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Understanding how climate risks to biodiversity will change over the coming decades is a major challenge and we therefore welcome Colwell's critique. We agree that the mechanisms discussed by Colwell—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, which is why we discussed each in our paper. However, Colwell does not provide any quantitative evidence to support his 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 the species exposure models (SEM) we introduced are an important step forward in ecological forecasting.

Abrupt exposure is a general pattern and not an artefact of homogenizing mountain regions.

Colwell asserts that risks of abrupt climate exposure are overestimated in our analysis because some 100km 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 already demonstrated in our paper (see Extended Figure 10[1]), 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 under RCP8.5 are projected to be at risk of abrupt ecological disruption by 2100, only 17% of these span ≥1000m elevation (Figure 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.

Species persistence at large spatial grains does not imply lack of ecological disruption.

Colwell suggests that the risk of ecological disruption is overestimated in our analysis because species may be able to persist within 100km 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 entirely agree and discussed in our paper. 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 portend potentially major disruption to the ecological systems these species leave behind[3]. For instance, few coral species on the Great Barrier Reef may yet have been driven extinct at the scale of 100km 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 exposure[4]. 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.

Abrupt exposure implies an elevated risk of ecological disruption regardless of spatial grain.

Colwell suggests that we should not define assemblages as the set of species that occur in a 100km 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 species[5]. 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 estimates[6]. 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 likely 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 (e.g., 1km) and temporal scales (e.g., monthly), as opposed to fine-scale modelling on only one of these dimensions[7].

Uncertainty in estimates of exposure and ecological disruption cut both ways.

While Colwell discusses mechanisms that 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 realised historical limits of a species for a run of 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 day[8]—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 adapted[11] or that species niches are determined by dependencies between multiple climate variables[12], both of which would increase the risk of exposure. Third, species may be sensitive to climate-driven disruption at temperatures below their realised thermal limits because they are impacted by the temperature-driven loss of essential habitat, such as sea ice fragmentation for polar bears[13] or mass mortality of habitat forming corals for marine animals[4], as well as by altered biotic interactions[14][15][16]—all factors not considered in our models.

For these reasons some may disagree with Colwell and think that our study has underestimated climate risks to biodiversity. Indeed, while our projections show that climate risks are likely to rapidly escalate over the coming decades, increases in sea surface temperatures over the last half century have already caused wide-spread dieoffs of fish[17], seagrass[18], macro-algae[19] and coral species[20], with these events often occurring abruptly and impacting multiple species, as in the case of mass coral bleaching[4]. Similarly, on land, climate driven population declines and local extinctions of both ectothermic and endothermic species are already underway[21–24].

A research agenda for understanding dynamic climate risks to biodiversity.

We think 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 in our paper that we project the risk of exposure to conditions beyond the known realised limits of a species, not the outcome of exposure (which may include evolution, dispersal, and local extinction). This distinction is important as it helps separate the sources of uncertainty inherent in biodiversity projections: (i) uncertainty in estimates of the timing of exposure due to limitations in species occurrence or climate data and (ii) uncertainty in the ecological consequences of exposure. From a methodological perspective, SEMs—which are based on fine temporal resolution climate data at monthly or annual scales rather than the mean conditions for a remote period of decades in the future—can help resolve these uncertainties. For example, estimating the future timing of exposure of local populations to unprecedented conditions can help understand the potential for evolutionary rescue from changing climates. Identifying those species and regions 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. Much work is now needed to improve and refine estimates of the timing of exposure and to understand its ecological consequences. But, as was the case with ecological responses to environmental upheavals in the past[25], our analysis suggests that in many places future changes in biodiversity due to anthropogenic climate warming are unlikely to be gradual and we should be prepared for that.

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Figure 1 Abrupt exposure is a general pattern and not an artefact of homogenizing mountain regions. Of those assemblages (100km grid cells, *n* = 6105) on land projected to be at risk of abrupt ecological disruption this century (≥20% of all species in an assemblages exposed in a single decade (see Figure 4[1])) most encompass a relatively narrow range of elevations (metres (m), calculated at 1 arc-minute resolution[2]) and thus have relatively small spatial climatic heterogeneity. Risk is calculated based on 22 General Circulation and Earth System Models developed for the Coupled Model Intercomparison Project 5 (CMIP5) under RCP 8.5, a high emissions scenario.

Contributions

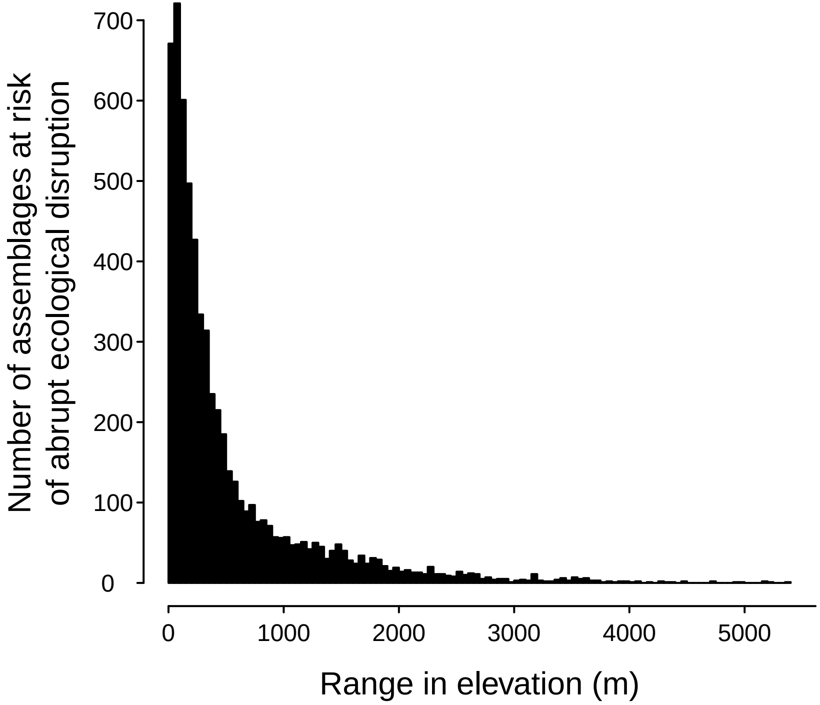
A.L.P., C.H.T. and C.M. contributed to writing the manuscript.

Data availability

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

Competing interests

The authors declare no competing interests.


Number of assemblages at risk of abrupt ecological disruption
700
600
500
400
300
200
100
0
0
1000
2000
3000
4000
5000
Range in elevation (m)