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ECOLOGY

Plant diversity rooted in pathogens

Ecologists have long pondered how so many species of plant can coexist locally in tropical forests. It seems that fungal pathogens have a central role, by disadvantaging species where they are locally common.

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Tropical forests routinely contain more than 200 tree species in a single hectare (Fig. 1). Why don't a few species come to dominate, by chance or by virtue of being better competitors? Multiple hypotheses have been proposed to answer this question, most of which invoke some sort of niche differentiation with respect to resources and/or natural enemies. But despite decades of research, the issue remains unresolved. In a paper published on *Nature*'s website today, Bagchi *et al.*[1] report the results of an elegant field study that clearly implicates natural enemies, specifically fungal pathogens, as crucial to maintaining tropical-plant diversity.

In 1970, ecologists Daniel Janzen[2] and Joseph Connell[3] proposed that natural enemies that target specific host plants maintain high tropical-plant diversity by elevating the mortality of each plant species in areas where it is abundant. Fundamentally, the idea is that host-specialized enemies, including pathogens and insect herbivores, can attack more efficiently and do more damage where their hosts are more plentiful. As a result, each host species fares better when it is rare and less well as it becomes more common — a phenomenon known as negative density dependence. Many empirical studies have found such negative density dependence in tropical forests[4,5], and the Janzen–Connell hypothesis is the most often cited explanation for these patterns and for high local diversity of plant species in tropical forests. However, niche differences in resource requirements or other factors could also cause negative-density-dependent patterns[6], and few studies have explicitly linked such patterns to particular natural enemies (although see ref. 7 for an exception).

Bagchi *et al.* tested this hypothesis experimentally by using pesticides to remove (or at least reduce) fungal pathogens and, separately, insects at the seedling-establishment stage. Working in a tropical forest in Belize, the authors censused seeds falling into seed traps and seedlings that became established in neighbouring 1-square-metre plots that were treated with a fungicide or with an insecticide, or not treated. In untreated plots, seedling establishment was negatively density dependent and there was a large increase in local species diversity from the seed to the seedling stage, consistent with previous work[4]. Bagchi and colleagues' crucial findings were that fungicide application resulted in the near disappearance of negative density dependence and a drop in seedling species diversity. By contrast, insecticide application merely weakened negative density dependence and led to no change in species diversity, although it did increase the total number of seedlings and caused a dramatic shift in species composition.

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Figure 1 | Shades of green. The forest canopy on Barro Colorado Island, Panama, provides visual evidence of how small areas can contain many different tropical tree species. Bagchi and colleagues' findings[1] suggest that fungal pathogens play a crucial part in maintaining this diversity.

This is the first study to explicitly link a particular group of natural enemies to negative density dependence and the maintenance of species diversity in tropical forest plants. It clearly implicates fungal pathogens as the most important drivers of these patterns at the seedling-establishment stage. In the past, there have been more studies of insects than of pathogens as agents of the Janzen–Connell effect — no doubt owing in large part to the greater ease of working with insects. Although insect attack has been found to increase with host-plant density in several tropical plant species[8], the ability of insects to respond to high host density, and thus induce negative density dependence, may ultimately be restricted by their own enemies, such as parasites or predators[9]. Pathogens seem less likely to be similarly checked, which may explain their greater contribution to negative density dependence.

Bagchi and colleagues' results demonstrate that fungal pathogens and insect herbivores influence tropical plant communities in qualitatively different ways. Their distinct roles relate to the two ways in which differences among plant responses to natural enemies can affect species diversity and composition. First, as discussed above, differences in natural enemies can contribute to niche differences that stabilize individual species' abundances and species diversity. Alternatively, or in addition, they can alter differences in competitive ability (fitness) among species[10], thereby modifying species abundances, and potentially which species can successfully compete at all. The large shifts in species composition seen during insecticide treatment suggest that insects have major impacts on fitness differences in this ecosystem. Overall, it seems that fungal pathogens are more important determinants of niche differences and thus species diversity, whereas insects have greater influence on fitness differences and thus species composition.

This work also contributes novel observations on the strength of negative density dependence in different species. Contrasting hypotheses predict either a negative relationship between a species' average abundance and its negative density dependence if greater abundance makes a species more apparent to its enemies, or a positive one if the causality is reversed and lower negative density dependence leads to increased abundance[5]. Previous studies[5,11] that quantified tree abundance over large areas have found that more-abundant species experience less negative density dependence. Bagchi *et al.* find that species that are more abundant as seeds suffer stronger negative density dependence, which at first seems to contradict these earlier findings. However, seed abundance depends not only on tree abundance but also on seed size, which varies widely among tropical tree species. Small-seeded species are likely to be particularly vulnerable to natural enemies, and small seeds are produced in greater numbers, and thus differences in seed size may reconcile Bagchi and colleagues' results with previous work. Future studies should seek to disentangle the roles of species traits and abundances in driving interspecific variation in negative density dependence.

Indeed, this groundbreaking experimental work lays the foundation for a host of studies exploring the roles of natural enemies in structuring tropical-plant diversity. Bagchi *et al.* investigated effects on seedling establishment, a single life stage — integration of such effects over the entire life cycle will ultimately provide a more complete picture. Replication of these experiments across climatic gradients could also test the idea that some climates are more conducive to natural enemies, and that this contributes to greater species diversity of forests in these areas. Furthermore, such comparative studies or others that explicitly manipulate temperature, rainfall or atmospheric carbon dioxide could address how global change affects interactions between plants and natural enemies and thereby illuminate the future of tropical plant diversity. ■

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