

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 birds⁶ 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 species⁹. But reverse speciation can also occur in terrestrial environments, particularly those similar to lakes, such as volcanic islands⁶.

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 study².

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 reappear¹⁰? Current theory does not provide a clear answer, but suggests that distinct species can re-emerge after a brief collapse¹¹. 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. ■

Jeffrey S. McKinnon is in the Department of Biology and North Carolina Center for Biodiversity, East Carolina University, Greenville, North Carolina 27858, USA.

Eric B. Taylor is in the Department of Zoology, Beaty Biodiversity Research Centre and Museum, and the Native Fishes Research Group, University of British Columbia, British Columbia V6T 1Z4, Canada. e-mails: mckinmonj@ecu.edu; etaylor@zoology.ubc.ca

1. Schluter, D. *Science* **323**, 737–741 (2009).
2. Vonlanthen, P. *et al.* *Nature* **482**, 357–362 (2012).
3. Schluter, D. *The Ecology of Adaptive Radiation* (Oxford Univ. Press, 2000).
4. Seehausen, O., van Alphen, J. J. M. & Witte, F. *Science* **277**, 1808–1811 (1997).
5. Taylor, E. B. *et al.* *Mol. Ecol.* **15**, 343–355 (2006).
6. De León, L. F. *et al.* *Evolution* **65**, 2258–2272 (2011).
7. Behm, J. E., Ives, A. R. & Boughman, J. W. *Am. Nat.* **175**, 11–26 (2010).
8. Rhymer, J. M. & Simberloff, D. *Annu. Rev. Ecol. Syst.* **27**, 83–109 (1996).
9. Dudgeon, D. *et al.* *Biol. Rev.* **81**, 163–182 (2006).
10. Turner, G. F. *Fish Fisheries* **3**, 225–229 (2002).
11. Gilman, R. T. & Behm, J. E. *Evolution* **65**, 2592–2605 (2011).

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 Stegman¹ 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 boundary². Therefore, the expression of plumes at Earth's surface should be independent of plate motions². 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 tail³. 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

Yellowstone track. In addition, the geochemistry of the flood basalt differs from that of the Yellowstone volcanics^{6,7}, complicating the plume hypothesis. Alternatively, the Steens–Columbia River flood basalt could be associated with extension of the upper plate behind the Cascades volcanic arc⁸ (back-arc spreading). But this phenomenon does not seem to explain the sudden appearance of the Steens–Columbia River flood basalt.

In their study, Liu and Stegman¹ (page 386) propose that the Steens–Columbia River flood basalt is a natural consequence of slowing convergence between the North American plate and the ancient Farallon plate. This slow-down was presumably associated with the approach of a mid-ocean ridge between the Farallon and Pacific plates 20 million years ago, now manifested as the active Juan de Fuca ridge. The authors performed geodynamic calculations with initial and boundary conditions constrained by observed relative plate motions and plate age. They show that stretching and eventual tearing of the Farallon plate accompanied the slow-down of convergence, resulting in detachment of the Farallon plate.

Liu and Stegman find that the model that best reproduces the presumed current location of the Farallon plate, as constrained from seismic tomography, predicts tearing to have begun about 16 million to 17 million years ago, when the Steens–Columbia River flood basalt initiated. Dynamic pressures generated from this tear resulted in rapid mantle upwelling through this gap in the slab, driving a magmatic flare-up that mimics the structural trend of the Steens–Columbia River flood basalt (Fig. 1).

If Liu and Stegman's model is correct, the implication is that some intraplate magmatism can be explained by the development of gravitational instabilities within subducting slabs. In their model, thermal upwelling is still responsible for flood basalts, but unlike traditional plumes, which derive from the lowermost mantle, an upper-mantle origin is implied. There are, however, some features that remain unresolved. For example, the model does not provide a good explanation for the eastward migration of the Yellowstone hot-spot track, the high ratio of helium-3 to helium-4 in Yellowstone volcanics⁷ or the presence of a seismic-velocity anomaly extending into the lower mantle beneath Yellowstone⁹. And it may not explain the isotopic signatures seen in the Steens–Columbia River flood basalt.

If accurate, Liu and Stegman's model should apply to other locations where slab tears have occurred. Such a tear clearly happened in central California about 20 million years ago, because the last remnants of the Farallon plate were captured on the coast of California, but the rest of the Farallon is no longer present beneath the state¹⁰. There is evidence of a flare-up in basaltic magmatism east of central California, for example on the border of California



Figure 1 | Columbia River Gorge, Oregon. Large, effusive outpourings of basalts, such as the Steens–Columbia River flood basalt in Oregon and Washington exposed here on the margins of the river, are usually attributed to the impingement of thermal plumes arising from the core–mantle boundary. Liu and Stegman show¹ that the timing and distribution of eruption may instead be related to tears developed within subducting slabs.

and Nevada, during this time. But the magnitude does not seem comparable to that of the Steens–Columbia River flood basalt, suggesting that different boundary conditions might need to be considered in the authors' model.

In any case, Liu and Stegman's study is pertinent because it draws more attention to subducting slabs in generating intraplate magmas. The following examples might be considered. Where a young oceanic plate is subducting, a slab tear, accompanied by large-volume magmatic flare-ups, should develop because young plates are difficult to subduct. This hypothesis may apply to the eastern Pacific. By contrast, when an old oceanic plate is subducting, a long segment of the slab might be expected to stagnate temporarily in the transition zone between the upper and lower mantle¹¹. The juxtaposition of cold slab material against hot mantle at depth would generate small-scale thermal upwellings along the edges of the slab¹². These upwellings could generate widespread basaltic magmatism far from the subduction trench, as seen in northeastern China. If the edges of the slab are migrating relative to the upper plate, hot-spot tracks could be generated¹³.

We note that all of these upwellings are sourced in the upper mantle and likely to be superimposed on magmatism associated with back-arc spreading; thus a complicated pattern of magmatism is expected. Should a subducting slab penetrate deep into the lower mantle, upwellings might be expected even further from plate boundaries.

In conclusion, there is reason to speculate that intraplate magmas might be intimately linked to subducting slabs^{12,14}. In other words, it is conceivable that plate tectonics generates many intraplate magmas. Differences in the magnitude and locations of intraplate

magmas may simply be controlled by the scale of subducting slabs. The debate over whether deep-seated thermal plumes exist¹⁵ remains unresolved because these narrow upwellings are difficult to detect. An alternative approach is to map out the geometry and length scale of subducting slabs, which may be easier to detect by various geophysical methods. Liu and Stegman's model shows how downwellings, such as subduction, must be considered when understanding the origin of upwellings and their associated magmatic activities. ■

Cin-Ty A. Lee is in the Department of Earth Science, Rice University, Houston, Texas 77005, USA. **Stephen P. Grand** is in the Department of Geological Sciences, University of Texas at Austin, Texas 78749, USA. e-mail: ctlee@rice.edu

- Liu, L. & Stegman, D. R. *Nature* **482**, 386–389 (2012).
- Morgan, W. J. *Nature* **230**, 42–43 (1971).
- Richards, M. A., Jones, D. L., Duncan, R. A. & DePaolo, D. J. *Science* **254**, 263–267 (1991).
- Smith, R. B. *et al. J. Volcanol. Geotherm. Res.* **188**, 26–56 (2009).
- Hooper, P. R., Camp, V. E., Reidel, S. P. & Ross, M. E. *Geol. Soc. Am. Spec. Pap.* **430**, 635–668 (2007).
- Leeman, W. P., Schutt, D. L. & Hughes, S. S. *J. Volcanol. Geotherm. Res.* **188**, 57–67 (2009).
- Graham, D. W. *et al. J. Volcanol. Geotherm. Res.* **188**, 128–140 (2009).
- Carlson, R. W. & Hart, W. K. J. *Geophys. Res.* **92**, 6191–6206 (1987).
- Schmandt, B. & Humphreys, E. *Earth Planet. Sci. Lett.* **297**, 435–445 (2010).
- Nicholson, C., Sorlien, C. C., Atwater, T. A., Crowell, J. C. & Luyendyk, B. P. *Geology* **22**, 491–495 (1994).
- Zhao, D. *Phys. Earth Planet. Inter.* **146**, 3–34 (2004).
- Faccenna, C. *et al. Earth Planet. Sci. Lett.* **299**, 54–68 (2010).
- James, D. E., Fouch, M. J., Carlson, R. W. & Roth, J. B. *Earth Planet. Sci. Lett.* **311**, 124–135 (2011).
- James, D. E., Fouch, M. J., VanDecar, J. C. & van der Lee, S. *Geophys. Res. Lett.* **28**, 2485–2488 (2001).
- Anderson, D. L. *Geol. Soc. Am. Spec. Pap.* **388**, 31–54 (2005).