

ECOLOGY

How latitude affects biotic interactions

Impacts of trees on neighboring trees from the same species are stronger in the tropics

By **Liza S. Comita**^{1,2}

Are biotic interactions, such as competition and predation, stronger in the tropics than at higher latitudes? Biologists have long speculated that more intense interactions tend to occur at lower rather than at higher latitudes as a result of year-round warm and wet conditions near the equator, particularly in lowland tropical rainforests (1). This idea is now well established in the ecologi-

cal literature (1, 2), but recent debate has questioned whether such a latitudinal gradient in biotic interactions actually exists (3). On page 1389 of this issue, LaManna *et al.* provide evidence that the intensity of at least some types of biotic interactions are indeed stronger closer to the equator (4).

In a recent study, Roslin *et al.* (5) experimentally assessed global patterns of predation rates on insects by using fake (plasticine) caterpillars placed at sites on six continents spanning a latitudinal gradient of >11,000 km. They found increasing rates of insect predation toward the equator. The higher predation risk at lower latitudes was driven by arthropod predators (such as ants) rather than birds or mammals. Use of standardized

methods to assess predation across multiple sites allowed Roslin *et al.* to make robust comparisons among sites and validate the existence of a latitudinal gradient in predation.

Similarly, LaManna *et al.* used data collected with standardized methods at multiple sites from around the world to test for a latitudinal gradient in the strength of biotic interactions. Rather than predation, they investigated interactions between neighboring trees, focusing on a phenomenon referred to as conspecific negative density dependence (CNDD), where an individual is negatively affected by the local density of other individuals of its own species (conspecifics).

Biologists have long hypothesized that plants should have lower performance (e.g.,

¹School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, USA. ²Smithsonian Tropical Research Institute, Panamá, República de Panamá. Email: liza.comita@yale.edu

growth, survival, or reproduction) when growing near conspecific neighbors. This is because individuals of the same species likely compete more strongly for resources than do unrelated species; they also tend to be susceptible to the same natural enemies, such as insect herbivores and fungal pathogens (6, 7). Hundreds of studies have tested this hypothesis, revealing that CNDD does occur in numerous ecological communities worldwide (8). Strong negative interactions between conspecifics have important implications for community diversity: When conspecifics have more negative effects on each other than on other species in the community, coexistence is possible because no single species can push other species to local extinction (9). Therefore, CNDD may play a critical role in helping to maintain diversity in ecological communities. Differences in the strength of CNDD among communities might drive global patterns of diversity (10), such as the higher diversity of tropical compared with temperate forests.

In their study, LaManna *et al.* quantified the strength of CNDD at 24 sites that range in latitude from 5.25°S to 48.66°N. They use data from a global network of forest research plots coordinated by the Smithsonian's Center for Tropical Forest Science-Forest Global Earth Observatory (CTFS-ForestGEO) (see the photos). At plots across the network, local researchers have used identical methods to identify, map, and measure millions of saplings and trees (11).

For each species at the 24 sites of their study, LaManna *et al.* modeled sapling abundance in local neighborhoods as a function of the density of conspecific adults. They found decreasing sapling recruitment with increasing conspecific adult density, consistent with CNDD. At the same time, sapling recruitment was relatively unaffected by the density of other species in the neighborhood. This observation suggests that conspecific interactions are indeed stronger than heterospecific interactions and may therefore promote coexistence and help to maintain tree diversity.

The authors then investigated whether the median strength of CNDD at each site was correlated with distance from the equator, as well as with several measures of species diversity. Their analyses revealed a latitudinal gradient in CNDD, with stronger negative effects of conspecific neighbors in more diverse, tropical forests compared to less diverse temperate forests. In a critical step,

they used a neutral model to confirm that these relationships did not arise spuriously as a result of differences in the numbers of individuals or species across the forest sites. Thus, the study provides robust evidence for a latitudinal gradient in the strength of interactions between neighboring trees.

LaManna *et al.*'s study also sheds light on a debate about the relation between the abundance of a species in a community and the strength of CNDD that the species experiences. In a tropical forest in Panama, locally rare tree species experience stronger CNDD than do locally common species (12), a pattern driven by higher susceptibility of rare species to soil pathogens (13). Scientists have



Scientists take tree measurements at a 50-ha CTFS-ForestGEO research plot in the Huay Kha Khaeng Wildlife Sanctuary (also shown in the first photo).

found the same relationship between CNDD and species abundance in other tree communities (10), but the opposite relationship has been reported for at least one temperate forest site (14). These differing results among studies have been attributed to differences in methods (14). Using the same method at each site, LaManna *et al.* now find that the CNDD-species abundance relationship varies systematically among sites. In the tropics, relatively rare species suffer stronger CNDD than do common species. By contrast, in temperate forests, common species experienced similar or stronger CNDD compared with rare species.

LaManna *et al.* offer several explanations for why CNDD may be stronger in the tropics. For example, intraspecific competition may be more intense, pressure from or susceptibility to specialized natural enemies may be higher, or seed dispersal may be more limited, resulting in more intense within-species interactions at lower latitudes. All of these explanations assume that biotic interactions are stronger in the tropics.

However, an alternate hypothesis is that biotic interactions are equally strong at all latitudes but that the impact of local abiotic conditions becomes more important at temperate latitudes. If species require specific habitats or prefer certain microenvironments, then higher sapling recruitment should occur where conspecific adult tree density is high because high conspecific adult densities would tend to be found in the species' preferred habitat. The relationship between sapling recruitment and local conspecific adult density is therefore the net outcome of both negative biotic interactions (such as competition and herbivory) and positive habitat effects. Similarly, positive biotic interactions, such as with mutualists like mycorrhizal fungi, may offset negative effects of conspecific density. Therefore, latitudinal shifts in the strength of CNDD could be driven by shifts in the importance of abiotic variables or positive biotic interactions instead of, or in addition to, negative biotic interactions.

Thus, although LaManna *et al.* clearly demonstrate a latitudinal gradient in the importance of conspecific interactions, many questions remain. Given the myriad threats facing forests around the world, a better understanding of the processes that shape these ecologically and economically valuable systems is urgently needed. Although logistically challenging, experimental tests of potential mechanisms causing CNDD, replicated across multiple sites spanning a wide latitudinal range, would offer valuable insights into the ecological processes shaping forests worldwide. ■

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