

# On Tropical Forests and Their Pests

Interactions with pest species may help to explain the high plant species diversity in tropical forests.

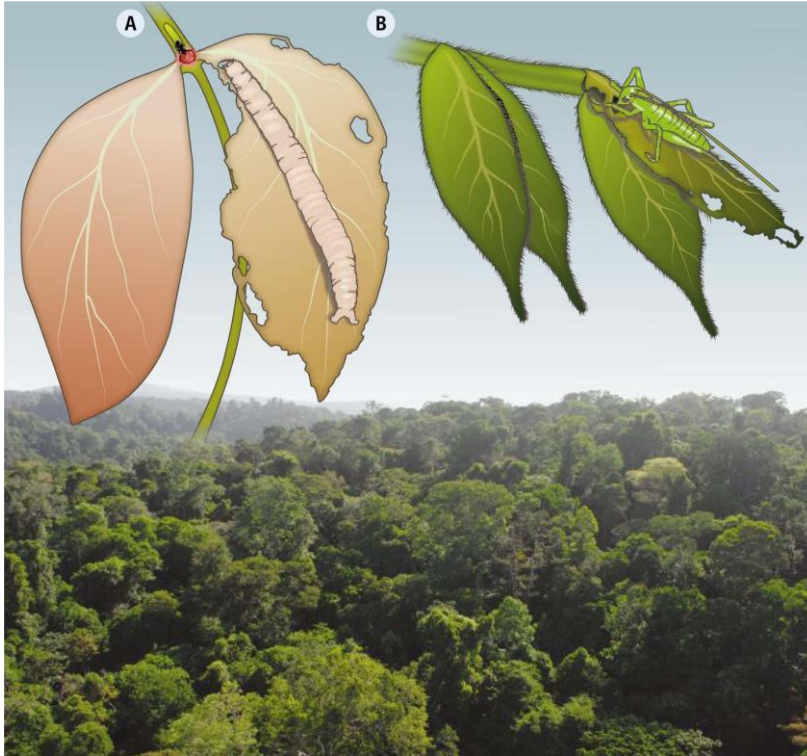
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Biologists have long been intrigued by the diversity of tropical forests, where 1 hectare may hold more than 650 tree species—more than in all of Canada and the continental United States. Ecological theory suggests that if species are too similar in their resource use, one will out-compete the others; hence, neighboring species must exploit different niches if they are to coexist. However, given that plants in one hectare of rainforest experience very similar physical environments, ecologists have struggled to demonstrate sufficient niche differentiation to support such high diversity (1). In addition to the puzzle of high local diversity, tropical forests also have high species richness overall. Recent studies show that interactions with pests may promote local plant diversity, accelerate plant evolution, and enhance the proliferation of species over evolutionary time.

Neighboring trees will experience similar abiotic challenges, such as the need to acquire light, water, and nutrients. It is therefore not surprising that neighbors in both temperate and tropical forests tend to have similar traits for resource acquisition (2–5). The diversity of tropical forests thus requires the existence of other niche dimensions along which species can differentiate, leading to a diversity of ways to make a living and thereby permitting coexistence. The origin and maintenance of high plant diversity in the tropics has been attributed to greater climatic stability, productivity, age, and area of the tropics than elsewhere. But these same factors also enable higher pest diversity. Biotic interactions, particularly between plants and their herbivores, may thus be stronger in the tropics (6, 7).

The evolutionary arms race between plants and their herbivores has produced a staggering array of plant defenses. For example, the leaves of a single tropical tree may contain hundreds of distinct chemical compounds that preclude attack by almost all herbivore species. An infinite number of defensive combinations are possible, with each combination susceptible only to a small subset of adapted, specialized herbivores. Moreover, the extent of herbivory may depend on the defensive profiles of the neighbors. Neighbors with similar defenses could share specialized herbivores and suffer more damage, whereas a neighbor with a locally novel profile would not be vulnerable to the common herbivores and would have a fitness advantage (see the figure).



Defense strategies. Two species of coexisting *Inga* (Leguminosae) (9) from the Amazon illustrate different defenses. (A) *Inga auristellae*. The leaves are light pink because they contain anthocyanin, an antifungal compound. They have delayed greening, hang down because they are expanding very quickly, are produced synchronously, have large extrafloral nectaries on the leaves, and produce chemical defenses. The caterpillar is a looper [*Coenipeta* (Noctuidae)] whose translucent body takes on the color of the food it is eating. (B) *Inga cayennensis*. The young leaves have normal greening, are covered in protective hairs, expand slowly, are produced continuously, have smaller extrafloral nectaries with low ant visitation rates, and produce a different set of chemical defenses. The herbivore is a katydid [Orthoptera (Tettigoniidae)]. The photo was taken in French Guiana, where both species shown above are found.

Consider, for example, *Inga*, a genus with more than 300 species, of which 45 can coexist in just 25 ha. In these as in all other tropical trees, 75% of the lifetime damage by herbivores happens during the few weeks of leaf expansion, as young leaves are tender and high in protein. To defend themselves, *Inga* leaves make a battery of chemical compounds and also have extrafloral nectaries that produce sugar to attract predatory ants as bodyguards against herbivores. Some species have normal greening, but others delay greening to minimize resources in the leaf during the vulnerable leaf expansion period (see the figure). Leaf expansion rates differ widely, with rapid expanders minimizing the vulnerable period. Leaf production can also be synchronous to satiate herbivores. Thus, young leaves have an arsenal of chemical, physical, and phenological defenses.

The few studies that have examined neighbors for divergence in defenses were conducted in the tropics, investigating dry forest trees in Mexico (8), rainforest trees in the Amazon (9), and understory shrubs in Panama (10). They all found that neighbors were more dissimilar in defenses than would be expected at random. Neighbors possessed similar adaptations to meet their local abiotic challenges (2–5, 9, 11), but differed in defenses against herbivores (8–10). Thus, niche differentiation with respect to defenses against pests may be the primary mechanism for coexistence in tropical forests.

Evidence from several lineages of tropical trees and shrubs shows that closely related species have diverged in defenses while differing little in nondefense traits (9–12). This supports the Red Queen

hypothesis (13), which states that antagonistic interactions between hosts and their pests lead to natural selection for beneficial adaptations and counteradaptations in both groups. Because herbivores are continually evolving counter- adaptations to plant defenses, plant defensive traits should evolve faster than adaptations to a more static abiotic environment.

In addition to promoting local diversity and accelerating defense evolution, plant- herbivore interactions may also enhance rates of speciation in the tropics. Plant radiations on islands and in mountains have been attributed to divergence in floral traits associated with shifts in pollinators or to divergence in traits for the physical environment. In contrast, none of the species-rich genera that constitute a large fraction of tree diversity in the lowland tropics have been explained by such mechanisms. The evolutionary arms race between plants and herbivores may be the missing explanation. Evidence in other systems shows that separate populations in different environments will diverge in their adaptations, and when populations reunite and interbreed, hybrid phenotypes can be inferior, leading to selection for reproductive barriers. Because defenses evolve more quickly than other traits, we suggest that divergence in defensive genes may be the main factor selecting for the evolution of reproductive isolation, thereby promoting speciation (6, 7). Additionally, selection for divergence in defenses can be genetically linked to reproductive barriers (14). For example, selection on leaf secondary metabolites could change the compounds expressed in floral scents, shifting pollinator preferences and hastening reproductive isolation.

For plant-herbivore interactions to explain high coexistence and diversity in the tropics, it is critical that herbivore pressure be greater in the tropics than in the temperate zone. Herbivore diversity, abundance, and host specificity, as well as rates of herbivory, are generally thought to be higher in the tropics. Conversely, temperate plants experience stronger abiotic selection due to a more severe and variable climate. Nonetheless, a robust answer to the role of herbivores in the maintenance and origin of plant diversity across latitudes needs more exploration. Given advances in metabolomics that allow chemical defenses to be quantified and in DNA sequencing for phylogenetics and species designations, progress is limited mainly by the need for time-intensive studies of plants and their enemies in the field.

#### References and Notes

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