

Spatial scale and the synchrony of ecological disruption

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In a rapidly changing global climate, the tempo and geography of threats to biodiversity and ecosystem function must guide regional responses. Trisos et al.¹ offer alarming predictions of “sudden and devastating effects on local biodiversity and ecosystem services” from the nearly simultaneous exposure of local assemblages to “climate conditions beyond their realized niche limits”. Here I suggest that both the synchrony of exposure of co-occurring species to intolerable climate regimes and the consequent synchrony and spatial extent of sudden, devastating effects—as envisioned in their study—may be exaggerated. Although threats to biodiversity and human well-being from climate change are urgent and real², predicting their timing and extent requires a finer spatial resolution that scales with ecosystem types, geographic ranges, and regional processes and topography.

The inferential problems with this study (and others that make similar assumptions) arise from the coarse spatial resolution of climate and biogeography modelled—uniformly 100 km × 100 km on land and sea³. This grid is used to map modelled historical and future climatic regimes (homogeneously, within each map cell) and to map the current geographical range of each of the more than 30,000 terrestrial and marine species in the study. The tolerance limits of each species’ realized thermal niche are then defined as the extremes of mean annual temperature (sea surface temperature for marine map cells) that were reached anywhere within the set of 100 × 100 km map cells that define that species’ current distribution, over 155 years (1850–2005) of modelled historical climate records.

When the projected future temperature in a given map cell first exceeds the estimated tolerance limits of a particular species mapped into that cell for five continuous years, that species is declared ‘exposed’ to unprecedented climatic conditions and is added to the cumulative ‘horizon profile’⁴ for the cell. A map-cell assemblage is designated ‘at risk of abrupt ecological disruption’ when at least 20% of the species currently mapping in that cell “are projected to undergo exposure to unprecedented temperatures within the same decade.” The authors state that they do not assume that local extinction (projected absence of a species from a 100 × 100 km map cell) is the inevitable consequence of local exposure, but instead, that “evidence for the ability of species to persist in the wild is largely absent” once its current niche limits are exceeded by future climate in a map cell. The practical difference between these consequences seems elusive.

Just how coarse is this spatial scale, in biological and climatic terms? Consider the biodiverse country of Costa Rica—there is a distance of just over 100 km between the Caribbean and Pacific coasts, traversing complex climatic gradients and distinct ecosystems with elevations of

up to 3,000 m, each with its characteristically distinct biota (Fig. 1a), including many endemic species with narrow, disjunct elevational ranges (Fig. 1b). As a marine equivalent, consider a 100 × 100 km map cell at the southern end of the Great Barrier Reef (Fig. 2), a cell that encompasses near-shore shallows, coral reef flat, reef face and continental shelf marine habitats, with depths down to 3,000 m.

Treating all the species in a 100 km × 100 km area such as those shown in Figs. 1, 2 (even only the top 200 m for marine cells, as the authors¹ do) as a co-occurring assemblage makes neither ecological nor biogeographical sense. Thus, predictions of ‘ecological disruption’, with the functional implications of this term (“sudden and devastating effects on local biodiversity and ecosystem services”¹), may be painted with far too broad a brush for topographically complex, terrestrial or marine regions—even for the vast open ocean, with its strong vertical temperature stratification³.

Nevertheless, mountains^{4,5} and complex marine habitats⁶ host a disproportionate number of species and offer rescue corridors for range-shifting species⁷. The coarse-scale approach used by Trisos et al.¹ creates more false than real presences for narrow-ranged species along steep temperature gradients, misleadingly uniting species with largely or even entirely disjunct ranges (Fig. 1b) into ‘assemblages’—a term that normally implies co-occurrence in space and time⁸.

The modelled¹ climate warms in lockstep for all species with distributions mapping in a single map cell. In the real world, many such cells encompass strong temperature and habitat gradients within a single cell (Figs. 1, 2). Regional temperatures (on the scale of tens of km) may be simultaneously both warmer and cooler than the single upper and lower limits assigned to the cell by the model. The temperature difference⁷ between sea level and 3,000 m of elevation within the single cell in Fig. 1, on any day of the year, is about 15 °C, more than three times the 4 °C scope of modelled future warming. The temperature gradient between sea surface and just 200 m depth³ (the depth limit for species considered by the authors¹) on the Great Barrier Reef (Fig. 2) is about 10 °C.

This unrealistic map scale obscures the potential for several, distinct, asynchronous and spatially heterogeneous mechanisms that allow species to persist over time, even within a single map cell, in the face of climatic changes. Cooler than average regions on a scale of tens of kilometres amount to thermal refugia, which blur the timing of exposure to inimical temperatures within the map cell, inevitably reducing the abruptness and synchrony of exposure to an unknown degree—perhaps quite substantially. The authors mention a possible role for microclimatic refugia in averting local extinction, but this term generally applies on a much smaller spatial scale^{6,9}.

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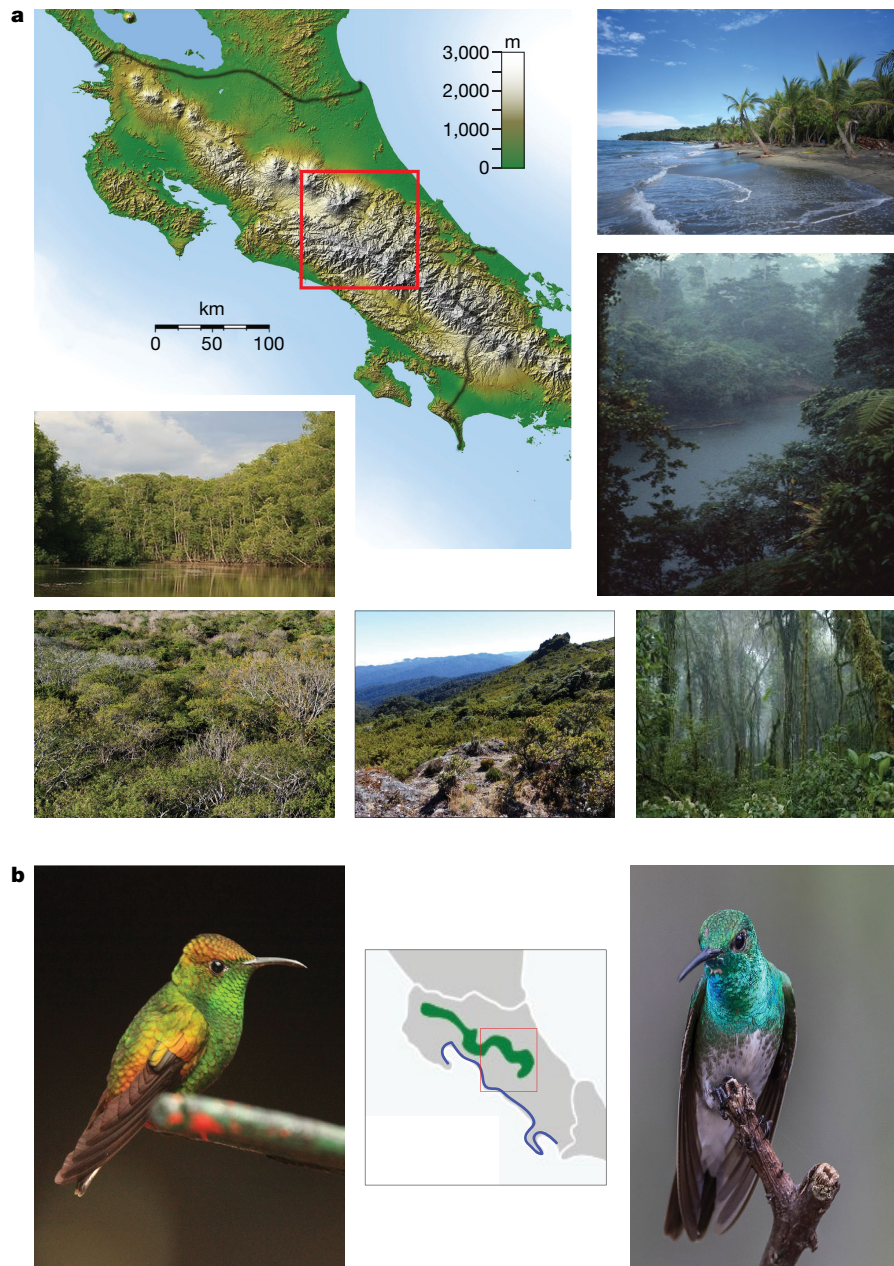


Fig. 1 | Spatial scale of terrestrial ecosystems and biogeography. a. A 100 km × 100 km map cell (red square) superimposed on the country of Costa Rica. Within this single cell, lie (clockwise from top right) Caribbean coastal forest, Atlantic lowland rainforest, mid-elevation cloud forest, high elevation paramo, Pacific coastal dry forest, and mangrove forest, each with its own, largely distinct biota. The entire country could be encompassed by just five such map cells. **b.** Two hummingbird species endemic to Costa Rica with disjunct, elevationally defined ranges. Left, male *Elvira cupreiceps* (coppery-headed emerald; range (green) superimposed on the map of Costa Rica). Right, male *Amazilia boucardi* (mangrove hummingbird; range (blue)

superimposed on the map). The red square on the map outlines a single, 100 km × 100 km map cell (Fig. 1a). Fig. 1a: Costa Rica digital map courtesy NASA/JPL-Caltech; photos clockwise from top right: Wilma Compton (CC BY 2.0, creativecommons.org/licenses/by/2.0/); Robert K. Colwell; Thejaan (CC BY 2.0, creativecommons.org/licenses/by/2.0/); courtesy Jack Donnelly; Florent Mechain/TravelMag.com (CC BY 2.0, creativecommons.org/licenses/by/2.0/); Mark Whatmough (CC BY 2.0, creativecommons.org/licenses/by/2.0/). Fig. 1b: range maps courtesy Simon Pierre Barrette; photos left and right: Tim Lenz (CC BY 2.0, creativecommons.org/licenses/by/2.0/); courtesy Jorge Obando.

Pervasive and ongoing range shifts along elevational, depth and latitudinal gradients driven by warming climate have been widely documented^{2,10}. Yet the model¹ holds distributions static, while isotherms inexorably are shifting both within real-world 100 × 100 km cells and into adjacent cells along these gradients as warming proceeds. In the model, by the time a species is declared exposed to unprecedented temperatures that exceed its niche limits in a particular map cell, the species' range may have shifted out of the cell. Regardless, such range-shifting species are added to the cell's horizon profile, once their

niche limits have been exceeded, further inflating the synchrony and extent of biotic change.

In their Methods section, the authors¹ acknowledge and demonstrate the directional effect of spatial scale on abruptness, noting that "individual grid cells at this resolution may contain...substantial...spatial climatic heterogeneity, thus...overestimating the abruptness of assemblage exposure dynamics." They conclude that "increasing the spatial resolution...would enable a more precise quantification of the timing of species exposure to changing climates..." It is not simply a matter

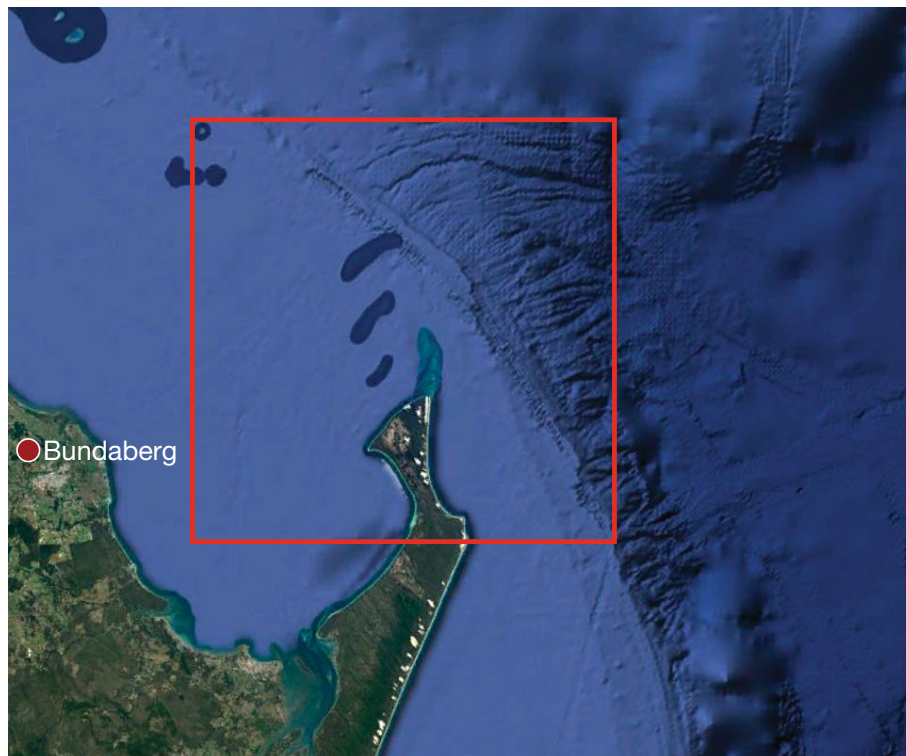


Fig. 2 | Spatial scale of marine habitats and biotas. A 100 km × 100 km map cell (red square) superimposed on the coast of Queensland, Australia at the southern end of the Great Barrier Reef. Within this single cell there are areas of near-shore shallows, coral reef flat, reef face and continental shelf marine habitats (all within the 200 m depth limit considered by the model¹, with a 10 °C temperature gradient), as well as depths down to 3,000 m in the Fraser Canyons (lower right side of the square)—each habitat with its own distinct biota. Even

topographically homogeneous regions of the open oceans have strong vertical temperature gradients inhabited by different communities at different depths³. Temperatures at the sea surface poorly reflect those at depths of hundreds or thousands of metres, and warming in the deep ocean is much less than at the surface¹⁵. Google Earth, Copyright 2021, Image Landsat/Copernicus, Data SIO, NOAA, US Navy, NGA, GEBCO.

of precision, however, but directional bias (accuracy)—synchrony of exposure is inflated to an unmeasured degree.

Finally, as Trisos et al. acknowledge¹, their model is blind to evolutionary rescue¹¹, a process that would also decrease the abruptness and synchrony of exposure to inimical temperatures. In fact, selection for evolutionary adaptation to warming climates is expected to be strongest in the trailing edge of species ranges^{12–14}, as they follow thermoclines across topographic or depth gradients. But these gradients are flattened or completely eliminated by coarse spatial scaling (Figs. 1, 2). It is precisely trailing-edge species that accumulate in the authors' horizon profiles¹.

Disjunct ranges, regional refugia, range shifts and evolutionary rescue—all mechanisms of survival hidden by coarse spatial scaling—add up to an unmeasured, but directional bias, exaggerating the abruptness and synchrony of exposure of species to inimical climates, especially in the most topographically complex map cells. This coarse spatial resolution drives a coarse temporal resolution, leading to overestimation of the spatial extent and coordination of the 'abrupt ecological disruptions' flagged in the title of the Article¹.

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Author contributions R.K.C. developed the ideas, wrote the manuscript, and prepared the figures.

Competing interests The author declares no competing interests.

Additional information

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Reply to: Spatial scale and the synchrony of ecological disruption

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REPLYING TO R. K. Colwell. *Nature* <https://doi.org/10.1038/s41586-021-03760-4> (2021)

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In the accompanying Comment¹, Colwell states that mechanisms such as evolution, range shifts, and localized climate refugia may enhance species persistence under climate warming, and that these mechanisms will be more likely to operate within larger spatial grains and mountainous regions. We agree that these mechanisms have important roles, and discussed each of them in our Article². However, Colwell does not provide any quantitative evidence to support the claim that our analysis overestimates the risk of abrupt climate exposure and presents a highly selective set of factors that are unlikely to have directionally biased our results. Here we explain why our conclusions are robust to the oversimplified subset of mechanisms discussed by Colwell and highlight why we believe that the species exposure models (SEMs) that we introduced are an important step forward in ecological forecasting.

Colwell asserts that risks of abrupt climate exposure are overestimated in our analysis because some 100-km grid cells contain substantial spatial climatic heterogeneity, particularly in mountainous regions. However, while mountains do undoubtedly provide more opportunities for local climate refugia, as we demonstrated² (see Extended Data Fig. 10), it is the relatively flat regions with little spatial climatic heterogeneity, such as the Amazon Basin, that are projected to experience the most abrupt exposure. Of the cells on land that are projected to be at risk of abrupt ecological disruption by 2100 under the very high Representative Concentration Pathway for greenhouse gases (RCP8.5), only 17% span more than 1,000 m of elevation (Fig. 1). Thus, our conclusion of abrupt exposure is not driven by the topographically diverse regions that Colwell suggests will be safe havens for biodiversity, but is instead a general pattern across assemblages and is especially strong in those areas where finer-scale climate heterogeneity is relatively small.

Colwell suggests that our analysis overestimates the risk of ecological disruption because species may be able to persist within 100-km grid cells by shifting their distribution to local refugia within the grid cell, either up mountain slopes or, in the oceans, to greater depths. The possibility that species may persist despite exposure to climate conditions beyond their historical limits is a point with which we agree and discussed². However, Colwell's interpretation that because species may persist, risks of ecological disruption are overestimated, misses the crucial point. Even if species are able to persist by retreating up mountains or to greater depths, the population contractions associated with these responses would still result in potentially major disruption to the ecological systems these species leave behind³. For instance, few coral species on the Great Barrier Reef may yet have been driven to extinction at the scale of 100-km grid cells, but this is clearly an unsuitable benchmark for assessing the massive ecological devastation caused by back-to-back mass bleaching and mortality of corals already impacting this and other regions as a result of thermal exposure⁴. Thus, just

as exposure should not be conflated with extinction, the chance that a species may persist somewhere should not be conflated with a low risk of ecological disruption.

Colwell suggests that we should not define assemblages as the set of species that occur in a 100-km grid cell, because these species may not interact at finer resolutions. This critique could be levelled at any spatial grain, and there is no single ideal grain size for describing a spatially diffuse assemblage of species⁵. While choosing a finer grain could better characterize local climate, it would lead to many false presences for each species, which could also lead to biased niche estimates⁶. More fundamentally, the decline or loss of a species will cause ecological disruption wherever it occurs in geographic space and our projections do not assume that species interact. Had we considered such interactions while studying exposure at finer grains, we would have been likely to project a greater risk of ecological disruption due to collapsing interdependencies among species. As with perhaps every pattern in biogeography, a critical study of scale dependence is warranted. A major challenge for future work is being able to model global or regional patterns of species exposure to future climates at both fine spatial (for example, 1 km) and temporal (for example, monthly) scales, as opposed to fine-scale modelling on only one of these dimensions⁷.

While Colwell discusses mechanisms that could make our risk projections pessimistic, he ignores other factors that could lead to exposure being underestimated. First, we defined exposure as the time when the mean annual or maximum mean monthly temperature consistently exceeds the realized historical limits of a species for at least five consecutive years. However, species may be at risk from much briefer periods of exposure—such as a single extreme year, month or even day⁸—leading to more immediate risks of ecological disruption than we projected^{9,10}. Second, our range-wide estimates did not account for the possibility that populations may be locally adapted¹¹ or that species niches are determined by dependencies between multiple climate variables¹², both of which would increase the risk of exposure. Third, species may be sensitive to climate-driven disruption at temperatures below their realized thermal limits because they are impacted by the temperature-driven loss of essential habitat, such as sea ice fragmentation for polar bears¹³ or mass mortality of habitat-forming corals for marine animals⁴, as well as by altered biotic interactions^{14–16}—all factors that are not considered in our models.

For these reasons, our study could be thought to underestimate climate risks for biodiversity. Indeed, while our projections show that climate risks are likely to escalate rapidly over the coming decades, increases in sea surface temperatures over the last half century have already caused widespread die-offs of fish¹⁷, seagrass¹⁸, macro-algae¹⁹ and coral species²⁰, with these events often occurring

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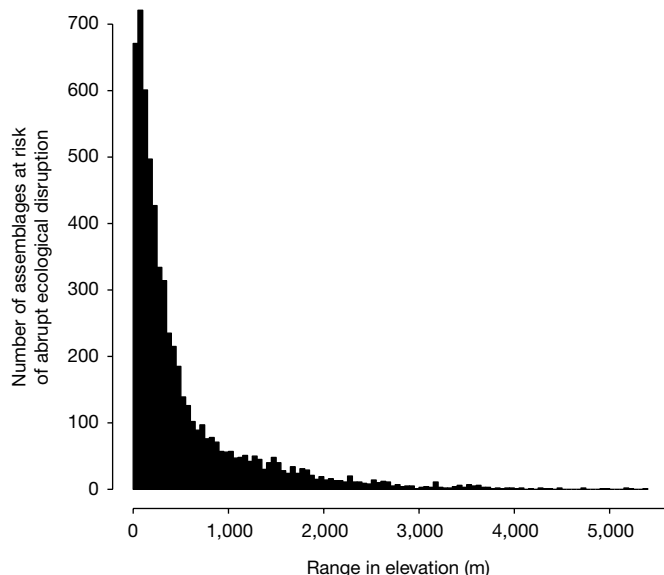


Fig. 1 | Abrupt exposure is a general pattern and not an artefact of homogenizing mountain regions. Of those assemblages (100-km grid cells, $n = 6,105$) on land projected to be at risk of abrupt ecological disruption this century ($\geq 20\%$ of all species in an assemblage exposed in a single decade (see Fig. 4 in ref. ²)), most encompass a relatively narrow range of elevations (calculated at 1 arcmin resolution²⁶) and thus have relatively small spatial climatic heterogeneity. Risk is calculated on the basis of 22 General Circulation and Earth System Models developed for the Coupled Model Intercomparison Project 5 (CMIP5) under RCP 8.5.

abruptly and impacting multiple species, as in the case of mass coral bleaching⁴. Similarly, on land, climate-driven population declines and local extinctions of both ectothermic and endothermic species are already underway^{21–24}.

It is our view that a primary value of the SEM framework will be to provide a conceptual and methodological foundation for addressing how various mechanisms balance out to either amplify or temper the risk of abrupt climate exposure and ecological disruption, thereby advancing understanding of how climate risks to biodiversity will unfold over time. From a conceptual perspective, we emphasized that we projected the risk of exposure in relation to conditions beyond the known realized limits of a species and not the outcome of exposure² (which may include evolution, dispersal and local extinction). This distinction is important, as it helps to separate the sources of uncertainty inherent in biodiversity projections: (1) uncertainty in estimates of the timing of exposure due to limitations in species occurrence or climate data, and (2) uncertainty in the ecological consequences of exposure. From a methodological perspective, SEMs—which are based on climate data with fine temporal resolution at monthly or annual scales rather than the mean conditions for a remote period decades in the future—can help to resolve these uncertainties. For example, estimating the future timing of exposure of local populations to unprecedented conditions can help to clarify the potential for evolutionary rescue from changing climates. Identifying those species and regions that are at immediate risk of exposure provides both a pragmatic early-warning system for climate risks to biodiversity and the opportunity to continuously update and refine projections as climate change unfolds and ecological responses are observed.

Our global analysis of exposure dynamics across terrestrial and marine systems remains a starting point. Further work is now needed to improve and refine estimates of the timing of exposure and to understand its ecological consequences. However, our analysis suggests that—similar to ecological responses to environmental upheavals in the past²⁵—in many places, future changes in biodiversity due to

climate change are unlikely to be gradual, and mitigation and adaptation approaches should reflect this.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-021-03760-4>.

Reporting summary

Further information on experimental design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

Elevation data are publicly available from <https://www.ngdc.noaa.gov/mgg/global/>. Code and data to reproduce Fig. 1 are available at Figshare (<https://doi.org/10.6084/m9.figshare.14730501>).

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Data collection No software was used in the data collection process

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Future climate projections from earth system models are combined with information on species geographic distributions to estimate species realised thermal niche limits and project the timing of future exposure to conditions beyond their niche. The risk of abrupt exposure to climate warming across equal area grid cells (100km) is compared to the elevation range (m) in each cell.
Research sample	We used expert verified range maps for 26,572 species from the International Union for Conservation of Nature (https://www.iucnredlist.org/resources/spatial-data-download) and BirdLife International (http://datazone.birdlife.org/species/requestdis), including; birds, mammals, reptiles, amphibians. This sample reflects availability of geographic range data for each organism group globally. From this data we identified those 100km grid cells at risk of abrupt ecological disruption by 2100 (n = 6105)
Sampling strategy	All grid cells estimated to be at risk of abrupt ecological disruption by 2100 are included.
Data collection	All data used here is already published and was downloaded from public data portals
Timing and spatial scale	The data on species distributions we use represents more than a century of collecting efforts and observations by scientists, naturalists and the public. The climate data we use is generated by simulations from computer models of the earth system. Both kinds of data are accurate to ~100km resolution and are available globally.
Data exclusions	Grid cells which our models indicate are not at risk of abrupt ecological disruption by 2100 were excluded.
Reproducibility	This is not an experimental study so experimental replication was not attempted. All data used in our analysis is publicly available. The results can be reproduced using the code and data available at Figshare (https://doi.org/10.6084/m9.figshare.14730501).
Randomization	No randomization was required. Our study was not experimental, but based on observed biodiversity and climate patterns.
Blinding	Our study was not experimental and so blinding is not relevant
Did the study involve field work?	<input type="checkbox"/> Yes <input checked="" type="checkbox"/> No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology and archaeology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data
<input checked="" type="checkbox"/>	<input type="checkbox"/> Dual use research of concern

Methods

n/a	Involved in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging