Ecology

The pace of biodiversity change in a warming world

Jennifer M. Sunday

The timing of disruptions to biodiversity associated with global warming is a key, but little-explored, dimension of change. Will losses in biodiversity occur all at once, or be spread out over time? **See p.496**

Projections of the effects of climate change on multiple species are often made by estimating the change predicted for a single future time point; for example, by asking how the geographical distributions of multiple species will differ in 2100 from those today[1]. However, this approach does not capture the pace, timing or possible synchrony of biodiversity changes across time. Acute synchronous impacts can potentially be more damaging to a system than those spread over time, in terms of both human adaptation to biodiversity losses and ecosystem resilience. On page 496, Trisos *et al.*[2] report an approach for predicting how climate change will affect future biodiversity patterns.

The authors estimated the timing and synchrony of climate impacts on organisms globally by asking when species in a given region will be exposed to temperatures outside their normal global experience (by considering projected future temperatures due to climate change). They did this by compiling geographical-range maps for approximately 30,000 species, including birds, mammals, reptiles, amphibians, fishes, marine invertebrates, corals and seagrasses, and using temperature-projection models to identify the warmest average annual temperature experienced between 1850 and 2005 by each species within its range. Dividing Earth into grid cells of 100 square kilometres and using predicted climate information, the authors determined when each species would experience annual average temperatures above its historical annual average, encountered anywhere in its range, for an extended period. The result provides an estimate of when a species will be exposed to unprecedentedly high temperatures.

Trisos and co-workers' approach builds on 'time of emergence', a concept used when analysing climate change. Time of emergence describes the time at which a climate variable, such as temperature, emerges beyond the historical values of variation observed for a particular location — in other words, when the average value of the measurement of interest becomes more extreme than the previously encountered natural variability. Trisos *et al.* offer innovation in applying this concept to the realm of biodiversity. First, rather than considering the variation experienced at just one location, they considered the full breadth of variation experienced across each species' geographical range, defining an organism as being 'exposed' in a specific grid cell only after it has experienced temperatures above its range-wide maximum (and with annual temperatures remaining above this value for a minimum of five years). Second, because the authors considered multiple species in an assemblage (the group of species present in a given grid cell), it was possible to assess the relative timing of exposure in a graphical format that the authors call a horizon profile (Fig. 1). This enables the synchrony in the timing of exposure events for the species in a region to be quantified and easily visualized.

The authors' results predict that the greatest levels of exposure will occur at latitudes nearer the Equator, and, most notably, that there will be high synchrony in the timing of exposure between species in the same grid cell, for grid cells both on land and in the ocean. Trisos *et al.* find that most species in a given cell will usually become exposed to unprecedentedly high temperatures within the same decade. If this exposure results in local extinction, it suggests the following disturbing scenario. We might initially see a small trickle of species being lost from an assemblage, but this will be followed by an abrupt loss of most species in the assemblage within the same decade.

What mechanism might explain this predicted pattern? The abruptness in exposures predicted by Trisos and colleagues is not due to any particular abruptness in the timing of climate change itself — although similar predictions of abrupt ecological change have been based on the additive effects of gradual climate change with abrupt natural climate variability, including weather[3]. Instead, it seems to be attributable to the similarity of the thermal niches occupied by the species in each grid cell. Trisos and
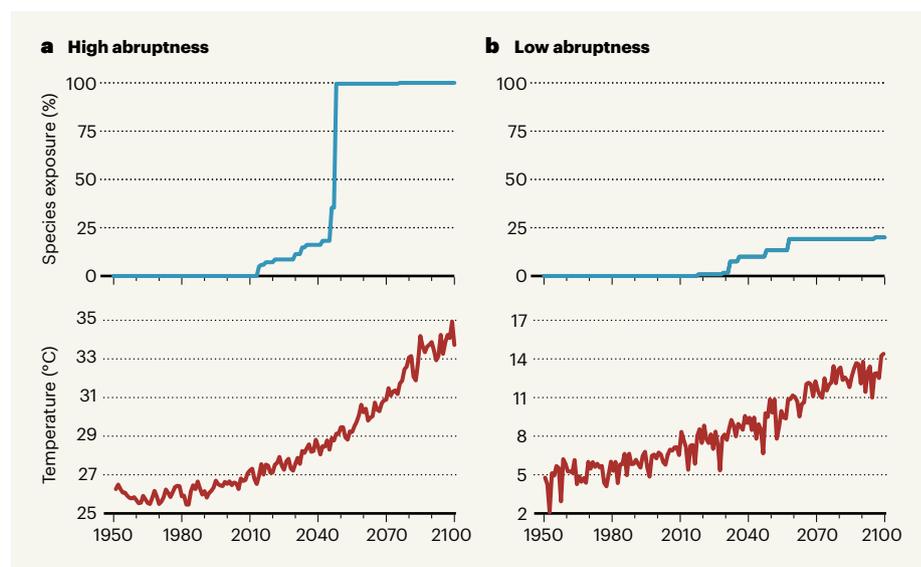
Figure 1 | Exposure of species to unprecedented temperatures owing to climate change. Trisos *et al.*[2] report a global analysis describing when species (as assessed in grids of 100 square kilometres) are predicted to encounter, for more than five years, higher annual average temperatures than they have previously experienced anywhere in their geographical range. This state is called species exposure, and the authors assessed more than 30,000 terrestrial and marine species. **a**, For the majority of locations, the timing of when most species in a grid are exposed occurs highly abruptly, as in this example from the Amazon basin. Temperatures are from projection models, and the predicted future temperatures due to climate change are from the RCP8.5 model, which depicts a scenario of high greenhouse-gas emissions[7]. **b**, By contrast, in the Gobi Desert (located in northern China and southern Mongolia), species exposure occurs with low abruptness. (Graphs based on Fig. 1 of ref. 2.)

colleagues find that more than half of the species in a given cell (and almost 90% in most marine assemblages) tend to have geographical ranges that encompass similarly warm temperatures, such that they would all face exposure at around the same time.

Such a striking pattern of shared thermal niches within assemblages has been observed before, in a global analysis of marine fishes and invertebrates[4]. In that study, species' thermal niches were found not to change gradually with latitude, but instead to have distinct transition points, indicating that species belong to what are termed thermal guilds[4]. These shared thermal niches could be due to physical boundaries or ecological interactions that restrict the ranges − and temperatures experienced − of multiple species similarly. Or this phenomenon might be the result of a low rate of evolution in the range of temperatures across which the species can fundamentally persist, leading to the maintenance of thermal guilds.

When does this abrupt exposure happen? It is predicted that it will occur at different times for grid cells around the world, from some predicted to be occurring already in the ocean, to others occurring towards the end of the projected time range, in 2100. That the timing is different across grid cells is a good thing, because at least all of the assemblages aren't predicted to experience abrupt losses at the same time. But, notably, the timing of exposure does not correlate with the timing of climate-change emergence in temperature, suggesting that the latter metric might be a poor predictor of major biodiversity change within a given grid cell.

Trying to project the timing of biodiversity shifts is a noble objective that will surely help us to develop management systems and anticipate crises. Although Trisos *et al.* provide an initial approach that offers useful insights, further studies should attempt to validate and qualify these predictions. For example, Trisos and colleagues used temperatures outside species' current thermal niches to define climate exposure, but we don't know what will really occur when species experience such temperatures − many can certainly tolerate temperatures beyond those found in their current ranges[5,6]. The timing of exposure to truly limiting environments might turn out to be more diverse across species than currently predicted by Trisos *et al.* if variation in species' fundamental climatic niches (the range of temperatures and other climate variables across which an organism can survive) is considered. It will also be useful to consider the flip side of the range-shift issue: the timing and abruptness with which new species enter an assemblage as a result of range extensions arising from climate change.

Most crucially, as climate change progresses, we should be able to test and refine

projections such as these using real-time observations. Where are biodiversity changes already occurring abruptly? The need for systematic global biodiversity monitoring has never been stronger.

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Evolution

Can't see the wood for the trees

Mark Pagel

Evolutionary-tree diagrams, which show the branching relationships between species, are widely used to estimate the rates at which new species arise and existing ones become extinct. New work casts doubt on this approach. **See p.502**

Scientists often want to make inferences about what the biological past was like, and how that past gave rise to the present, because doing so allows them to understand the processes that drive evolution. But on page 502, Louca and Pennell[1] challenge a major aspect of that enterprise.

Specifically, their work regards the issue of estimating past rates of speciation and extinction, which are, respectively, the rates at which new species arise and existing species go extinct. These rates determine the number of contemporary species of various forms. There are, for instance, around 6,600 species

> **"Assumptions are being made about the things that we would like to estimate."**

of songbird (passerines), which constitute more than half of all existing bird species, and we might therefore be tempted to say that songbirds have a high rate of speciation in comparison with that of other birds. But it's also possible to speculate that they have a low extinction rate. Louca and Pennell show that the uncertainty is even worse than this: not only can we not estimate these two rates, but also there is an infinite number of different sets of these two parameters that are equally good at describing any particular outcome, such as the number of species of contemporary songbird.

Because fossils are scarce or non-existent

for the vast majority of species, evolutionary scientists instead estimate speciation and extinction rates from phylogenies − tree diagrams that describe the patterns of descent among a group of contemporary species (Fig. 1a,b). For any such phylogeny, it is easy to construct what is termed a lineage-through-time plot; this records the cumulative number of lineages up to that point in time on the tree that will eventually leave one or more living descendent species (Fig. 1c). The slope of the curve fitted to such a plot, often denoted by λ, is the net speciation rate. This is equal to the difference between the rate of speciation, termed b (or birth), and the rate of extinction, termed d (or death). It is described by the equation $\lambda = b − d$.

However, it is known that a difficulty arises in estimating b and d, because if all that is available is the number of species that have survived to the present, such as our 6,600 songbirds, any pair of b and d that returns the same value of λ will produce an identical lineage-through-time curve, and there is an infinite number of these pairs. In fact, it turns out that for the simple case of estimating $b − d$, such as described here, a feature of the shape of the lineage-through-time curve can be exploited to estimate the rate of extinction, and then the rate of speciation can be found by subtraction[2]. But to do so requires making the assumption that both of these rates are constant throughout the entire time span of the tree, when instead they almost certainly vary between the different branches (lineages) of the phylogeny, and through time.

This is where Louca and Pennell step in,