

1 **Matters Arising**

2 **Why spatial scale matters in predicting synchrony of ecological disruption**

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10 In this provocative study¹, Trisos, Merow, and Pigot offer alarming predictions of “sudden and
11 devastating effects on local biodiversity and ecosystem services” from the nearly simultaneous
12 exposure of “local assemblages” to “climate conditions beyond their realized niche limits.” The
13 headline claim is the abruptness and synchrony of effects on these species assemblages. Without
14 any doubt, the fate of species and habitats under ongoing climate change is genuine and urgent²,
15 with serious consequences for ecosystems and human well-being³, and nothing I say here should
16 be interpreted to the contrary. But I suggest that both the synchrony of exposure of co-occurring
17 species to intolerable climate regimes and the consequent synchrony and spatial extent of
18 sudden, devastating effects—as envisioned in this study—may be overestimated.

19 **Spatial scale of climate and biogeography**

20 The most salient problems with this study arise from the coarse spatial resolution of the
21 analysis—uniformly 100 km x 100 km, on land and sea. This grid is used to map modeled
22 historical and future climatic regimes (homogeneously, within each map cell) and to map the
23 current geographical range of each of the more than 30,000 terrestrial and marine species in the

24 study. The tolerance limits of each species' realized thermal niche are then defined as the
25 extremes of mean annual temperature (sea surface temperature, for marine map cells), over 155
26 years (1850–2005) of modelled historical climate records, reached anywhere within the set of
27 100 x 100 km map cells that define that species' current distribution. (The authors also
28 considered precipitation, for terrestrial map cells, but focused on temperature, as I will do here.)

29 When the projected future temperature in a given map cell first exceeds the estimated
30 upper (or lower) tolerance limits of a species mapped into that cell, that species is declared
31 “exposed” to unprecedented climatic conditions and is added to the cumulative “horizon profile”
32 for the assemblage. A map-cell assemblage is designated “at risk of abrupt ecological disruption”
33 when at least 20% of the species currently mapping in that cell “are projected to undergo
34 exposure to unprecedented temperatures within the same decade.” The authors state that they do
35 not assume that local extinction (absence from a map cell) is the inevitable consequence of local
36 exposure, but instead, that “evidence for the ability of species to persist in the wild is largely
37 absent” once niche limits are exceeded in a map cell. The practical difference seems elusive.

38 Just how coarse is this spatial scale, in biological and climatic terms? Consider the
39 biodiverse country of Costa Rica. It is little more than 100 km from the Caribbean coast to the
40 Pacific, as the toucan flies, traversing complex climatic gradients and distinct ecosystems up to
41 3000 m elevation, each with its characteristically distinct biota (Fig. 1), including many endemic
42 species with narrow, disjunct elevational ranges (Fig. 2). A single 100 km x 100 km map cell
43 encompasses ecosystems ranging from mangroves and coastal forest, to lowland rainforest,
44 seasonal dry forest, cloud forest, and treeless alpine paramo (Fig. 1). The entire country could be
45 encompassed by just 5 such map cells.

46 For a marine equivalent, I suggest a 100 x 100 km map cell with its NW corner on Lady
47 Elliot Island, at the southern end of the Great Barrier Reef, a cell that would encompass near-
48 shore shallows, coral reef flat, reef face, and continental shelf marine habitats, with depths down
49 to 3000 m in the Fraser Canyons (Fig. 3). But even topographically relatively homogeneous
50 regions of the open oceans have strong vertical temperature gradients, inhabited by different
51 communities at different depths⁴, and open-ocean pelagic systems cover ~50% of the planet
52 surface and occupy 99% of the volume of the biosphere⁵. Unlike terrestrial regions with little
53 topographic complexity (e.g. Saskatchewan prairies or the Amazon), in which mean annual
54 temperature can be reasonably treated as a spatially homogeneous condition, temperatures at the
55 sea surface poorly reflect those 100s or 1000s of metres deep, and warming in the deep ocean is
56 much less than at the surface⁶.

57 Treating all the species in a 100 km x 100 km areas such as those shown in Figs. 1 and 3
58 as a “co-occurring assemblage” (even for a major group, such as amphibians or marine fishes)
59 makes neither ecological nor biogeographical sense. Thus, predictions of “ecological disruption,”
60 with the functional implications of that term (“...sudden and devastating effects on local
61 biodiversity and ecosystem services”¹), may be painted with far too broad a brush for
62 topographically complex, terrestrial or marine regions—and even for the open ocean, with its
63 strong vertical temperature stratification⁷.

64 For the purposes of the Trisos et al. study¹, such a coarse scale may well be adequate for
65 flat, climatically homogeneous terrestrial regions or oligotrophic ocean gyres, which tend to have
66 homogeneous biotas because of shared range limits⁸. But the same coarse scale fails to capture
67 the more varied fates of terrestrial species that inhabit topographically and climatically rugged

68 regions (Figs. 1 and 2), coastal bottom-dwelling fish (Fig. 3), or pelagic species that inhabit
69 thermal fronts or seamounts⁹.

70 Yet mountains^{10,11} and complex marine habitats⁹ host a remarkable number of species,
71 disproportionate to their area. The authors' rationale for using such a coarse scale—to avoid
72 "incurring false presences" in smaller map cells, arising from inaccurate range maps and patchy
73 distributions¹²—paradoxically creates more false than real presences for narrow-ranged species
74 on steep climatic gradients on land, misleadingly joining species with largely or even entirely
75 disjunct ranges (Fig. 2) into supposed "assemblages"—a term that normally implies co-
76 occurrence in space and time¹³. In the sea, the same approach likewise unites all species in a map
77 cell, regardless of depth ranges, habitat preference, and differences in temperature tolerances.

78 **Spatial scale and synchrony of exposure**

79 What are the dynamic consequences of modeling niches and exposure to the risk of local
80 extinction in topographically varied regions under warming climates, on such a coarse
81 geographic scale? As the modeled climate warms, in lock-step for all species with distributions
82 mapping in a single cell, the temperature of each 100 x 100 km cell is assumed spatially uniform.
83 However, in the real world many such cells are spatially heterogeneous, encompassing strong
84 temperature and habitat gradients within the geographical limits of a single cell (Figs. 1 and 3).
85 Regional temperatures (on the scale of tens of km) may be simultaneously both hotter and cooler
86 than the single value assigned to the cell by the authors' model. For example, the temperature
87 difference between sea level and 3000 m elevation, within the single 100 x 100 km cell in Fig. 1,
88 on any day of the year, is about 15°C¹⁴, more than three times the 4°C total scope of modeled
89 future warming. The temperature gradient between sea surface and just 200 m depth (the depth
90 limit for species considered by the authors) on the Great Barrier Reef (Fig. 3) is about 10°C⁴.

91 The unrealistic uniformity assumed by the author’s method obscures the potential for
92 several, distinct, asynchronous and spatially heterogeneous mechanisms that allow species to
93 persist over time, even within a single 100 x 100 km cell, in the face of climatic changes. Cooler
94 than average regions within such a cell, on a scale of tens of km, amount to thermal refugia, in
95 the context of the model, protecting species from local extirpation or total extinction. These
96 regional refugia spread out the timing of exposure to inimical temperatures within the map cell,
97 inevitably reducing abruptness and synchrony of exposure, to an unknown degree—perhaps
98 quite substantially. The authors mention a possible role for “microclimatic refugia” in averting
99 local extinction, but that term generally applies on a much smaller spatial scale^{9,15}.

100 Pervasive and ongoing range shifts along elevational, depth, and latitudinal gradients,
101 driven by warming climate, have already been widely documented^{3,16}. Yet the model holds
102 distributions static, while isotherms inexorably shift both within real-world 100 x 100 km cells
103 and also into adjacent cells along these gradients as warming proceeds. In the authors’ model, by
104 the time a species is declared “exposed” to unprecedented temperatures that exceed its niche
105 limits, in a particular map cell, the species’ range may have shifted out of the cell. Regardless,
106 such range-shifting species are added to the cell’s “horizon profile,” once their ghost niche limits
107 have been exceeded by cell-averaged climate, inflating the synchrony of biotic change. Perhaps
108 the authors would include such fugitive range shifts—although they may well rescue individual
109 species from extinction—as contributing to “sudden and devastating effects on local biodiversity
110 and ecosystem services,” but their model does not take account of these potential range-shift-
111 escapes, nor are they discussed.

112 In the Methods section, the authors acknowledge the directional effect of spatial scale on
113 abruptness, writing, “...individual grid cells at this resolution may contain ...substantial

114 ...spatial climatic heterogeneity, thus...overestimating the abruptness of assemblage exposure
115 dynamics.” As a rough index of the internal climatic heterogeneity of each terrestrial 100 x 100
116 km cell (marine cells were not considered), they recorded the range of interpolated
117 temperatures¹⁷ at a 1° x 1° resolution and showed that this index is negatively correlated with
118 horizon abruptness. From this exercise, they conclude that “...increasing the spatial resolution at
119 which species niche limits and assemblages are defined would enable a more precise
120 quantification of the timing of species exposure to changing climates...” It is not simply a
121 matter of precision, however, but directional bias (accuracy)—synchrony of exposure is inflated
122 to an unmeasured degree.

123 Regional-scale refugia and range shifts are not the only escapes from inimical climates
124 that would be expected to reduce the apparent abruptness of climate horizons, though they are
125 probably the most affected by coarse spatial scale. Another issue is the vexing question of
126 unexpressed tolerance, as highlighted by Sunday¹⁸ in her commentary on this study. Do some
127 species fondly remember the Miocene, when global temperatures were 6°C hotter than today?¹⁹
128 In other words, do their fundamental thermal niches maintain unexpressed adaptations to past,
129 warmer climates²⁰? Are their realized niches truncated by topographic boundaries²¹? If so, the
130 effects of future warming may be overestimated by the approach taken by the authors, and shared
131 current geographical boundaries may falsely synchronize future projections. We know, for many
132 terrestrial ectotherms, that thermal tolerance limits are surprisingly high, even for species from
133 higher latitudes. For marine species, the thermal safety margin is smaller ²², particularly in
134 tropical seas ^{7,23} The corresponding data for long-lived endotherms are much scarcer. The
135 authors mention this issue as a complication, but their quantitative predictions do not take
136 account of it. Nonetheless, it is not a neutral source of uncertainty, but represents a directional

137 bias towards overestimating exposure—and synchrony of exposure—of co-occurring species to
138 future, adverse climates.

139 Finally, as the authors acknowledge, their model is blind to evolutionary rescue²⁴, yet
140 another mechanism that would be expected to decrease the abruptness and synchrony of
141 exposure to inimical temperatures. In fact, selection for evolutionary adaptation to warming
142 climates is expected to be strongest in the trailing edge of species ranges²⁵⁻²⁷, as they follow
143 thermoclines across topographic or depth gradients. But these gradients are flattened or
144 completely eliminated (Fig. 1) by coarse spatial scaling. It is precisely trailing-edge species that
145 accumulate in the authors' horizon profiles.

146 Taken together, disjunct ranges, regional refugia, range shifts, and evolutionary rescue—
147 all mechanisms of survival hidden by coarse spatial scaling—add up to an unmeasured, but
148 directional bias, exaggerating the abruptness and synchrony of exposure of species to inimical
149 climates, especially in the most topographically complex map cells. Put another way, the coarse
150 spatial resolution drives a coarse temporal resolution of exposure—overestimating the spatial
151 extent and coordination of the “abrupt ecological disruptions” of the title of Trisos et al.¹.

152 The coarse spatial resolution (for distributions, climate, and assemblages) could have
153 been avoided, on land and for bottom-dwelling species in the oceans, by using a hybrid spatial
154 scale—smaller cells for diverse topography, larger ones for flatter topography, as done by
155 Rangel et al.²⁷. The bookkeeping is more complicated, but entirely feasible. For pelagic systems
156 in the open ocean, a different approach would need to be devised, to account for depth-related
157 heterogeneity within map cells. In conclusion, I do not question the ongoing impact of
158 anthropogenic climate change on ecosystems presented, but I have reservations about the degree
159 of abruptness and synchrony of the projected changes that Trisos and colleagues¹ predict.

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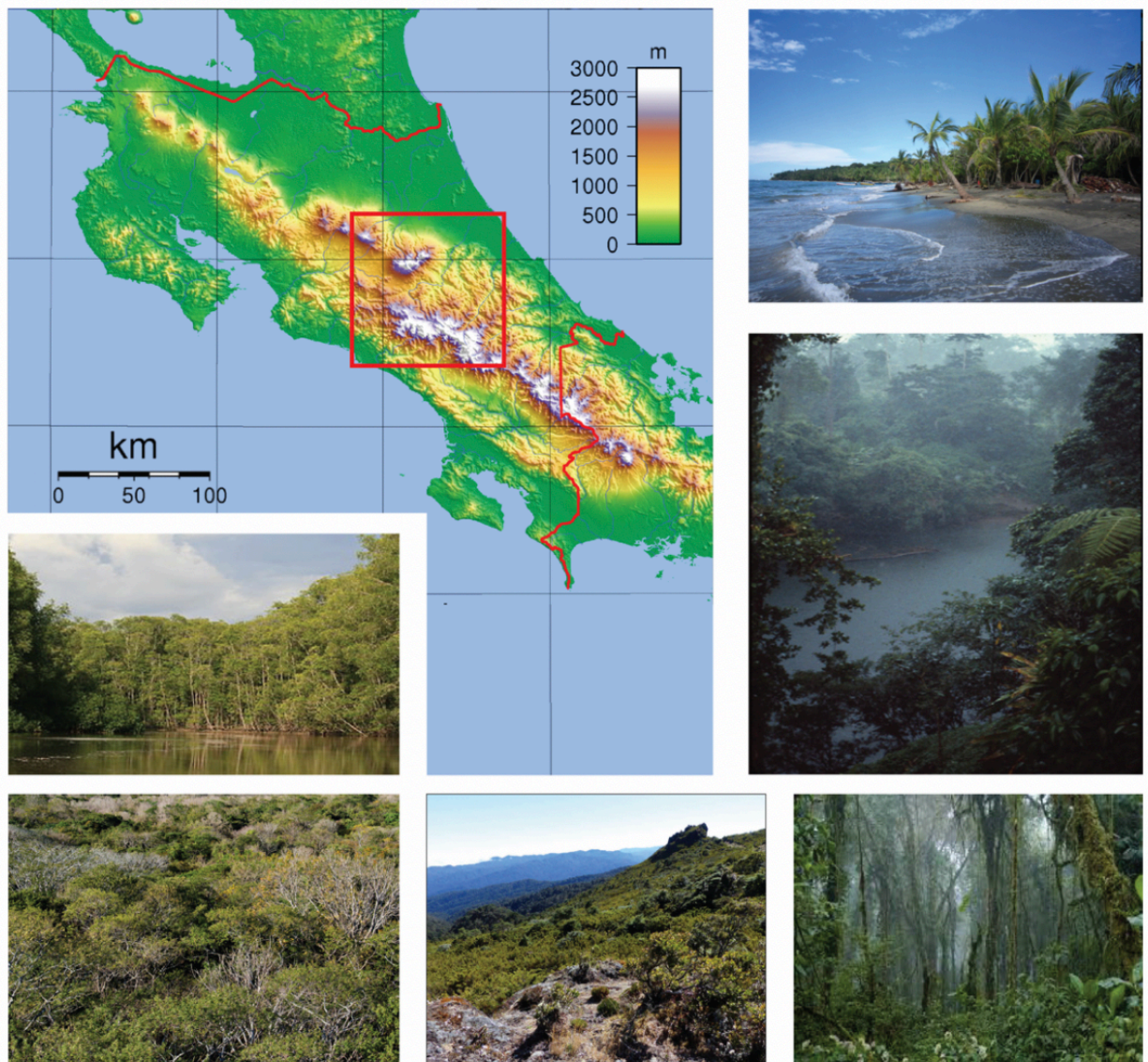
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165 **Author contributions** R.K.C. developed the ideas, wrote the manuscript, and prepared the
166 figures.

167 **Competing interests** The author declares no competing interests.

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172 **Fig. 1.** A 100 km x 100 km map cell (red square) superimposed on the country of Costa Rica.

173 Within this single cell, lie (clockwise from top right) Caribbean coastal forest, Atlantic lowland

174 rainforest, mid-elevation cloud forest, high elevation paramo, Pacific coastal dry forest, and

175 mangrove forest, each with its own, largely distinct biota. [*Map and photo credits will be added*

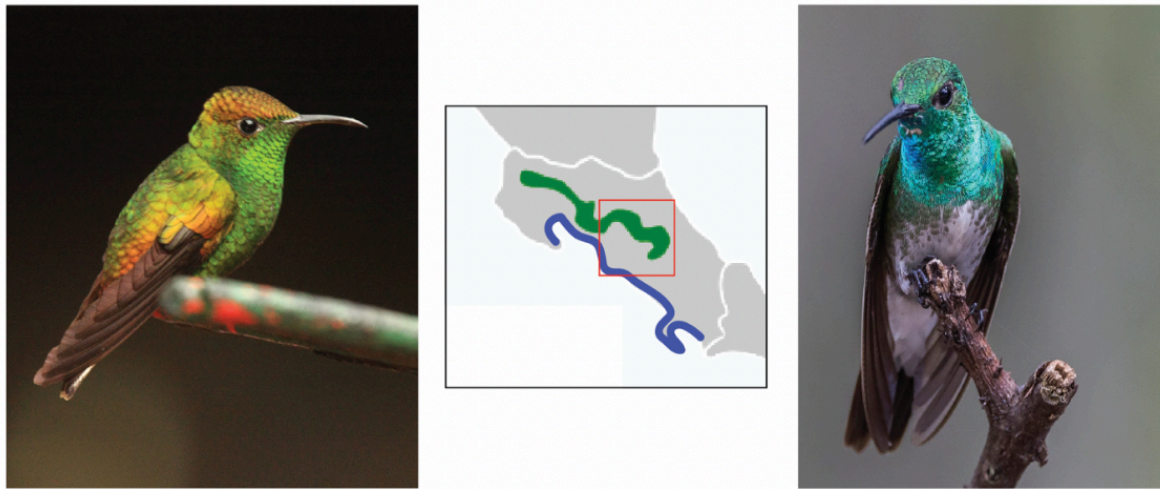
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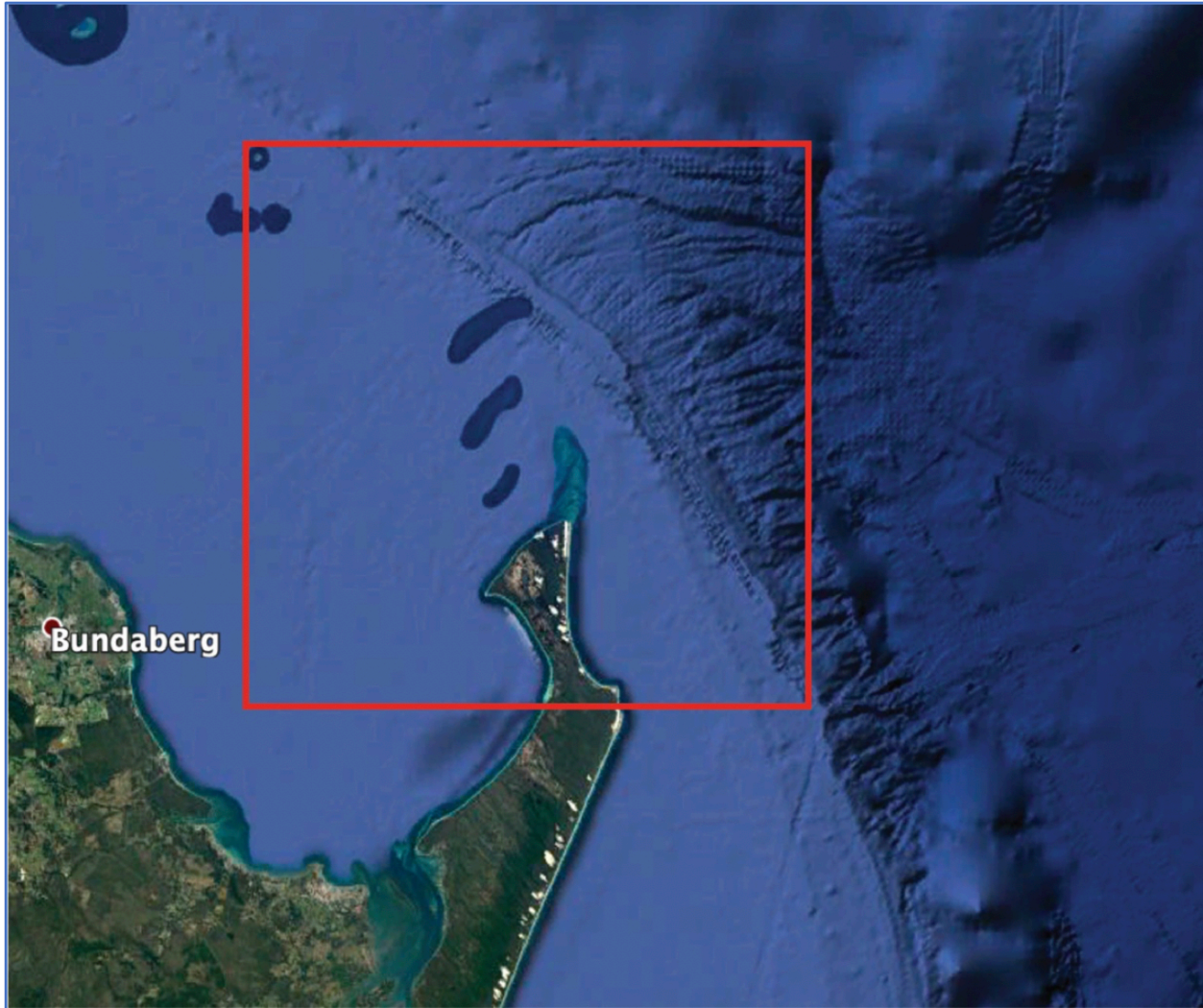
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182 **Fig. 2.** Two hummingbird species endemic to Costa Rica with non-overlapping (disjunct),
183 elevationally-narrow ranges. *Left:* Male *Elvira cupreiceps* (coppery-headed emerald), green on
184 the map of Costa Rica. *Right:* Male *Amazilia boucardi*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

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191 **Fig. 3.** A 100 km x 100 km map cell (red square) superimposed on the Queensland, Australia,
192 coast at the southern end of the Great Barrier Reef. Within this single cell lie areas of near-shore
193 shallows, coral reef flat, reef face, and continental shelf marine habitats, with depths down to
194 3000m in the Fraser Canyons, each habitat with its own distinct biota. [*Map from Google Earth.*]

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