

AMOC, although other secondary processes also influence Pa/Th (6). Another AMOC proxy is the standardized carbon isotope ratio in the fossil shells of bottom-dwelling (benthic) foraminifera ( $\delta^{13}\text{C}_{\text{BF}}$ ); these organisms record the carbon isotope ratios of dissolved inorganic carbon in the water column.  $\delta^{13}\text{C}_{\text{BF}}$  is also affected by other processes, but those can be simulated in three-dimensional (3D) models (7) and differ from the secondary processes affecting Pa/Th.

Thus, if secondary processes dominated the variations of Pa/Th and/or  $\delta^{13}\text{C}_{\text{BF}}$ , we would not expect to see any correlation between them. However, Henry *et al.*'s Pa/Th and  $\delta^{13}\text{C}_{\text{BF}}$  records are highly correlated both with each other and with sea surface temperature (SST) variations in a nearby sediment core. In their reconstruction, cold phases in the North Atlantic are  $\sim 2^\circ\text{C}$  cooler in the subtropical North Atlantic. Pa/Th increases during these cold phases, approaching the production value, and  $\delta^{13}\text{C}_{\text{BF}}$  decreases by  $\sim 0.5$  per mil. In 3D climate model simulations, collapse and resumption of the AMOC caused by freshwater perturbations to the North Atlantic results in similar changes in SSTs and  $\delta^{13}\text{C}_{\text{BF}}$  at the core location (8).

This agreement indicates that at least some of the ice age D-O events, particularly those accompanied by massive ice berg rafting, were associated with large AMOC changes and perhaps even AMOC collapses. But Henry *et al.*'s data also indicate a variety of responses, with other events showing smaller changes.

In the future, combining high-quality paleoceanographic reconstructions with 3D circulation models that directly simulate the proxies may allow AMOC changes to be quantified throughout the most recent ice age. This could help to better assess how AMOC changes affect ecosystems and societies, such as shifts in the inter-tropical convergence zone, ocean productivity, and carbon cycle, and how likely they are to occur in the future as a result of human-caused climate change (9). ■

#### REFERENCES

1. L. G. Henry *et al.*, *Science* **353**, 470 (2016).
2. T. Kuhlbrodt *et al.*, *Rev. Geophys.* **45**, RG2001 (2007).
3. T. J. Crowley, *Paleoceanography* **7**, 489 (1992).
4. C. Buizert *et al.*, *Nature* **520**, 661 (2015).
5. T. F. Stocker, S. J. Johnsen, *Paleoceanography* **18**, 1087 (2003).
6. C. T. Hayes *et al.*, *Deep Sea Res.* **116**, 29 (2015).
7. A. Schmittner *et al.*, *Biogeosci.* **10**, 5793 (2013).
8. A. Schmittner, D. C. Lund, *Clim. Past* **11**, 135 (2015).
9. W. Cheng, J. C. H. Chiang, D. X. Zhang, *J. Climate* **26**, 7187 (2013).

10.1126/science.aag3156

#### ECOLOGY

## Plant extinctions take time

Many plant species may already be functionally extinct

By **Quentin Cronk**

**T**he recent *State of the World's Plants* report from the Royal Botanic Gardens, Kew (1) estimates that 50,000 of the  $\sim 390,000$  known vascular plant species are at risk of extinction. Given the rarity of so many plants, coupled with widespread environmental destruction over the past quarter-century, we might expect that a lot of plants should have gone extinct. Indeed, estimates made in the early 1990s suggest that up to 30,000 species should have gone extinct by 2015 (2, 3). Yet, the International Union for Conservation of Nature (IUCN) Red List of Threatened Species database for 2016 has fewer than 150 extinct species. How can we explain this discrepancy?

Proving an absence is an age-old problem in science. To prove the existence of an organism, one can collect a specimen and put it in a museum collection. Proving that an organism does not exist is more problematic. It is always possible that we have not looked hard enough. As a result, the answer to the seemingly simple question of how many plant species have become extinct in the Anthropocene is that no one really knows. But this does not mean that there is no problem. Many plant species may be on an inevitable path to extinction, even though isolated specimens can survive for decades or more.

To derive global plant extinction rates expected by 2015, multiple studies in the early 1990s estimated likely species losses based on the habitat area expected to be lost (2, 3). This species-area model is potentially problematic (4). But even if the model is flawed, the underlying concept is uncontroversial: less habitat, fewer species. The studies arrived at the conclusion that between 4000 and 30,000 species would be extinct by 2015 (2, 3). In contrast, the IUCN Red List database of 2016 lists only 142 extinct plants; 105 of these are completely extinct, and the remaining 37 are extinct in the wild but survive in cultivation. The discrepancy between the recorded extinctions and earlier expectations cannot be explained by lower-than-expected habitat destruction. In fact, many new threats to tropical forest ecosystems have emerged since 1990, notably the expan-

sion of industrialized agriculture driven by increased demand for soy and palm oil.

Two possible explanations present themselves. First, there may be many undocumented extinctions. It is true that extinction lists are highly conservative. Compilers have to be cautious, because even when an organism is declared extinct, there is always the possibility that it will be rediscovered. How much searching has to be done before a species that has not been seen for more than 50 years is declared extinct? And who will do the searching? Biologists generally prefer to do fieldwork in places where species survive, not degraded areas where extinction has occurred. For practical reasons, a complete list of extinct plants may be impossible to obtain. Even so, it is hard to imagine that we would miss thousands of predicted extinctions.

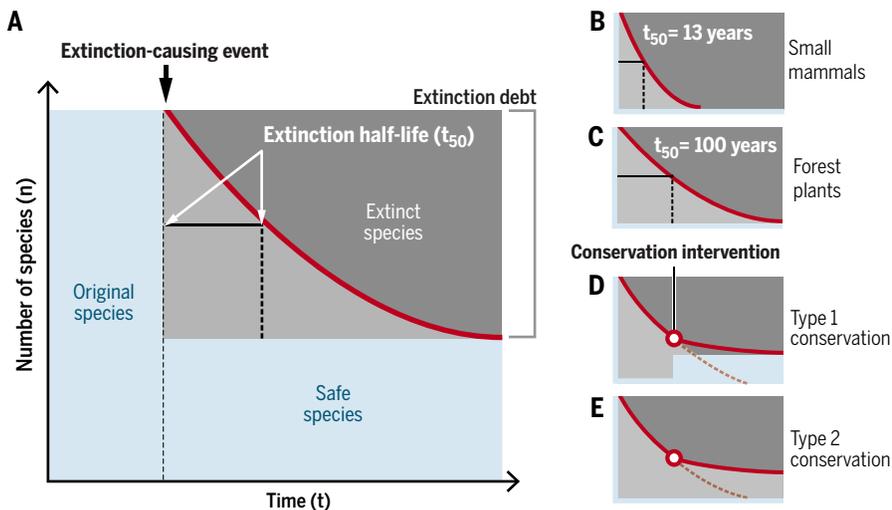
Second, there may be a long extinction lag time. The species-area curve is driven by equilibrium phenomena, and ecosystems may take a long time to equilibrate. Diamond has used the term "relaxation time" to describe this extinction lag (5). Janzen calls the species in this extinction waiting room "the living dead" (6). He noticed that the agricultural landscapes that replaced native forest in Costa Rica were not devoid of native trees. Forest remnants hung on at field margins and in small forest patches. However these trees could not regenerate because habitat suitable for seedlings no longer existed. The trees, although living out their physiological life, were "just as dead... as if they were in the back of a logging truck" (6).

Numerous factors influence the extinction lag time (7). Broadly, these can be divided into those intrinsic to species (such as longevity of individuals, presence of a seed bank, and sensitivity to inbreeding depression) and extrinsic factors (such as spatial scales and patch structure). Long-lived species in large areas will have long extinction lag times and vice versa.

There are several reasons that plants should survive longer than animals as living dead. First, plants may have seed banks in the soil; until these seed banks are ex-

**"...we [may be] facing slow-creeping biodiversity loss on a large scale."**

Beaty Biodiversity Research Centre, University of British Columbia, Vancouver, BC, Canada. Email: [quentin.cronk@ubc.ca](mailto:quentin.cronk@ubc.ca)



**The slow-burning fuse of plant extinction.** (A) This conceptual scheme relates the extinction debt (the number of species expected to become extinct as the result of an extinction-causing event) to the relaxation time (the lag time to complete this process). (B) Small areas and fast demographic turnover promote rapid extinction and hence short persistence of the extinction debt. (C) Large areas or slow demographic turnover promote slow extinction and long persistence of extinction debt. (D and E) Conservation interventions can have different effects. Type 1 conservation reduces the extinction debt and thus prevents extinction (D); type 2 conservation extends the extinction lag time and thus delays extinction (E).

hausted, occasional plants may appear. Some invertebrates have stages that can diapause in lake mud for multiple years, but this strategy is generally rarer in animals than in plants. Second, few animals have life spans matching those of woody plants, which may live hundreds of years. An exception is Lonesome George, the last known Pinta tortoise (*Chelonoidis abingdoni*), who extended the living-dead phase to almost plantlike proportions by his longevity. Third, many plants can reproduce asexually or self-fertilize, and the last individual plant may therefore produce occasional successors, whereas the single last animal rarely does.

There are thus strong reasons to expect the relaxation times for plant extinction to greatly exceed that of animals. Indeed, the processes and parameters of plant extinction may be quite different from those of animals. It is therefore important to understand what happens during the relaxation time. In this vein, Downey and Richardson recently introduced the concept of a plant extinction trajectory that passes through several defined stages (8).

How long can plant relaxation times be? The South Atlantic island of St. Helena provides an interesting case study. The Portuguese navigators who discovered it in 1502 quickly introduced goats. Without predators, the goats multiplied into huge flocks. Most vegetation was destroyed, and plants became extinct. What is remarkable, however, is the tenacity of the living dead. For instance, the St. Helena olive (*Nesiotia elliptica*) fell to an unsustainable population level of 12 to 15 plants in the mid-19th century (9) but only became extinct in 2003. It was arguably just

as extinct with a population of less than 10 in 1900 as it is now. The extinction lag times for woody plants on St. Helena are thus measured in many centuries. Studies on temperate forest herbs similarly indicate lag times of more than 100 years (10), whereas small mammals in tropical forest fragments have median extinction lag times of only 13 years (11).

This slow-burn extinction in plants raises a number of questions. The first is a practical one. If human actions over the past 25 years have set in train a mass extinction that will take 100 years or more to play out, then how do we identify the living dead and what should be our response? At the very least, the long plant relaxation time allows us to sequence the whole genomes of the rarest plants, so that we will know a little more about the organisms we lose (and understand, or even address, some of the genetic problems they face). As sequencing costs drop, a coordinated global program of rarity genomics is something that can be considered.

The second question is whether we can use the relaxation time as a window of opportunity for conservation. Can we drive the equilibrium back to a state that retains more species? The answer is probably a cautious yes. Another way of expressing the difference between functional extinction (that is, the living dead) and census extinction (where no individuals survive) is through the concept of “extinction debt,” a term coined by Tilman *et al.* from metapopulation dynamics (12). Extinction debt is the number of extinctions expected to result, sooner or later, from an extinction-causing event. Facing the slippery

problem of quantifying census extinction, extinction debt may be a more useful approach (13). It may be possible, by smart ecological restoration and reserve selection, to pump “species credit” into ecosystems to reduce extinction debt (14).

There are some hopeful stories of species brought back from the brink sustainably. An example of a critically rare species that has possibly been moved into the sustainably safe zone is the Mauritius kestrel, which was made almost extinct by anti-malarial DDT use in the 1950s and 1960s, but intensive management from 1974 worked (15). The kestrel escaped irreversible genetic problems only because of the very short duration of its bottleneck and the total cessation of DDT use in 1970. The success of conservation projects will depend on whether they merely prolong the extinction lag time or whether they reduce the extinction debt by dealing with fundamental ecosystem and genetic problems, moving species into the sustainably safe zone (see the figure).

At this juncture, rather than estimating census extinction, it is important that scientists develop better models for assessing global extinction debt and maximizing species credit. If the high 1990s estimates of plant extinction by 2015 are accurate estimates of extinction debt, then we are facing slow-creeping biodiversity loss on a large scale. Failing to notice this because the time scale is too long would not be smart. ■

#### REFERENCES AND NOTES

1. Royal Botanic Gardens, Kew, *The State of the World's Plants* (Royal Botanic Gardens, Kew, UK, 2016).
2. M. Jenkins, in *Global Biodiversity: Status of the Earth's Living Resources* (World Conservation Monitoring Centre, Cambridge, UK, 1992); <http://dx.doi.org/10.5962/bhl.title.44956>.
3. W. V. Reid, in *Tropical Deforestation and Species Extinction*, T. C. Whitmore, J. A. Sayer, Eds. (Chapman Hall, London, UK, 1992), pp. 55–73.
4. F. He, S. Hubbell, *Ecology* **94**, 1905 (2013).
5. J. M. Diamond, *Proc. Natl. Acad. Sci. U.S.A.* **69**, 3199 (1972).
6. D. H. Janzen, *Encyclopedia of Biodiversity* **4**, 590 (2001).
7. K. Hylander, J. Ehrlén, *Trends Ecol. Evol.* **28**, 341 (2013).
8. P. O. Downey, D. M. Richardson, *AoB Plants* **10**, 1093/aobpla/plw047 (2016).
9. Q. B. C. Cronk, *The Endemic Flora of St Helena* (Nelson, Oswestry, 2000).
10. M. Vellend *et al.*, *Ecology* **87**, 542 (2006).
11. L. Gibson *et al.*, *Science* **341**, 1508 (2013).
12. D. Tilman *et al.*, *Nature* **371**, 65 (1994).
13. O. R. Wearn *et al.*, *Science* **337**, 228 (2012).
14. I. Hanski, *Ann. Zool. Fennici* **37**, 271 (2000).
15. J. J. Groombridge *et al.*, *J. Anim. Ecol.* **70**, 401 (2001).

#### ACKNOWLEDGMENTS

I thank the organizers and participants of the State of the World's Plants Symposium at Royal Botanic Gardens, Kew (May 2016) for helpful discussion. Research in the author's laboratory is funded by the Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants Program (grant no. RGPIN-2014-05820).

10.1126/science.aag1794