

The knowledge that large-scale rearrangements in two key proteins in the spliceosome likely play key roles in the cycling of the spliceosome provide a new perspective on prior genetic and biochemical data, and should provide opportunities to further explore the functional consequences of these arrangements. Cryo-EM reconstructions of other steps in the splicing pathway, previously imaged at much lower resolution (2 to 4 nm) (8)—too low for accurate docking of the new models—are now primed to be imaged at resolutions better than 1 nm, given the rapid advances in cryo-EM in the past 3 years (10). Higher-resolution structures of the spliceosome in these other steps are likely to reveal additional conformational changes required for splicing to occur.

The recent structural models of the spliceosome in different steps of the splicing reaction represent a turning point for the field, reminiscent of the change that occurred when structures of the protein-synthesizing machine—the ribosome—were resolved in 2000 (11). Now, dozens of ribosome and ribosomal subunit structures are determined every year. With the advent of high-resolution cryo-EM, the same is likely to be true for the spliceosome over the next decade. New structures will be needed to understand the catalytic cycle and the process by which pre-mRNAs can be alternatively spliced to form many different mature mRNAs encoding different proteins. Model organisms such as fungi, which were needed for the first high-resolution cryo-EM structures (2–5), will likely continue to provide important insights into alternative splicing—for example, into exon skipping (12) (see the figure, panel B). In the meantime, it will be exciting to see how the present burst of spliceosome structural knowledge permeates through the field to inspire new genetic, biochemical, and biophysical experiments aimed at unraveling the fundamental properties of this ancient regulator of gene expression. ■

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ECOLOGY

Thermal trouble in the tropics

Tropical species may be highly vulnerable to climate change

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Early Victorian naturalists marveled at the profusion of diversity they encountered as they traveled from temperate to tropical latitudes. The inverse relationship between latitude and species richness that these naturalists first observed is now referred to as the latitudinal diversity gradient. Various ecological and evolutionary explanations have been proposed for the latitudinal diversity gradient. Of these, perhaps none are more relevant to contemporary conservation issues than Janzen's hypothesis of latitudinal differences in species' climatic tolerances and thermal selectivity (1). On page 1437 of this issue, Chan *et al.* (2) advance Janzen's early theories by elucidating some of the potential selective pressures imposed by climate and climate variability.

In 1967, Daniel Janzen published his seminal treatise discussing why "mountain passes are higher in the tropics" (1). He argued that in climates with low variability, as occur throughout much of the tropics, species should evolve to have narrow thermal

tolerances. In contrast, the high climatic variability that occurs in most temperate regions should select for broader thermal tolerances. Therefore, species at lower latitudes will generally have smaller elevational ranges because they have narrower thermal tolerances, making mountains less surmountable, and hence "higher," from the perspective of tropical species. The real importance of Janzen's ideas lies in the revelation that thermal tolerances are traits shaped by selection and that they manifest in the realized elevational and geographic ranges of species.

However, climate varies not just with latitude and elevation, but also through time. Increasing atmospheric concentrations of CO₂ and other greenhouse gases are driving rapid changes in Earth's climate. Alongside rising mean annual temperatures, there have been dramatic and complex changes in the temporal variability of climatic conditions over the past century (3). Compared to their temperate counterparts, tropical species are particularly vulnerable to changes in global climate, because they have evolved under stable climates and thus have narrow thermal niches (see the figure) (4, 5). In other words, just as mountain passes are "higher in the tropics," so, too, are the effects of climate change on species predicted to be more severe in the tropics—despite absolute rates of warming being slower there than at higher latitudes (6).

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Thermal specialists. Tropical species such as those living in these mountains in Pahang, Malaysia, tend to have narrow thermal tolerances and may therefore be especially vulnerable to climate change.

Using data from more than 16,000 vertebrate species and over 150 elevational transects from around the globe, Chan *et al.* provide macroecological evidence supporting Janzen's original thesis, inject the pertinent context of climate change, and—perhaps most importantly—identify how temporal variation in climatic factors is likely to select for the breadths of species' thermal tolerances. More specifically, the authors show that high seasonal temperature variability and low diurnal temperature variability both favor thermal generalist species over specialist species with narrower thermal tolerances.

Several studies have shown that thermal specialists will need to quickly migrate and/or evolve to track the movement of suitable climatic zones (6), potentially leading to extinctions as some species fail to keep pace (7). The results of Chan *et al.* suggest that additional evolutionary pressures may act against thermal specialists at a global scale. Long-term increases in seasonal temperature variability (3) due to the increasing frequency and severity of extreme climatic events (8), coupled with decreases in diurnal temperature variability due to faster nighttime versus daytime warming (9), will both select against thermal specialists. The combined ecological and evolutionary pressures of climate change on specialists may eventually lead to global biodiversity losses and biotic homogenization.

To better predict the impacts of climate change on biodiversity, further research is paramount, especially on tropical species, which are expected to be most sensitive to changes in climate and climate variation. Several influential and oft-cited reviews claim to have uncovered coherent fingerprints of climate change across Earth's ecosystems

(10, 11). In reality, however, a clear understanding of how climate change is affecting tropical species is precluded by a paucity of studies, and hence data, from low-latitude systems. This geographic bias is further magnified by taxonomic biases: Nearly all studies that do exist for the tropics come from just a handful of taxa, generally dominated by endothermic vertebrates, which may be unrepresentative of broader patterns in other species groups. Geographic and taxonomic biases result, in part, from the traditional difficulties of working with diverse taxa in often-inaccessible locations. Growing collaborative data networks, combined with new methods of large-scale data collection (12), are helping researchers to bypass some of these limitations and will hopefully soon provide us with a more complete understanding of how tropical species are responding to climate change.

The potential effects of climate change on natural systems are complex and remain poorly understood. However, the ecological and evolutionary risks to specialist species appear particularly ominous. A lamentable lack of basic ecological and biogeographic data from the tropics limits our ability to extrapolate macroecological patterns or to model future environmental responses to changes in climate. Chan *et al.* present a novel framework for how long-term and short-term climatic variability combine to shape the evolution of thermal niche breadths and hence geographic distributions. Additional studies looking at the adaptability and plasticity of climatic tolerances of species are now required to improve predictions of how these species will respond to increasing environmental variability in a rapidly changing world. ■

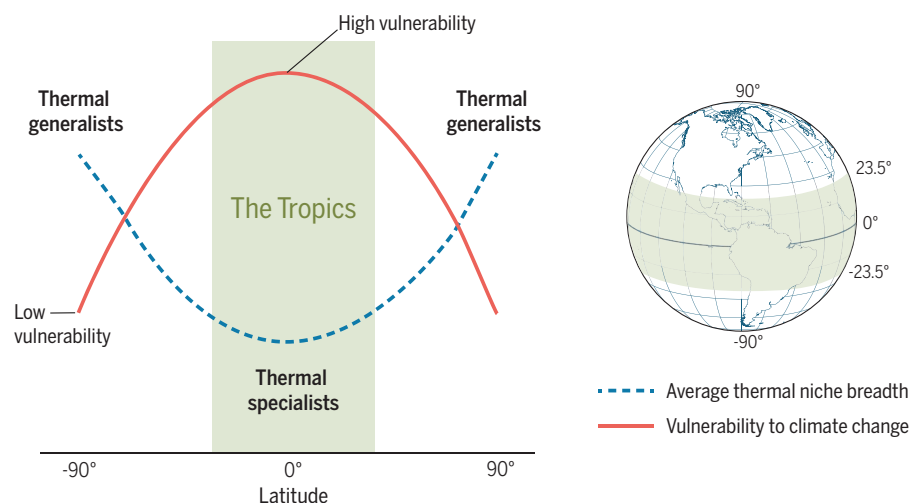
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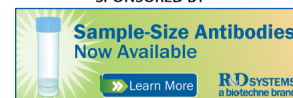
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