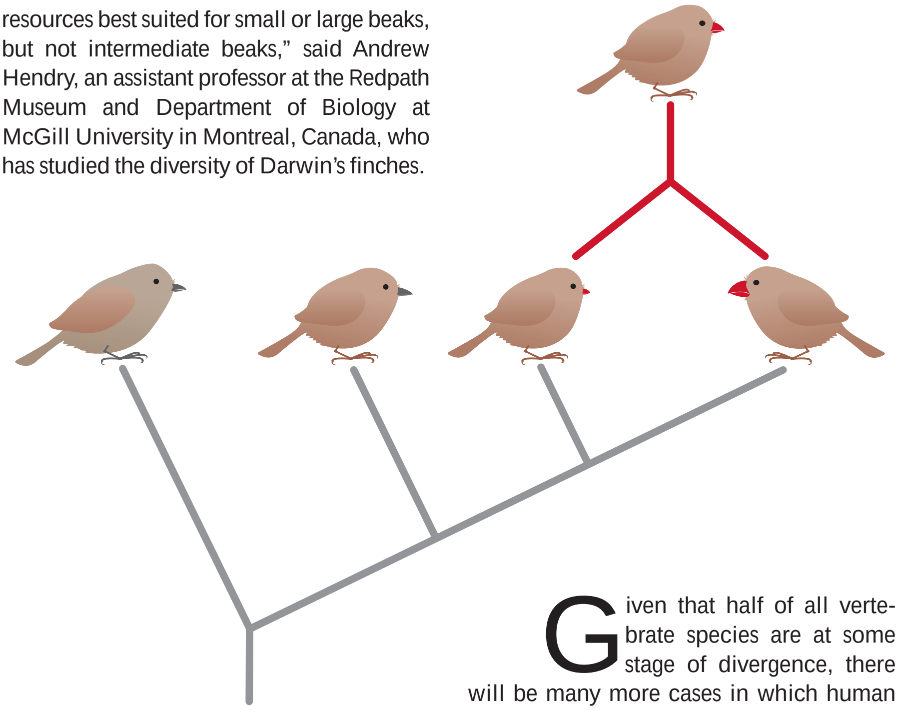
In reality, the ecological landscape changes much more rapidly than the geological landscape—even without human intervention—as a result of changes in climate, threats from new predators, competition with rivals and varying availability of food. Recent research has attempted to identify how these changes accelerate divergence or bring about the opposite process, called reverse speciation, whereby populations on the point of separation reunite.

In any case, the starting point is forward speciation, in which a lineage splits to create two or more new species. This can take place over a wide variety of time scales, depending on the selective force exerted by competitive, ecological or other factors. The key point is that adaptation can occur on ecological time scales of hundreds of years or a few thousand years through selection within existing gene pools, overturning Darwin's original theory that species evolved slowly over millions of years.

These processes have been studied among three-spine stickleback fish in western Canada, where retreating glaciers formed several lakes at the end of the last ice age, 11,000 years ago. The sticklebacks entered the lakes from the sea, and were then isolated from their original marine habitat. In each of the six lakes, the fish subsequently followed similar evolutionary paths. Some evolved slender bodies for fast swimming to hunt small invertebrates in the open water, while others became bulky and remained near the lake floor in shallow waters. Reproductive isolation between the two groups has not yet occurred, and about one per cent of the members of each new generation are hybrids.

At least, that was the case until the mid-1990s, and still is in most of the lakes. However, in one lake, Enos on Victoria Island, the two species suddenly seemed to converge again, as the number of hybrids increased rapidly. These fish have more intermediate body shapes and a mixture of previously distinct genetic markers. According to Eric Taylor, Associate Director of the Biodiversity Research Centre at the University of British Columbia in Vancouver, Canada, this might have been caused by the introduction of crayfish into the lake, which encouraged reverse speciation among the sticklebacks in three possible ways: by destroying nest materials and/or nests, thus reducing differences in nest-building preferences; by increasing the turbidity and, therefore, cloudiness of the water, making it harder for fish to select mates with their own shape; or by predation on eggs or the fish themselves, reducing the numbers of both species and, therefore, mate choice. "All of these are speculative for sticklebacks, but have precedents in other systems," said Taylor.

Humans can also trigger reverse speciation more directly—for example, by opening up new food choices, which can reduce the adaptive advantages of the diverging species. One such example emerged during the 1990s on the Galapagos Islands with Darwin's finches, which comprise 14 species found nowhere else in the world. They exhibit a wide range of beak sizes and have evolved to feed on different types of food. On one of the islands, Santa Cruz, the birds have diverged into two clusters: one with large beaks adapted for feeding on large seeds, and one with small beaks adapted for feeding on small seeds. Although some cross-mating produces offspring with medium-sized beaks, natural selection strongly selects those with either large or small beaks because they are more successful at feeding. "The idea is that there are resources best suited for small or large beaks, but not intermediate beaks," said Andrew Hendry, an assistant professor at the Redpath Museum and Department of Biology at McGill University in Montreal, Canada, who has studied the diversity of Darwin's finches.



However, the divergence was dramatically reversed in one area of the island—Academy Bay—where humans settled late in the last century. Hendry observed that the number of finches with medium-sized beaks increased significantly after 1999. He suggested that the birds now feed on rice and other crops planted by humans, for which beaks of all sizes are equally suitable. "The large and small beaks are not lost, you instead see an increase in the frequency of intermediate beaks," said Hendry. "In essence you change a two-humped distribution into a one-humped distribution but that one hump still spans the full range of beaks that were present in the original two-humped distribution." Hybrids produced by cross-mating now have better survival chances and the relative reproductive isolation that previously existed between the large-beaked and small-beaked populations has disappeared because both groups mate more readily with those with medium-sized beaks.

> Given that half of all vertebrate species are at some stage of divergence, there will be many more cases in which human activities are reversing speciation

Given that half of all vertebrate species are at some stage of divergence, there will be many more cases in which human activities are reversing speciation. However, natural factors, such as volcanic activity, climate change or invasion of an ecosystem by a new predator, can also cause speciation to go into reverse. The main question is what causes species to split in the first place. It is easy to understand how geographical separation causes speciation, because it reduces or eliminates opportunities for cross-mating and gene flow. In the absence of geographic isolation, the processes at work involve feeding and mating choices, and sometimes adaptations to avoid predators. In many cases, two species start drifting apart, but the two populations continue to mate with each other, thus maintaining gene flow and reproductive compatibility. "Many species probably start to move toward becoming separate from one another, but then speciation might often not go all the way to completion," said David Pfennig, a professor in the Department of Biology at the University of North Carolina at Chapel Hill, USA.

Pfennig has identified the importance of food sources as a trigger for speciation, a phenomenon known as character displacement. He studied populations of Mexican spadefoot toads in southeastern Arizona. At high elevations, the tadpoles are polymorphic, developing into either large-headed carnivorous polymorphs that feed on shrimps, or small-headed omnivorous polymorphs that feed on a variety of detritus. Pfennig compared the survival of offspring produced within each of the two populations with hybrids resulting from crosses, both in isolation and in competitive situations (Pfennig & Murphy, 2000). "Between-population offspring performed as well as within-population offspring when reared in isolation," said Pfennig. "When each was reared under conditions mimicking competitive environments in high- or low-elevation ponds, however, between-population offspring performed significantly worse than within-population offspring." This showed that the offspring of crosses between the populations suffered from reduced competitiveness rather than intrinsic genetic incompatibilities.

The next question is how reproductive isolation occurs in the absence of initial mating incompatibilities. Pfennig is now testing the theory that individuals evolve a tendency to mate with others from their own population, given the competitive advantages that their offspring would have. "Once that sort of 'assortative mating' evolves, then populations may become reproductively isolated," he said.

Although most speciation in animals occurs when a single lineage splits, there are rare examples of two closely related species hybridizing to form a new species. Often this happens between two neighbouring populations that have only recently evolved into different species from a single lineage and which still have the same chromosome number. In such cases, reproductive isolation between hybrid offspring and their parents—and therefore speciation—is unlikely to occur.

However, Chris Jiggins from the Institute of Evolutionary Biology at the University of Edinburgh, UK, and colleagues have recently found an example of genuine speciation by hybridization in *Heliconius* butterflies in lower Mesoamerica and the Andes (Mavarez *et al*, 2006). The authors studied two closely related species, *Heliconius cydno* and *Heliconius melpomene*, the speciation of which was associated with shifts in wing-colour patterns. These two species were found to cross-mate occasionally in the wild and produce a hybrid called *Heliconius heurippa*. The scientists established that *H. heurippa* was genetically isolated from its parent species by studying polymorphisms of nuclear genes. The two parent species had no alleles in common at these sites, whereas *H. heurippa* had alleles from both parents, and this allelic variation persisted among the offspring of the hybrid. Furthermore, the authors found assortative mating. The hybrid *H. heurippa* had a wing pattern that differed from those of both parent species, and males of all three species were much more likely to mate with females with the same wing pattern. Experiments with paper dummies showed that this preference was associated with the wing pattern itself, rather than associated pheromones.

> …this more diffuse view of speciation implies that such endangered species should enjoy protection, and many conservationists and researchers in the field are now inclined to agree

In plants, hybridization is a more common mechanism of speciation, and has played a much more significant role during their evolution. It is closely associated with polyploidy, which occurs when an organism has three or more complete sets of chromosomes. This can occur via one of four mechanisms: somatic doubling during mitosis; failure to reduce the number of chromosomes during meiosis, leading to unreduced gametes; polyspermy, which is the fertilization of an egg by two or more male nuclei; and endoreplication, whereby DNA is replicated without cell division.

Hybrids formed through polyploidy, whether within species through vegetative propagation or between species through cross-fertilization, are immediately cut off reproductively. The more interesting and controversial question is whether plant speciation can proceed sympatrically—without geographic isolation, in the absence of polyploidy and in the face of gene flow.

"The potential for behavioural isolation [assortative mating by choice] is much greater in animals," noted Troy Wood, an associate professor of chemistry at New York State University in Buffalo, USA. However, there has been increased attention towards sympatric speciation in plants, according to Wood, and recently an example was found among palm trees in the small and isolated Lord Howe Island in the South Pacific (Savolainen *et al*, 2006). The phylogenetic, ecological and genomic data indicate that a common ancestor reached the island around 5 million years ago, probably from Australia, but then split into two groups each favouring a different soil type. This, in turn, led to the key step in speciation—reproductive isolation—by evolving different flowering times in response to different soil substrates.

"To our knowledge this is the first plausible example of sympatric speciation in plants," said Christian Lexer, a population geneticist at the Royal Botanic Gardens, Kew, UK, and one of the paper's co-authors. Lexer argues that the selective mechanisms causing sympatric speciation in diploids—without changes in chromosome number—should in principal be similar for plants and animals. However, while animals can exercise choice through feeding and mating preferences, plants cannot, although it is possible that a plant species could split as a result of choices exercised by pollinating insects.

These insights into speciation are significant beyond a purely academic interest because they shed light on the fundamental mechanisms of evolution and therefore provide researchers with clues as to how best to preserve biodiversity and minimize human impact on ecosystems. They might also provide better arguments for those who want to save and preserve seriously endangered species, such as the mountain gorillas, Siberian tiger and white rhinoceros, even when there are closely related populations with higher numbers. In fact, this more diffuse view of speciation implies that such endangered species should enjoy protection, and many conservationists and researchers in the field are now inclined to agree. "Surely we should be interested in biodiversity generally," said Jiggins. "So if the mountain and lowland gorillas are distinct genetically and ecologically, then they are both worth preserving whether or not we give them the title of species."

Ole Seehausen, the Head of Aquatic Ecology and Evolution at the University of Berne, Switzerland, takes a similar stand. "The conservation value of populations in my eyes is independent of their species status, and is instead determined by the amount of genetic and functional uniqueness and by the adaptive potential," he said. Indeed, Seehausen calls for a paradigm shift in conservation biology, away from the concept of distinct species that exist in total reproductive isolation with nothing in between. This new view of evolution in action might help us to appreciate the intricate mechanisms at work and the resulting richness of all species on Earth.

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