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Matters Arising

Why spatial scale matters in predicting synchrony of ecological disruption

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ABSTRACT The fundamental assumption behind this provocative study ¹ is that current and future climatic tolerance limits for a species can be inferred from the last 170 years of climate records within its current distribution. Using this approach, the authors project the probable fate, in time, of sets of supposedly co-occurring species “assemblages,” under modeled future climates. Without any doubt, the fate of species under ongoing climate change is urgent and alarming, but I suggest that both the synchrony of exposure to intolerable climate regimes and the “ecological disruptions” arising from such exposure may be substantially overestimated in by this study.

Spatial scale and assemblages

The most serious problems arise from the coarse spatial resolution of the analysis—uniformly 100 km x 100 km. This grid is used (1) to map current species geographical ranges, (2) to map historical and future climatic regimes, and (3) to define the spatial extent and species composition of each “assemblage” as the current occupants of each map cell.

Just how coarse is this spatial scale, in biological and climatic terms? (I will focus on terrestrial species, because that is where my own expertise lies.) 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 gradients from sea level to 3400 m that span diverse and distinct climate zones, each with its characteristically distinct biota (Fig. 1), including many endemic species with narrow 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 covered by just 5 such map cells. Treating all the species in a 100 km x 100 km area as a “co-occurring assemblage” in such a region makes neither ecological nor biogeographical sense. Thus, predictions of “ecological disruption,” with the functional implications of that term (“...near-simultaneous exposure among multiple species could have sudden and devastating effects on local biodiversity and ecosystem services”¹), may be painted with far too broad a brush for such topographically complex regions.

For the purposes of this study¹, such a coarse scale may well be adequate for flat, climatically homogeneous regions (e.g. Saskatchewan prairies or the Amazon), which tend to have homogeneous biotas, but not for topographically and climatically rugged regions (the Canadian Rockies or the Andean slopes). Yet mountains host a remarkably disproportionate number of terrestrial species^{2,3}. 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 distributions⁴—paradoxically creates more false than real presences for narrow-ranged species on steep climatic gradients, and misleadingly joins species with largely or even entirely disjunct ranges into supposed “assemblages” (Fig. 2).

Spatial scale and synchrony of exposure

What are the dynamic consequences of modeling niches and exposure to the risk of extinction in topographically rugged regions under warming climates, on such a coarse geographic scale? As the modeled climate moves in lock-step for all species with distributions mapping into a single cell, the climate of each 100 x 100 km cell is assumed spatially uniform, whereas in the real world many such cells are spatially diverse, encompassing strong climatic gradients even within the geographical limits of a single cell (Fig. 1). This unrealistic uniformity obscures the potential for asynchronous and spatially heterogeneous mechanisms that allow species to persist over time. Range shifts along elevational (and thus, climatic) gradients have been widely documented^{5,6}, yet the model holds distributions static, while climatic regimes may shift into adjacent cells, upslope or poleward. As the authors acknowledge, persistence in microclimate refugia and evolutionary adaptation to novel climates are also invisible to the model. These hidden mechanisms of survival add up to an unmeasured, but directional bias, overestimating the simultaneity of exposure of species to inimical climates, especially in the most topographically complex map cells.

On balance, this coarse spatial scale yields biased results, exaggerating estimates of the synchrony of local exposure of assemblages to climate change. Put another way, a coarse spatial resolution drives a coarse temporal resolution of exposure—overestimating the extent and coordination of the “abrupt ecological disruptions” of the title.

In fact, the authors were aware of this very issue (“...individual grid cells at this resolution may contain...substantial...spatial climatic heterogeneity, thus...overestimating the abruptness of assemblage exposure dynamics”¹), and they even demonstrate the problem by changing the climate resolution (but not the species mappings) to a 1 km resolution. 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 exaggerated to an unknown but perhaps substantial degree.

The coarse spatial resolution (for distributions, climate, and assemblages) could have been avoided by using a hybrid spatial scale—smaller cells for diverse topography, larger ones for flatter topography, as done by ⁷. The bookkeeping is more complicated, but entirely feasible.

The problem of unexpressed tolerance

A related issue is the vexing question of unexpressed tolerance, as highlighted by ⁸. Do some species fondly remember the Miocene, when maximum temperatures were up to 6-11°C hotter than today⁹? In other words, do their fundamental thermal niches maintain unexpressed adaptations to past, warmer climates¹⁰? 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, although the corresponding data for long-lived endotherms are much scarcer. The authors ¹are aware of this issue, but their quantitative predictions do not (cannot) take account of it. Nonetheless, it is not a neutral source of uncertainty. It represents a directional bias towards overestimating exposure—and synchrony of exposure—to future, adverse climates.

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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.

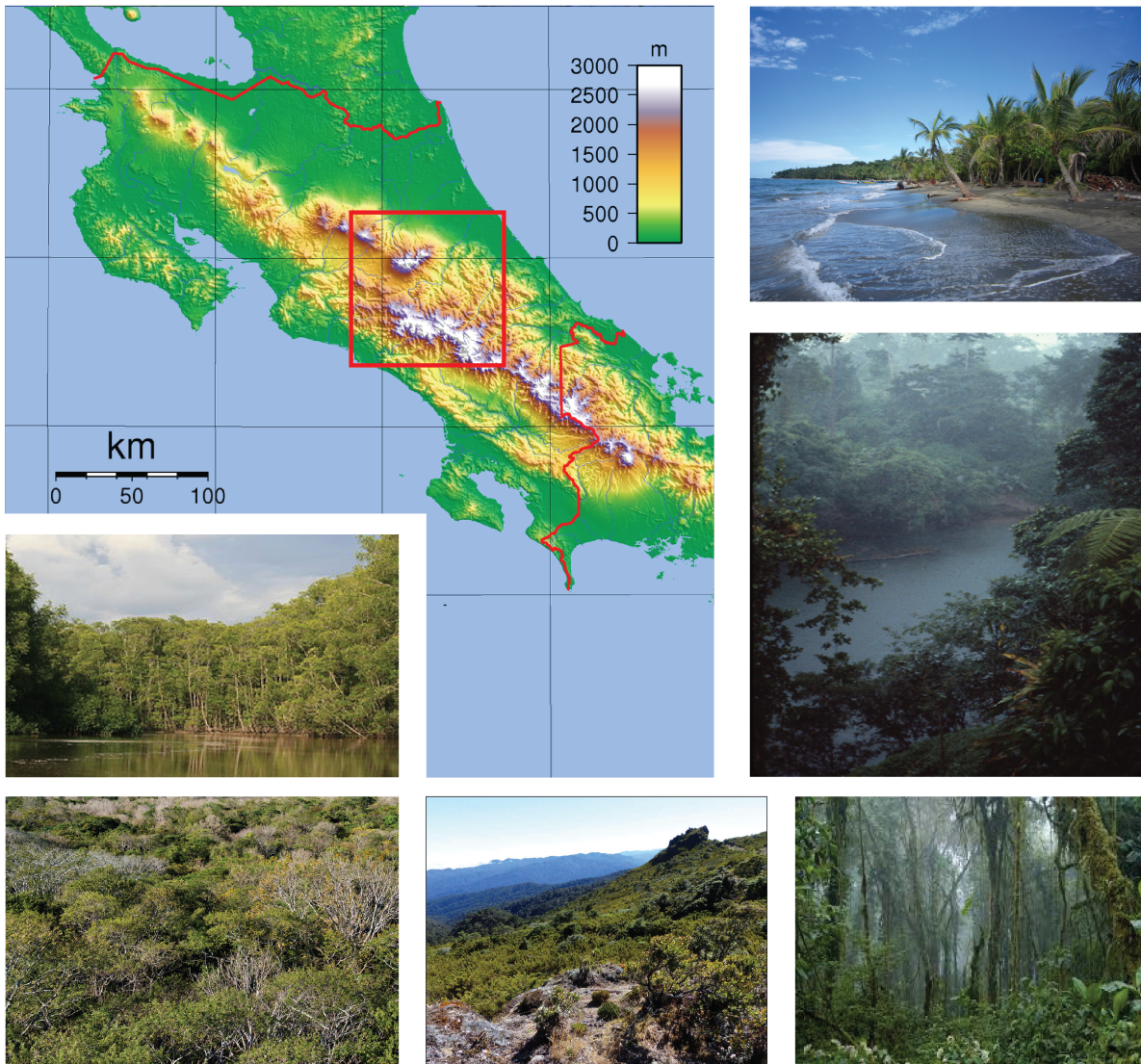


Fig. 1. A 100 km x 100 km map cell (red square) superimposed on the country of Costa Rica. Within this single cell, lie (clockwise from top right) Caribbean coastal forest (Puerto Viejo de Limón), Atlantic lowland rainforest (La Selva Biological Station), mid-elevation cloud forest (Monteverde), high elevation paramo (Cerro de la Muerte), Pacific coastal dry forest (Santa Rosa NP), and mangrove forest (Manuel Antonio), each with its own, largely distinct biota. *Credits:* Map adapted from Sadalmelik (Wikipedia, CC-BY-SA 3.0). Photos clockwise from top right:

Wilma Compton (CC 2.0 Generic), Robert K. Colwell (CC-BY-SA 3.0), Florent Mechain/TravelMag.com (CC BY 2.0) Jack Donnelly, QCostaRica.com, Thejaan (CC BY 2.0), Mark Whatmough (Wikimedia, CC 2.0 Generic).

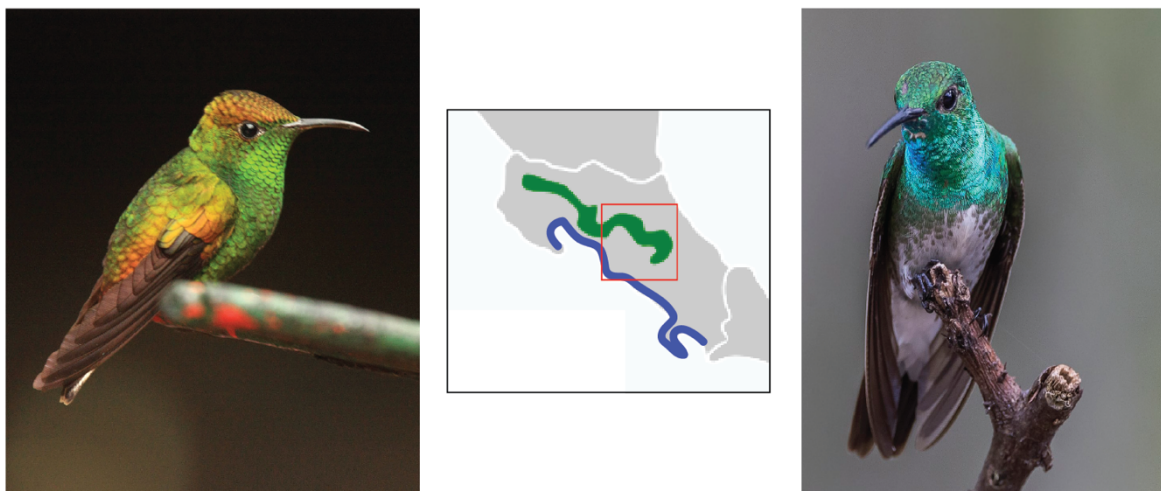


Fig. 2. Two hummingbird species endemic to Costa Rica with restricted, narrow ranges, separated by habitat and elevation . *Left:* Male *Elvira cupreiceps* (copper-headed emerald), green on the map of Costa Rica. *Right:* Male *Amazilia boucardi* (mangrove hummingbird), blue on the map. The red square on the map outlines a single, 100 km x 100 km map cell (Fig. 1). *Photo credits:* *left*, Tim Lenz, Wikipedia (CC BY 2.0); *right*, Jorge Obando, Wikipedia (CC BY-SA 2.0). *Map credit:* modified from map by Cephas, Neotropical Birds Online (CC BY-SA 3.0).