Revised version, submitted to Nature 24 September 2020

Preprint only, not peer-reviewed

Matters Arising

Why spatial scale matters in predicting synchrony of ecological disruption

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Arising from: C. Trisos et al. *Nature* **580**, 496–501, https://doi.org/10.1038/s41586-020-2189-9 (2020).

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In this provocative study[1], Trisos, Merow, and Pigot 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." The headline claim is the abruptness and synchrony of effects on these species assemblages. Without any doubt, the fate of species and habitats under ongoing climate change is genuine and urgent[2], with serious consequences for ecosystems and human well-being [3], and nothing I say here should be interpreted to the contrary. But 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 this study—may be overestimated.

Spatial scale of climate and biogeography

The most salient problems with this study arise from the coarse spatial resolution of the analysis—uniformly 100 km x 100 km, on land and sea. This grid is used to map modeled 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), over 155 years (1850–2005) of modelled historical climate records, reached anywhere within the set of 100 x 100 km map cells that define that species' current distribution. (The authors also considered precipitation, for terrestrial map cells, but focused on temperature, as I will do here.)

When the projected future temperature in a given map cell first exceeds the estimated upper (or lower) tolerance limits of a species mapped into that cell, that species is declared "exposed" to unprecedented climatic conditions and is added to the cumulative "horizon profile" for the assemblage. 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 (absence from a 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 niche limits are exceeded in a map cell. The practical difference seems elusive.

Just how coarse is this spatial scale, in biological and climatic terms? Consider the biodiverse country of Costa Rica. It is little more than 100 km from the Caribbean coast to the Pacific, as the toucan flies, traversing complex climatic gradients and distinct ecosystems up to 3000 m elevation, each with its characteristically distinct biota (Fig. 1), including many endemic species with narrow, disjunct elevational ranges (Fig. 2). A single 100 km x 100 km map cell encompasses ecosystems ranging from mangroves and coastal forest, to lowland rainforest, seasonal dry forest, cloud forest, and treeless alpine paramo (Fig. 1). The entire country could be encompassed by just 5 such map cells.

For a marine equivalent, I suggest a 100 x 100 km map cell with its NW corner on Lady Elliot Island, at the southern end of the Great Barrier Reef, a cell that would encompass near-shore shallows, coral reef flat, reef face, and continental shelf marine habitats, with depths down to 3000 m in the Fraser Canyons (Fig. 3). But even topographically relatively homogeneous regions of the open oceans have strong vertical temperature gradients, inhabited by different communities at different depths[4], and open-ocean pelagic systems cover ~50% of the planet surface and occupy 99% of the volume of the biosphere [5]. Unlike terrestrial regions with little topographic complexity (e.g. Saskatchewan prairies or the Amazon), in which mean annual temperature can be reasonably treated as a spatially homogeneous condition, temperatures at the sea surface poorly reflect those 100s or 1000s of metres deep, and warming in the deep ocean is much less than at the surface[6].

Treating all the species in a 100 km x 100 km areas such as those shown in Figs. 1 and 3 as a "co-occurring assemblage" (even for a major group, such as amphibians or marine fishes) makes neither ecological nor biogeographical sense. Thus, predictions of "ecological disruption," with the functional implications of that 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—and even for the open ocean, with its strong vertical temperature stratification[7].

For the purposes of the Trisos et al. study[1], such a coarse scale may well be adequate for flat, climatically homogeneous terrestrial regions or oligotrophic ocean gyres, which tend to have homogeneous biotas because of shared range limits[8]. But the same coarse scale fails to capture the more varied fates of terrestrial species that inhabit topographically and climatically rugged regions (Figs. 1 and 2), coastal bottom-dwelling fish (Fig. 3), or pelagic species that inhabit thermal fronts or seamounts[9].

Yet mountains[10,11] and complex marine habitats [9] host a remarkable number of species, disproportionate to their area. The authors' rationale for using such a coarse scale—to avoid "incurring false presences" in smaller map cells, arising from inaccurate range maps and patchy distributions [12]—paradoxically creates more false than real presences for narrow-ranged species on steep climatic gradients on land, misleadingly joining species with largely or even entirely disjunct ranges (Fig. 2) into supposed "assemblages"—a term that normally implies co-occurrence in space and time[13]. In the sea, the same approach likewise unites all species in a map cell, regardless of depth ranges, habitat preference, and differences in temperature tolerances.

Spatial scale and synchrony of exposure

What are the dynamic consequences of modeling niches and exposure to the risk of local extinction in topographically varied regions under warming climates, on such a coarse geographic scale? As the modeled climate warms, in lock-step for all species with distributions mapping in a single cell, the temperature of each 100 x 100 km cell is assumed spatially uniform. However, in the real world many such cells are spatially heterogeneous, encompassing strong temperature and habitat gradients within the geographical limits of a single cell (Figs. 1 and 3). Regional temperatures (on the scale of tens of km) may be simultaneously both hotter and cooler than the single value assigned to the cell by the authors' model. For example, the temperature difference between sea level and 3000 m elevation, within the single 100 x 100 km cell in Fig. 1, on any day of the year, is about 15°C[14], more than three times the 4°C total scope of modeled future warming. The temperature gradient between sea surface and just 200 m depth (the depth limit for species considered by the authors) on the Great Barrier Reef (Fig. 3) is about 10°C[4].

The unrealistic uniformity assumed by the author's method obscures the potential for several, distinct, asynchronous and spatially heterogeneous mechanisms that allow species to persist over time, even within a single 100 x 100 km cell, in the face of climatic changes. Cooler than average regions within such a cell, on a scale of tens of km, amount to thermal refugia, in the context of the model, protecting species from local extirpation or total extinction. These regional refugia spread out the timing of exposure to inimical temperatures within the map cell, inevitably reducing 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 that term generally applies on a much smaller spatial scale[9,15].

Pervasive and ongoing range shifts along elevational, depth, and latitudinal gradients, driven by warming climate, have already been widely documented[3,16]. Yet the model holds distributions static, while isotherms inexorably shift both within real-world 100 x 100 km cells and also into adjacent cells along these gradients as warming proceeds. In the authors' 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 ghost niche limits have been exceeded by cell-averaged climate, inflating the synchrony of biotic change. Perhaps the authors would include such fugitive range shifts—although they may well rescue individual species from extinction—as contributing to "sudden and devastating effects on local biodiversity and ecosystem services," but their model does not take account of these potential range-shift-escapes, nor are they discussed.

In the Methods section, the authors acknowledge the directional effect of spatial scale on abruptness, writing, "…individual grid cells at this resolution may contain …substantial …spatial climatic heterogeneity, thus…overestimating the abruptness of assemblage exposure dynamics." As a rough index of the internal climatic heterogeneity of each terrestrial 100 x 100 km cell (marine cells were not considered), they recorded the range of interpolated temperatures[17] at a 1º x 1º resolution and showed that this index is negatively correlated with horizon abruptness. From this exercise, they conclude that "…increasing the spatial resolution at which species niche limits and assemblages are defined would enable a more precise quantification of the timing of species exposure to changing climates…" It is not simply a matter of precision, however, but directional bias (accuracy)—synchrony of exposure is inflated to an unmeasured degree.

Regional-scale refugia and range shifts are not the only escapes from inimical climates that would be expected to reduce the apparent abruptness of climate horizons, though they are probably the most affected by coarse spatial scale. Another issue is the vexing question of unexpressed tolerance, as highlighted by Sunday[18] in her commentary on this study. Do some species fondly remember the Miocene, when global temperatures were 6°C hotter than today?[19] In other words, do their fundamental thermal niches maintain unexpressed adaptations to past, warmer climates[20]? Are their realized niches truncated by topographic boundaries[21]? If so, the effects of future warming may be overestimated by the approach taken by the authors, and shared current geographical boundaries may falsely synchronize future projections. We know, for many terrestrial ectotherms, that thermal tolerance limits are surprisingly high, even for species from higher latitudes. For marine species, the thermal safety margin is smaller [22], particularly in tropical seas [7,23] The corresponding data for long-lived endotherms are much scarcer. The authors mention this issue as a complication, but their quantitative predictions do not take account of it. Nonetheless, it is not a neutral source of uncertainly, but represents a directional bias towards overestimating exposure—and synchrony of exposure—of co-occurring species to future, adverse climates.

Finally, as the authors acknowledge, their model is blind to evolutionary rescue [24], yet another mechanism that would be expected to 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[25-27], as they follow thermoclines across topographic or depth gradients. But these gradients are flattened or completely eliminated (Fig. 1) by coarse spatial scaling. It is precisely trailing-edge species that accumulate in the authors' horizon profiles.

Taken together, 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. Put another way, the coarse spatial resolution drives a coarse temporal resolution of exposure—overestimating the spatial extent and coordination of the "abrupt ecological disruptions" of the title of Trisos et al.[1].

The coarse spatial resolution (for distributions, climate, and assemblages) could have been avoided, on land and for bottom-dwelling species in the oceans, by using a hybrid spatial scale—smaller cells for diverse topography, larger ones for flatter topography, as done by Rangel et al. [27]. The bookkeeping is more complicated, but entirely feasible. For pelagic systems in the open ocean, a different approach would need to be devised, to account for depth-related heterogeneity within map cells. In conclusion, I do not question the ongoing impact of anthropogenic climate change on ecosystems presented, but I have reservations about the degree of abruptness and synchrony of the projected changes that Trisos and colleagues[1] predict.

Acknowledgements

I am grateful to Anthony J. Richardson and an anonymous peer reviewer for suggestions, and to Editor Anna Armstrong for her patience.

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

Competing interests The author declares no competing interests.

Figures

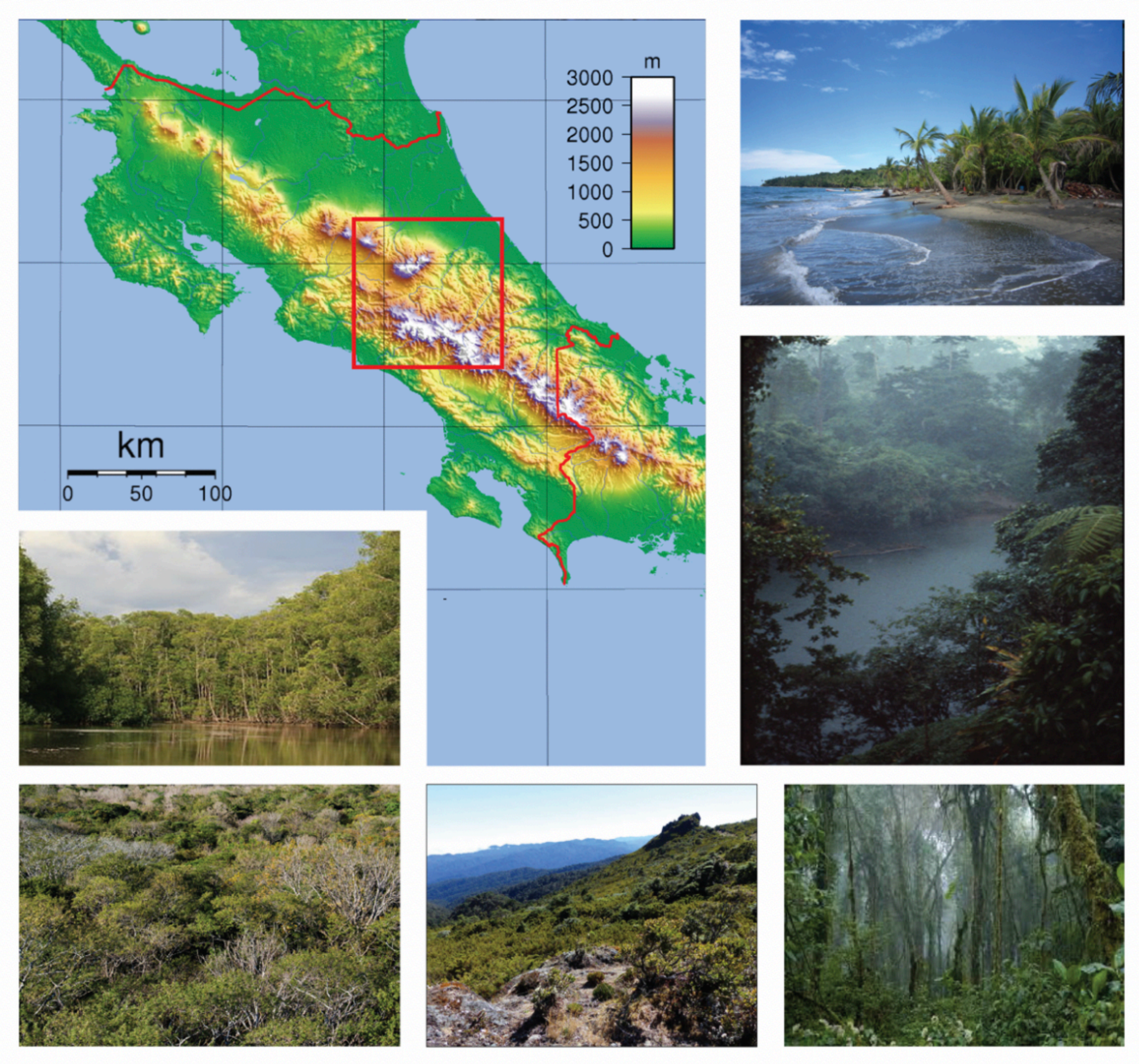

Fig. 1. A 100 km x 100 km map cell (red square) superimposed on the country of Costa Rica. Within this single cell, lie (clockwise from top right) Caribbean coastal forest, Atlantic lowland rainforest, mid-elevation cloud forest, high elevation paramo, Pacific coastal dry forest, and mangrove forest, each with its own, largely distinct biota. [*Map and photo credits will be added if the MS is accepted. All elements are either my own photographs or images and maps labeled*

Creative Commons *or designated for* Non-commercial Use with Modification *in Google Images*.]

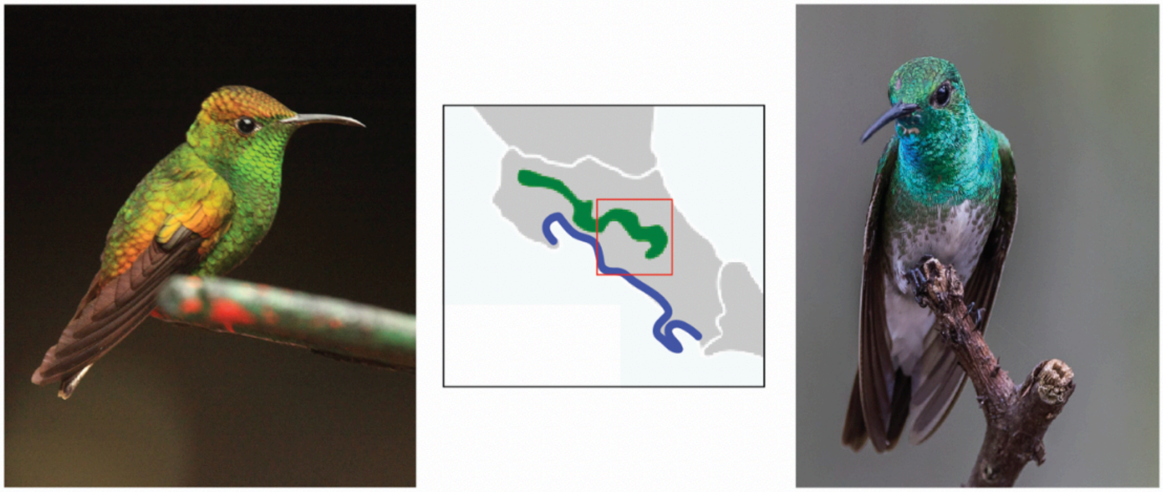

Fig. 2. Two hummingbird species endemic to Costa Rica with non-overlapping (disjunct), elevationally-narrow ranges. *Left*: Male *Elvira cupreiceps* (coppery-headed emerald), green on the map of Costa Rica. *Right*: Male *Amazilia boucardi* (mangrove hummingbird), blue on the map. The red square on the map outlines a single, 100 km x 100 km map cell (Fig. 1). [*Map and photo credits will be added if the MS is accepted. All elements labeled Creative Commons.*]

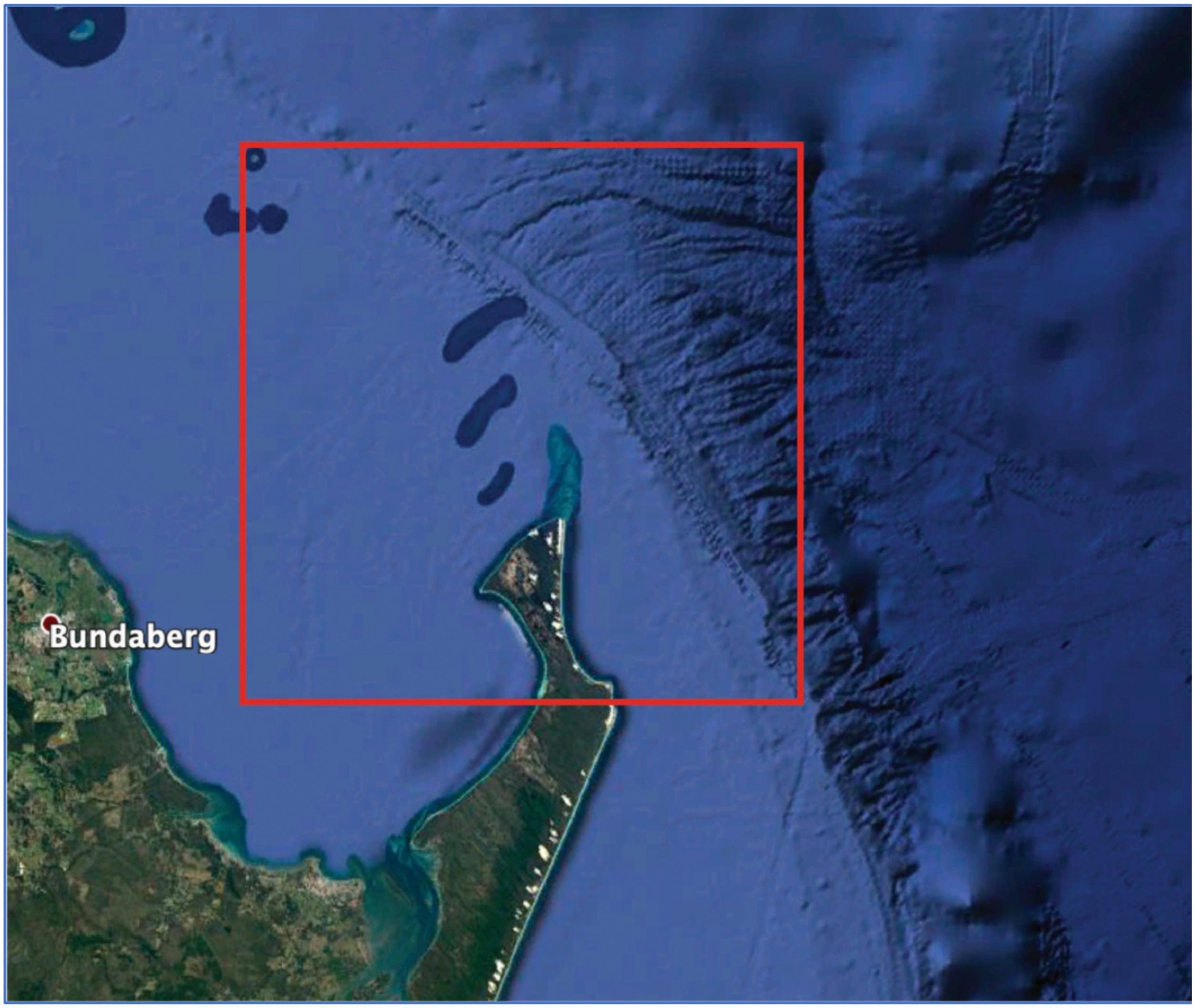

Fig. 3. A 100 km x 100 km map cell (red square) superimposed on the Queensland, Australia, coast at the southern end of the Great Barrier Reef. Within this single cell lie areas of near-shore shallows, coral reef flat, reef face, and continental shelf marine habitats, with depths down to 3000m in the Fraser Canyons, each habitat with its own distinct biota. [*Map from Google Earth.*]

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