a widely used tool in determining the origins of materials used for a broad range of purposes, from environmental monitoring to medical research. ■

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BIODIVERSITY

Species choked and blended

The appearance of new ecological niches propels the evolution of species, but the converse can also occur. A study shows that changing lake habitats have caused extinctions and reduced the genetic differences between species. SEE ARTICLE P.357

JEFFREY S. MCKINNON & ERIC B. TAYLOR

Conventional wisdom long held that even if individuals of two different species could mate with each other, their offspring were doomed to early death or sterility. But a different view is taking hold: that it is often adaptations to different environments that cause species to separate, such that hybrid offspring fail because of their poor fit to resources, rather than through intrinsic shortcomings[1]. As a consequence, changes to particular environmental conditions that previously kept species distinct could increase genetic mixing, and thereby reduce species number. On page 357 of this issue, Vonlanthen *et al.*[2] provide evidence that human alterations to lake habitats have eroded barriers between species and contributed to extinctions.

The authors' study of 17 Swiss lakes shows that glacial melting in the past 12,000 years provided ecological opportunities, in the form of new environmental niches, that led to diversification of whitefish species, as has been reported for other freshwater fishes[3]. Whitefish species divergence is characterized by, for example, differences in body size and the number of 'gill rakers' — cartilaginous structures that protrude from fish gills and are involved in feeding (Fig. 1). Large-bodied whitefish, which have fewer gill rakers, typically feed from the bottom of lakes and spawn in shallow water in winter, whereas smaller species, which have more gill rakers, tend to feed in open water and spawn much deeper.

However, increased human activity around the lakes dramatically altered the lakes' ecology during the twentieth century. Higher nutrient levels in the water caused eutrophication, in which algal populations increase, water quality is reduced and oxygen levels at the lake bottom decrease. Vonlanthen *et al.*[1] propose that these conditions compressed the depth range in which whitefish could spawn, bringing previously separated species together to breed, forming hybrids. Whitefish feeding patterns were probably also affected, through reductions in zooplankton diversity and possibly in the density of bottom-dwelling prey (Fig. 1), which would also have reduced opportunities for exploiting ecological variation.

Vonlanthen and colleagues' data show that the extent of species loss for each lake correlates with the severity of that lake's eutrophication. But did these extinctions result exclusively from demographic decline — the extinction process we usually think of, in which deaths outnumber births? Or was reverse speciation at play, in which characteristics that once defined distinct species are merged into a single hybrid species?

The authors report[2] several lines of evidence suggesting a role for reverse speciation in the lakes. First, the severity of eutrophication is the best predictor of genetic differentiation of modern whitefish — lakes that suffered the greatest eutrophication contain species that are the least genetically different from each other. Historical DNA samples also allowed Vonlanthen and colleagues to document a progressive reduction in whitefish genetic differentiation in one of the lakes (Lake Constance) between 1926 and 2004. Furthermore, they find strong genetic traces of the extinct whitefish species

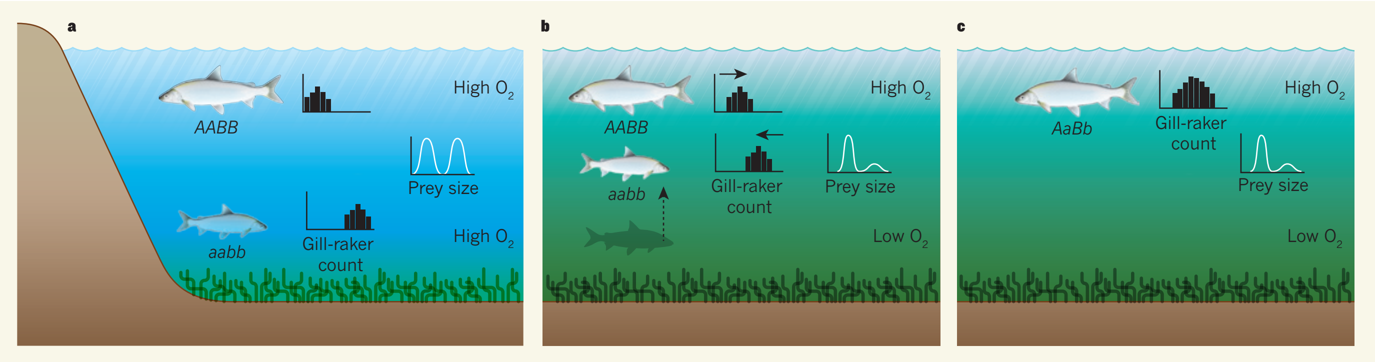

Figure 1 | Loss of fish biodiversity through eutrophication. a, Before human activity raised nutrient levels in lake waters, the Swiss lakes studied by Vonlanthen *et al.*[2] were well oxygenated at all depths, and there were diverse invertebrate prey communities in both the open water (suggested by other studies to be generally smaller prey, represented by the left side of the prey-size distribution) and at the bottom (generally larger prey, right side of distribution). These resources supported genetically distinct species of whitefish (represented as *AABB* and *aabb*) with different characteristics, including their body size and number of gill rakers — cartilaginous protrusions from the gills. Large-bodied whitefish with fewer gill rakers generally fed from the bottom and spawned in shallow water, whereas small-bodied species with more gill rakers typically fed in open water and spawned much deeper. **b,** Lake eutrophication led to lower oxygen levels, especially at depth, driving deep-spawning species into shallower water, where they spawned with other species to form hybrids. Simultaneously, the fishes' prey became less diverse, thereby reducing divergent selection — the process by which different ecological niches provide a selective pressure for species to have distinct characteristics. **c,** Increased hybridization and reduced divergent selection, as well as demographic decline, resulted in extinction of the deeper-spawning species, with the remaining species being a genetic hybrid (*AaBb*) and possessing an intermediate number of gill rakers.

Coregonus gutturosus in extant sister species, implicating hybridization in that extinction. The authors also document lessened differences in the fishes' gill-raker numbers, a key characteristic, in the most polluted lakes. This finding is consistent with the hypothesis that eutrophication reduced ecological opportunity, which in turn weakened selection for differences in feeding traits.

Previous cases of reverse speciation in fishes[4,5] and birds[6] have shown that altered ecological conditions[7,8] can erode fragile reproductive barriers and allow the formation of viable hybrids. However, the mechanisms of species collapse have often remained obscure. The current study is noteworthy because it establishes strong links among changed environmental conditions, reduced ecological opportunity and reverse speciation. The scale of the effect in whitefish, studied over decades and across 17 lakes, is also exceptional. The work highlights an under-appreciated aspect of biodiversity loss — 'cryptic extinction', whereby considerable morphological and genetic variability is maintained within hybrids, but previously species-specific combinations of these features are lost.

Cryptic extinction may have a particularly high impact on fish biodiversity because individual lakes often contain unique species, and fresh waters contain about 40% of all fish species[9]. But reverse speciation can also occur in terrestrial environments, particularly those similar to lakes, such as volcanic islands[6].

The major limitation of Vonlanthen and colleagues' study is its correlational nature. Whitefish hybridization clearly increased in the Swiss lakes as pollution and disturbance increased, but factors in addition to those highlighted by the authors may have contributed to the loss of diversity. One of these is a by-product of demographic decline — as one species becomes rare, finding mates becomes more difficult, and so more frequent hybridization would be expected. Other potential confounding processes include the introduction of whitefish from hatcheries, overfishing and the impact of invasive species. However, despite these other influences, a convincing effect of eutrophication levels on biodiversity emerges from the study[2].

The work raises a number of additional important questions. How much, and which parts, of the genomes of extant whitefish species are 'original' compared with hybrid in origin? Which genes are responsible for the critical differences between whitefish species, and how has the prevalence of variants of these genes altered in response to ecological changes? In addition, what are the relative roles of the two processes of increased hybridization and reduced divergent selection (in which the existence of multiple ecological niches promotes the divergence of distinct species) in driving reverse speciation? Genome-wide analyses of both historical and modern whitefish samples will help to address these questions.

A more practical concern is what happens next. Eutrophication has now been eliminated or greatly reduced in most of the lakes studied, so they more closely resemble their previous state. Can we expect 're-speciation', in which fishes with characteristics of extinct species reappear[10]? Current theory does not provide a clear answer, but suggests that distinct species can re-emerge after a brief collapse[11]. If Vonlanthen and colleagues are correct and speciation reversal is an under-appreciated threat to biodiversity, we need to understand how to prevent and correct the ecological changes responsible — and perhaps learn how to recognize when it truly is too late. ■

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EARTH SCIENCE

Intraplate volcanism

The origin of volcanic activity occurring far from tectonic-plate boundaries has been a subject of contention. The latest geodynamic model offers a fresh take on the matter. SEE LETTER P.386

CIN-TY A. LEE & STEPHEN P. GRAND

In this issue, Liu and Stegman[1] present a hypothesis for the generation of volcanic centres that might change our view of how plate tectonics influences the distribution of volcanic activity on Earth.

The theory of plate tectonics describes the uppermost of Earth's layers as made up of rigid plates, the relative motions of which are confined to narrow plate boundaries. The boundaries come in three types: divergent, where plates move away from one another and create systems such as mid-ocean ridges; convergent, where one plate slides beneath another, forming subduction zones; and transform margins, where plates slide past one another, as in the San Andreas Fault system.

Plate tectonics successfully explains most of Earth's geological features. For example, volcanism at mid-ocean ridges can be explained by decompression melting associated with passive upwelling of hot (asthenospheric) mantle in response to plate divergence. Volcanism at subduction zones can be described by a combination of two effects: partial melting of the mantle, driven by return flow in the mantle wedge overlying the subduction zone, and melting-point depression, caused by the influx of water released from the descending plate of the subduction zone.

Volcanoes that occur far from plate boundaries — for example, intraplate magmatism — are more difficult to explain with plate tectonics. Some intraplate volcanic systems, such as the Hawaiian volcanic chain in the Pacific plate and the Yellowstone volcanic field in North America, migrate along tracks that seem independent of plate-boundary processes. The effusive but short-lived outpourings of basalts, known as flood basalts, some of which are so large that they cover substantial areas of continents or even entire plates, are also not easily described by the interaction of slowly moving plates.

One popular view is that intraplate magmatism is driven by narrow mantle upwellings (plumes) originating from a hot thermal layer at the core–mantle boundary[2]. Therefore, the expression of plumes at Earth's surface should be independent of plate motions[2]. Flood basalts are thought to record the initial impingement of the anomalously hot plume head, whereas the volcanic track, known as the hot-spot track, records the passage of the plate over the plume's tail[3]. For example, the eruption of the Steens–Columbia River flood basalt about 17 million years ago is thought to represent the initiation of the currently active Yellowstone hot-spot track, and so is conjectured to fit into the plume theory[4,5].

However, the eruption area of the Steens–Columbia River flood basalt is oriented north–south, perpendicular to the