speciation. This insistence now seems misplaced and has led to an artificial dichotomy. In fact, allopatric and sympatric speciation lie at the opposite ends of a continuum, which runs from zero to maximal gene flow between diverging populations. These new studies provide good evidence that fully sympatric speciation can occur, but most examples probably lie somewhere in between these two extremes. For example, the sticklebacks cited above likely arose from two invasions of each lake, but must have continued to diverge once sympatric. Hence a combination of both allopatric and sympatric divergence was probably involved.

Given the difficulty of proving the case one way or another, we should abandon the common assumption that allopatric speciation is the 'null hypothesis' with all the burden of proof lying on the hypothesis of speciation with gene flow. Instead, speciation research should concentrate on the more proximal causes of speciation, rather than intractable questions of geography. Key questions that we can answer include whether speciation results from natural selection and/or genetic drift, and what traits and genetic architectures are causal in divergence.

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Institute of Evolutionary Biology, School of Biology, University of Edinburgh, Edinburgh EH9 3JT, Scotland, UK.
E-mail: chris.jiggins@ed.ac.uk

Conservation: Losing Biodiversity by Reverse Speciation

A large fraction of the world's species diversity is of recent evolutionary origin, and has evolved as a by-product of divergent adaptation in heterogeneous environments. Recent research provides a dire warning that homogenizing environments may cause the rapid loss of such species through a reversal of the speciation process.

Ole Seehausen

Adaptive divergence between populations in response to divergent or disruptive selection is the cause of ecological speciation [1,2]. In its course, gene flow between diverging populations becomes reduced, either indirectly as a by-product of divergent adaptation, or by direct selection when intermediate genotypes are ecologically less successful [3]. Reproductive isolation in ecological speciation is due to prezygotic mechanisms (mate choice) and extrinsic (ecology-dependent) postzygotic mechanisms in the absence of intrinsic postzygotic hybrid dysfunction. Better studied examples include insect host races [4], and adaptive radiations of birds [5] and fish [3,6], but ecological speciation is widespread and common [2].

Whether or not divergent selection results in ecological speciation depends on the strength of divergent selection relative to gene flow. This balance is dynamic and can itself evolve, generating a feedback loop in which gene flow can impede divergence, and divergent adaptation can impede gene flow [7]. It follows that irreversible speciation requires sufficiently long persistence of the environmental conditions that started it in the first place. Unless species that are not geographically isolated have been isolated by selection and/or mate choice long enough for strong intrinsic (environment-independent) hybrid dysfunction to emerge, ecological speciation is reversible through increasing gene flow, weakening ecological selection or both. The critical time window can encompass a million years or more [2], several orders of magnitude longer than the time required for ecological speciation [1,2,6].

The concept of extinction through introgressive hybridization is established in conservation biology in the context of anthropogenic species translocations which bring into contact otherwise allopatric species [8]. However, the genetic re-admixture of species with a sympatric history, as a corollary of changes in the selection/gene flow balance, is less well established [9], even though the phenomenon was described more than 70 years ago [10]. If species originated in response to divergent selection/gene flow balance, then re-admixture because of a change in the balance is appropriately termed speciation in reverse.

Taylor *et al.* [11] and Gow *et al.* [12] have recently described this process in detail for one of the best
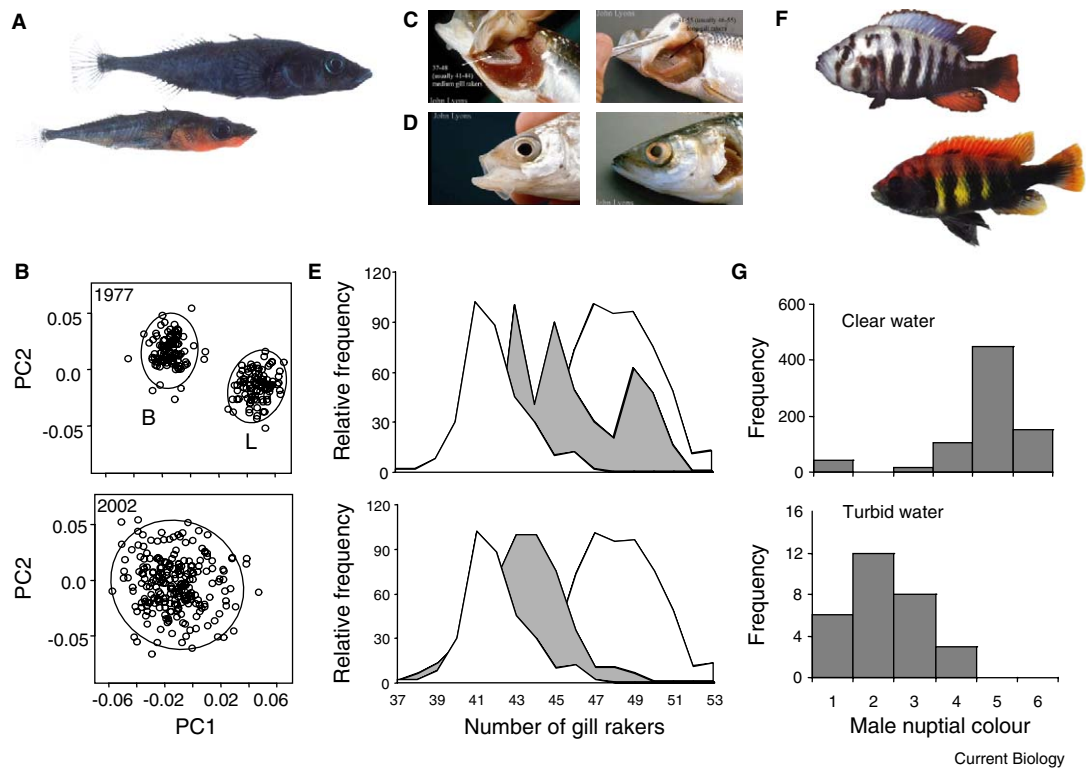
Figure 1. Three examples of speciation reversal.

(A) Males in nuptial coloration of the endemic stickleback species pair of Enos Lake, benthic (top) and limnetic (bottom). (B) Samples of Enos lake stickleback from 1977 (B, benthic; L, limnetic) and 2002 plotted along the first and second axis of morphological variation. Ellipses encircle about 95% of the individuals. (C) Gill rakers of the sparsely rakered *Coregonus hoyi* (left) and the densely rakered *C. artedi*, adapted to feed on benthic versus planktonic food respectively. (D) Heads of *C. hoyi* (left) and *C. artedi* (right). (E) Frequency distributions of gill raker counts in *C. artedi* (gray in top panel), and *C. hoyi* (gray in bottom panel) from 1984/85, and (white) in *C. hoyi* (left) and *C. artedi* (right) in 1917. (F) Males in nuptial coloration of the cichlid species pair *Pundamilia pundamilia* and *P. nyererei*. (G) Frequency distributions of male nuptial colour phenotypes — 1, no red on body like the top fish (F); 6, very red like the bottom fish in (F) — at a clear water station (top panel; note that absolute frequencies cannot be directly compared between the two species because the blue and red species live in different microhabitats that require different fishing techniques) and a turbid water station (bottom panel). A, courtesy Eric B. Taylor/University of British Columbia; B, adapted from [11]; C,D, courtesy John D. Lyons/Wisconsin Department of Natural Resources; E, adapted from [15]; F,G, courtesy O. Seehausen/University of Berne.

known vertebrate speciation models, the sympatric sticklebacks of Enos Lake (Vancouver Island, Figure 1A). Enos Lake is one of six lakes along the British Columbia coast that once harbored endemic, postglacially arisen species pairs of sympatric sticklebacks, a larger benthic and a smaller limnetic species [13]. The Enos Lake pair is the best studied of these. The species differed in size, shape, habitat, feeding, color vision and male breeding colors [3]. Some gene flow between them has probably always occurred [13], but it was strongly constrained by several different and synergistically interacting forces: nesting site segregation, size assortative mate choice, sexual selection and ecological selection against the intermediate morphology [3].

Several years ago, indications appeared that the species pair may be collapsing into a hybrid swarm. Kraak *et al.* [14] reported 17% intermediate phenotypes in July 1999, many more than the 1% reported in samples from the 1980s and early 1990s [13]. Taylor *et al.* [11] conducted a morphological analysis for samples spanning a time frame of 1977 to 2002, and a genetic analysis for samples from 1994 to 2002. Two distinct and non-overlapping morphological groups were evident in 1977 and 1988, but by 1997 these got replaced by a single highly variable cluster (Figure 1B). Microsatellite DNA analysis of a sample from 1994 indicated two genetically distinct populations, but only a single population was evident in 1997 and later years, including distinct hybrid genotypes.

Even though the exact causes of the breakdown of reproductive isolation in the Enos Lake sticklebacks are not yet known, the temporal coincidence with important changes in the habitat is highly suggestive. The Signal crayfish (*Pascifasticus leniesculus*) became established after the late 1980s, and the lake changed dramatically from relatively clear with a zone of submerged vegetation to now highly turbid without submerged macrophytes. Taylor *et al.* [11] suggest the most obvious effect of crayfish in Enos Lake is the destruction of aquatic vegetation and an associated increase in turbidity from crayfish movements. Increased turbidity makes mate choice less effective. Destruction of the macrophytes removes nesting habitat partitioning. The distribution of

food resources may have changed too, such that intermediate phenotypes may no longer be at a fitness disadvantage. It is also possible that the appearance of the crayfish and the increased turbidity are two responses to a third change in the environment, namely increased nutrient influx due to increased urbanization [11].

Gow *et al.* [12] confirmed the results of Taylor *et al.* [11] and extended the analysis to two other lakes, using for each lake a suite of species-diagnostic markers selected from 288 stickleback-derived loci. Whereas this study provided further evidence for the breakdown of the Enos Lake species pair into a hybrid swarm, it revealed less, namely 5% recent hybridization in Priest and Paxton lakes. The long-term estimates of gene flow were even lower by more than one order of magnitude, which can be taken as evidence that reduced hybrid fitness constrains gene flow between the species. Interestingly, the Paxton Lake species pair showed molecular evidence of historical introgression. Between the late 1950s and late 1970s the lake level fluctuated greatly because of water extraction for quarry-mining, and coho salmon were introduced that prey on sticklebacks but went extinct again five years later. During this period of disturbance, the proportion of intermediate phenotypes was larger than after this period. Hence, it appears this species pair has once been close to collapsing by speciation reversal too, and is now recovering from that period of intensified introgression.

The parallels between the sticklebacks and several other cases of recent and sudden loss of species diversity in fish are striking. Increased levels of introgressive hybridization have been invoked both in the loss of a diverse species flock of ciscoes (*Coregonus* spp.) in the Laurentian Great Lakes [15] and in the rapid breakdown of cichlid species diversity in Lake Victoria [16]. Loss of species richness was in both cases associated with increased phenotypic variability of the few remaining species. Even though

the exact causes of increased introgression are not fully known, changes to the costs and benefits of mate selectivity are likely. Such changes have the potential to simultaneously increase gene flow between species and reduce selection against hybrids.

Removal of some and addition of other predators caused large shifts in the abundances among Great Lake ciscoes, with six of eight species becoming very rare in the first half of the 20th century. By the 1960s, hybrid phenotypes dominated the catches in Lake Michigan, and several species had disappeared [17]. Morphological data for the last two abundant species in Lake Huron, *Coregonus artedi* and *C. hoyi*, suggest that even these collapsed into a hybrid swarm [15] (Figure 1C–E). In Lake Victoria a crash in cichlid populations due to introduction of a top predator coincided with loss of visibility due to rapid eutrophication. Intermediate cichlid phenotypes came to dominate in turbid waters with complete collapse of some species complexes (Figure 1F,G). Several populations that recovered after heavy fishing suppressed predation intensity are made up of new phenotypes [18]. Reduced mate encounter rates through reduced visibility and reduced population density make mate choice more costly, while reducing visibility also makes it less effective, increasing the fitness of randomly mating relative to choosy individuals. It seems likely that these cases are just the more visible among a much larger number of cases of speciation reversal.

A critical question is what the fraction of biodiversity is that is vulnerable to reversal of speciation when environments change. I suggest that a comparison of the ratio of selection/gene flow balance-dependent species versus older species in a given taxon is a first useful approximation. McKinnon and Rundle [3] listed at least 18 (and up to 1000) postglacially evolved species of Threespine sticklebacks, six times as many as the three older species in the genus *Gasterosteus*. Similarly, Hudson *et al.* [19] list at

least 100 postglacial species of coregonines, more than five times the number of older species [20]. Similar or higher ratios occur in African cichlid fish [6]. These ratios illustrate the fact that a very large proportion of global species richness must be maintained by selection/gene flow balance and is therefore vulnerable to reversal of speciation.

It is likely that incipient speciation and its reversal naturally characterize evolutionary dynamics of ecological speciation and adaptive radiation. Indeed the level of reproductive isolation between species of Darwin's Finches varies between years with and without selection against hybrids [5]. Such alternation between progress and regress in speciation during adaptive radiations may even increase the adaptability of genomes [6]. High temporal turnover of young species is also implicated by the large ratios of young to old species in many taxa. It is likely that in many cases of ecological speciation the selection/gene flow balance tilts through natural processes before speciation becomes irreversible.

But no matter how long-lived the average species is, collapsing the diversity of young 'ecological' species back into the fewer older ones would be a tremendous loss of biodiversity with likely major repercussions on ecosystem function. With the ongoing homogenization of the environment, associated with the rapid transition from natural to managed systems, we are unfortunately almost certainly already well on the way towards that less diverse world. As conservationists, we should therefore perhaps be as much concerned about the maintenance of the ecological mechanisms that generate and maintain species diversity at the evolutionary front, as we already are about the maintenance of genetic diversity.

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Department of Aquatic Ecology and Evolution, Institute of Zoology, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland; EAWAG Ecology Research Centre, Kastanienbaum, Switzerland.
E-mail: ole.seehausen@aqua.unibe.ch

Cell Migration: Neurons Go with the Flow

Cilia lining the surfaces of the brain ventricles may be responsible for the graded distribution of chemorepellents that drive the directed migration of neurons.

Jon Clarke

I bet the words 'cerebrospinal fluid flow' do not exactly set the hearts of cell or developmental biologists racing. But a recent paper [1] suggests we should pay more attention to this phenomenon, as new evidence suggests the flow of cerebrospinal fluid in the ventricles of the adult mammalian brain can direct the migration of new-born neurons towards their destination in the olfactory bulb.

The olfactory bulb is one of the few areas of the mammalian brain that recruits new neurons into its circuitry throughout life. The adult-generated neurons, however, do not originate in the olfactory bulb itself (Figure 1), but rather in a specialised stem cell niche, some distance away from the olfactory bulb, adjacent to the lateral ventricles of the brain [2]. This stem cell zone is known as the Sub-Ventricular Zone (SVZ) and lies just subjacent and parallel to the ventricular surface. From here, new-born neuroblasts migrate in chains of cells towards the anterior end of the lateral ventricle. There, the many chains of migrating cells that lie close to the ventricular surface merge into a single stream directed anteriorly away from the ventricle and towards the olfactory bulb. This stream is known as the 'rostral migratory stream'.

Sawamoto *et al.* [1] compared the patterns of neuroblast migration to the flow of cerebrospinal fluid in the adjacent ventricles using dye injection and analysis of the extended morphology of migratory neuroblasts in fixed tissue. This revealed that the direction of migration of new neurons in the SVZ closely matches the cerebrospinal fluid flow in the lateral ventricle, which is especially striking in the dorsal region of the ventricle (Figure 1A). In fact, adjacent to the anteriormost border of the ventricle almost half of the neuroblasts are surprisingly aligned ventrally away from the entrance to the rostral migratory stream, which correlates with the direction of the cerebrospinal fluid flow in this. Whether these anterior-ventral cells eventually find their way into the rostral migratory stream or have another fate is not known. While these observations demonstrate a common directionality of cerebrospinal fluid flow and olfactory neuroblast migration, they do not provide insight into whether the flow is instructive for migration.

Cerebrospinal fluid flow is driven by the beat of cilia that protrude from the ependymal cells that line the surfaces of the ventricles (Figure 1B). Thus, if cerebrospinal fluid flow is really directing cell migration, mutations affecting the cilia should also alter cell migration. Mice mutant for *polaris*, a gene essential for cilia assembly [3], have only very few functional cilia and thus cerebrospinal fluid flow is negligible in the lateral ventricles. In *polaris* mutants, the chains of migrating neuroblasts are severely