Local to global

Uncovering drivers of global tree diversity

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Plant species diversity declines from tropical to temperate latitudes. Local neighbourhood interactions among species that favour heterospecifics over conspecifics may have a role in shaping this latitudinal diversity gradient, but perhaps not as traditionally thought.

One of the most notable biodiversity patterns on Earth is the decline in plant species diversity from the Equator to the poles[1]. One hectare of tropical forest can contain up to hundreds of plant species, whereas one hectare of temperate forest can contain up to several dozen. Biodiversity can determine essential ecosystem functions and is being lost at alarming rates[2]; a better understanding of the mechanisms that contribute to global biodiversity is therefore critically important.

Many hypotheses might explain the latitudinal diversity gradient, including faster rates of evolution, greater productivity and more stable climates in tropical than temperate environments[3]. The Janzen–Connell hypothesis is another prominent hypothesis that might explain the high diversity of plant species in tropical forests[4,5]. This hypothesis suggests that relatively host-specific natural enemies (for example, pathogens, parasites and herbivores) are more prominent in tropical than temperate forests. Such antagonists accumulate where their host species is at high densities, which can increase mortality for nearby younger individuals of the same species (conspecifics). However, these antagonists should also favour the growth and survival of individuals of other plant species (heterospecifics) in the area, which may maintain higher local levels of plant species diversity (Fig. 1). If conspecifics reduce plant survival more than heterospecifics, then locally dense stands of conspecifics should become less dense over time; this would open space for other species and increase species diversity. By contrast, if conspecifics have similar or more positive effects on survival than heterospecifics, then plant species diversity should erode over time.
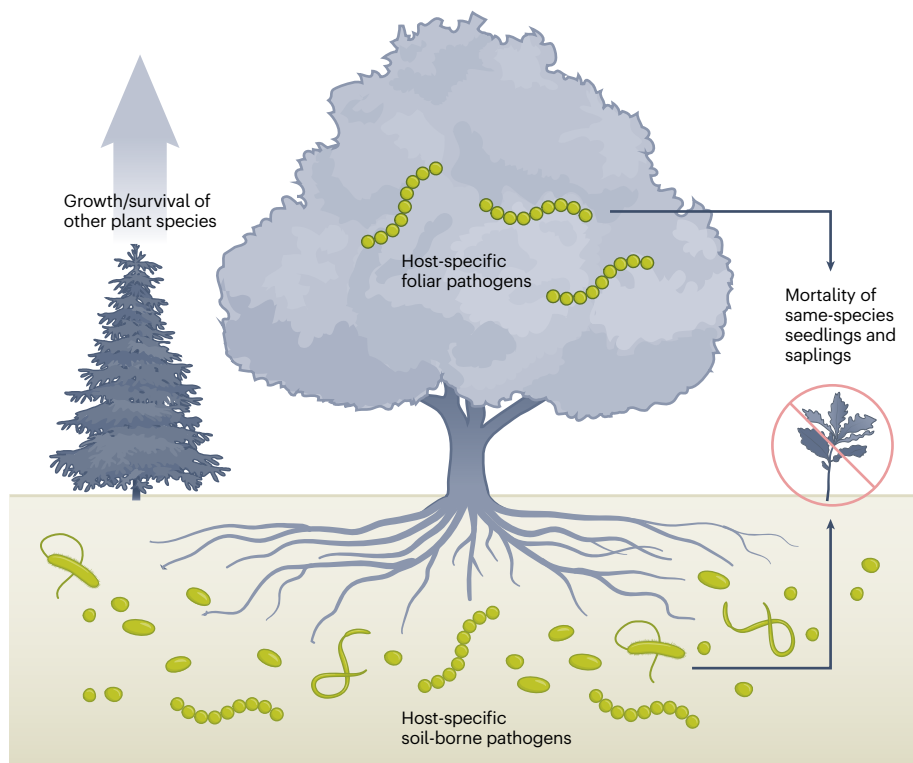

Fig. 1 | Example mechanisms that generate stabilizing CDD, which may contribute to latitudinal gradients in plant species diversity. Relatively host-specific natural enemies (including both above- and belowground pathogens, parasites and herbivores) usually accumulate around an adult individual. Such enemies can be devastating for younger conspecifics in the neighbourhood, and potentially cause their mortality. However, these antagonists also favour the growth and survival of heterospecifics in the area, which may maintain higher levels of local plant-species diversity. These mechanisms generate what is known as stabilizing CDD, which means that increases in conspecific density reduce plant survival more than similar increases in heterospecific density. Stabilizing CDD is thought to be stronger in tropical than temperate forests, but a recent study suggests this idea may be more nuanced than traditionally thought[11].

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In these ways, tropical plant-species diversity might be maintained at high levels by strong interactions with relatively host-specific natural enemies, whereas a comparative lack of these interactions in temperate forests might lead to lower species diversity. Studies over the past several decades have found widespread evidence for these negative conspecific interactions (also known as negative conspecific density dependence (CDD)) across plant species[6,7]. Spatial distributions of trees also appear to fit those predicted by the Janzen–Connell hypothesis[8–10]. However, global tests of this idea using data on plant survival are lacking.

In a recent article in the journal *Nature*, Hülsmann et al. used data from 23 stem-mapped forest plots in the Smithsonian Forest Global Earth Observatory (ForestGEO) network to test whether increases in conspecific tree density reduce sapling survival rates more than comparable increases in heterospecific tree density[11]. They call this difference 'stabilizing CDD', because more-negative effects from conspecifics than heterospecifics are theorized to stabilize population abundances and potentially allow species coexistence (all else being equal). They find that stabilizing CDD is present, on average, across the global array of forest plots they examined. They also find slightly greater average stabilizing CDD in tropical than temperate forests, but this relationship between average stabilizing CDD and latitude is by itself not significant. Such a finding appears to falsify the Janzen–Connell hypothesis. Perhaps local interactions mediated by relatively host-specific natural enemies have little to do with the latitudinal diversity gradient.

However, one of the most exciting findings from Hülsmann et al. comes from examining latitudinal patterns in stabilizing CDD for species at different abundances in their communities (that is, rare versus common species). They find that stabilizing CDD is significantly stronger in tropical than temperate forests for species at low to moderate abundances. Approximately two-thirds of tree species in their analysis had abundances at which significant latitudinal differences in stabilizing CDD were observed. Latitudinal differences in stabilizing CDD were especially pronounced for tree species at low abundances in forest communities. These findings support a reframing of the Janzen–Connell hypothesis, and raise the question of whether differences in stabilizing CDD for species at low to intermediate abundances could be enough for local interactions to contribute to the latitudinal diversity gradient. Some have suggested that as long as common species are held in check by some degree of stabilizing CDD, then stronger stabilizing CDD for species at low to moderate abundances in tropical forests should stabilize their populations and lead to their persistence over long periods of time[8,9,12]. It may seem counterintuitive to think of natural enemies as stabilizing. But as host populations decline so do their host-specific enemies, which causes host populations to rebound and stabilize at relatively low to moderate abundances[12]. This mechanism — if more pronounced in tropical forests — would enable the tropics to act as a 'museum' of plant species diversity, potentially preventing extinction for species at low to moderate abundances because their populations are stabilized by interactions with relatively host-specific natural enemies. Indeed, one of the notable differences between tropical and temperate forests is that tropical forests hold many more rare species, but similar numbers of common species.

Hülsmann et al. tested for latitudinal differences in stabilizing CDD using data on sapling survival, but stabilizing CDD may also differ across tropical and temperate forests for other life stages. For example, if stabilizing CDD for seedling survival follows the same pattern as Hülsmann et al. observed for sapling survival (or exhibits a more pronounced latitudinal gradient), then the cumulative effect across both life stages might be an even stronger latitudinal gradient in stabilizing CDD. Such a finding would be consistent with strong spatial repulsion among conspecific adults in tropical forests and global differences in spatial repulsion of saplings from conspecific adults — patterns that reflect processes acting across multiple life stages, including seed germination and seedling establishment as well as seedling, sapling and adult survival[8–10]. Global tests of stabilizing CDD at other life stages will enable more confident conclusions about the effect of local interactions on global diversity gradients.

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