Plant diversity increases with the strength of negative density dependence at the global scale


Theory predicts that higher biodiversity in the tropics is maintained by specialized interactions among plants and their natural enemies that result in conspecific negative density dependence (CNDD). By using more than 3000 species and nearly 2.4 million trees across 24 forest plots worldwide, we show that global patterns in tree species diversity reflect not only stronger CNDD at tropical versus temperate latitudes but also a latitudinal shift in the relationship between CNDD and species abundance. CNDD was stronger for rare species at tropical versus temperate latitudes, potentially causing the persistence of greater numbers of rare species in the tropics. Our study reveals fundamental differences in the nature of local-scale biotic interactions that contribute to the maintenance of species diversity across temperate and tropical communities.

Theory predicts that higher biodiversity in the tropics is maintained by negative density–dependent interactions among species and their specialized natural enemies (2–6). Conspecific negative density dependence (CNDD) is the process by which population growth rates decline at high densities as a result of natural enemies (e.g., predators, pathogens, or herbivores) and/or competition for space and resources (2–4, 7). Numerous studies have documented the existence of CNDD in one or several plant species (8–12), and most of these studies explicitly or implicitly assume that stronger CNDD maintains higher species diversity in communities. However, only a handful of studies have explicitly examined the link between CNDD and species diversity (4, 11, 13, 14), and no study has examined this relationship across temperate and tropical latitudes. Despite decades of study, our understanding of how processes at local scales—such as density-dependent biotic interactions—influence global patterns of biodiversity remains in flux (1, 15).

Both species-specific and more generalized mechanisms can cause CNDD, but only CNDD caused by species-specific mechanisms can maintain diversity (2, 3, 16, 17). Species-specific causes of CNDD include intraspecific competition or pressure from host-specific natural enemies (6, 9, 10, 16). These specialized interactions stabilize populations of individual species, causing population growth rates to decrease when a species is locally common and increase when a species is locally rare (6, 9, 10, 17). Thus, CNDD caused by specialized interactions results in the maintenance of diversity via negative frequency dependence at local scales (17–19). However, negative density dependence may also result from interactions that are more generalized with respect to species identity, such as interspecific competition or pressure from generalist natural enemies (6, 16, 20). In this case, high densities of either conspecifics or heterospecifics similarly reduce population growth rates of a given species, and one or a few better-performing species could exclude others (6, 16, 20). Thus, negative effects of conspecific densities on the recruitment or survival of a given species (i.e., CNDD) are expected to maintain diversity only when they are stronger relative to any negative effects from heterospecific densities (hereafter, heterospecific negative density dependence [HNDD]) (17). Increases in CNDD

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1Tyson Research Center, Washington University in St. Louis, St. Louis, MO, USA. 2Department of Biology, Washington University in St. Louis, St. Louis, MO, USA. 3Center for Conservation and Sustainability, Smithsonian Conservation Biology Institute, National Zoological Park, Front Royal, VA, USA. 4National Research Program - Eastern Branch, U.S. Geological Survey, Reston, VA, USA. 5Ecology Laboratory, BIOTEC, National Science and Technology Development Agency, Science Park, Pathum Thani, Thailand. 6Institute of Molecular Biosciences, Mahidol University, Salaya, Nakhon Pathom, Thailand. 7Research Office, Department of National Parks, Wildlife and Plant Conservation, Bangkok, Thailand. 8Institute of Forest Resource Management, National Research Program - Eastern Branch, U.S. Geological Survey, Reston, VA, USA. 9Department of Life Science, Tunghai University, Taichung, Taiwan. 10Department of Botany and Plant Physiology, University of Buea, Buea, Cameroon. 11Department of Biology, Indiana University, Bloomington, IN, USA. 12Smithsonian Tropical Research Institute, Balboa, Ancon, Republic of Panama. 13Institute of Pacific Islands Forestry, U.S. Department of Agriculture Forest Service, Hilo, HI, USA. 14Center for Tropical Forest Science–Forest Global Earth Observatory, Smithsonian Tropical Research Institute, Panama City, Republic of Panama. 15Department of Botany, National Museum of Natural History, Washington, DC, USA. 16Wildland Resources Department, Utah State University, Logan, UT, USA. 17Department of Botany, Faculty of Science, University of Peradeniya, Peradeniya, Sri Lanka. 18Joint Lab for Biodiversity Conservation, Sun Yat-sen University (SYSU)–University of Alberta, State Key Laboratory of Biocontrol, School of Life Sciences, SYSU, Guangzhou 510275, China. 19Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada. 20Department of Natural and Applied Sciences, University of Wisconsin–Green Bay, Green Bay, WI, USA. 21Department of Ecology and Evolutionary Biology, University of California, Los Angeles, Los Angeles, CA, USA. 22Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan. 23Department of Forest Ecology, Silva Tarouca Research Institute, Brno, Czech Republic. 24Los Alamos National Laboratory, Los Alamos, NM, USA. 25Department of Forest Management, College of Forestry and Conservation, University of Montana, Missoula, MT, USA. 26Center for Tropical Forest Science–Forest Global Earth Observatory, Smithsonian Environmental Research Center, Edgewater, MD, USA. 27Forest Ecology Group, Smithsonian Environmental Research Center, Edgewater, MD, USA. 28Institut de Recherche en Ecologie Tropicale, Centre National de la Recherche Scientifique et Technologique, Libreville, Gabon. 29Institute of Plant Science, University of South Bohemia, Bráníková 31, Ceske Budejovice 370 05, Czech Republic. 30Institute of Biology, University of the Philippines Diliman, Quezon City, Philippines. 31Institute of Forest Science, University of Florida, Gainesville, FL, USA. 32Faculty of Science, University of the Philippines, Diliman, Quezon City, Philippines. 33School of Biology, Washington State University, Vancouver, WA, USA. 34Institute of Tropical Forest Sciences, Washington State University, Pullman, WA, USA. 35Institute of Biology, University of Wisconsin–Green Bay, Green Bay, WI, USA. 36Institute of Arts and Sciences, Far Eastern University Manila, Manila, Philippines.

*Corresponding author. Email: joe.a.lamanna@gmail.com

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Fig. 1. Species richness increased with the strength of conspecific negative density dependence (CNDD) across tropical and temperate forests. (A) World map of stem-mapped forest plots \((n = 24\) forest plots) examined, which are part of the Smithsonian Center for Tropical Forest Science–Forest Global Earth Observatory (CTFS-ForestGEO) network. The median strength of CNDD measured at (B) 10-m-by-10-m and (C) 20-m-by-20-m scales declined (lower values indicate stronger CNDD) with increasing distance from the equator. Forest-wide rarefied species richness increased across latitudes with the median strength of CNDD measured at (D) 10-m-by-10-m or (E) 20-m-by-20-m scales. Patterns were similar for observed (nonrarefied) species richness and diversity (figs. S1 and S2). Density dependence was estimated with the Ricker model, but qualitatively similar results were obtained using another functional form (25) (figs. S5 and S6). Numbers next to plots (at right) are observed and rarefied species richness, respectively, of live trees. Plots are colored by increasing distance from the equator. Lines are best fits from linear [(B) and (C)] or Poisson [(D) and (E)] regression, and correlation coefficients \((r)\) are from Spearman-rank tests. BCI, Barro Colorado Island; SERC, Smithsonian Environmental Research Center; SCBI, Smithsonian Conservation Biology Institute.
relative to HNDD indicate greater specificity of the mechanisms underlying CNDD and are expected to maintain higher levels of species diversity (9, 10, 17–19).

The relative strength of CNDD can also vary among common and rare species in a community (9, 10), with important implications for the maintenance of diversity across latitudes. A notable feature of many tropical communities is that they harbor extremely large numbers of rare species (1), Assuming that CNDD is stronger than HNDD and limits local abundances of common species, the maintenance of diversity may depend on the degree to which populations of rare species are stabilized by CNDD. First, strong CNDD caused by host-specific enemies or intraspecific competition can reduce extinction risk by stabilizing the population dynamics of rare species (10, 18, 21, 22), leading to the persistence of greater numbers of rare species in a community. For example, strong CNDD caused by soil-borne pathogens may allow tropical tree species to recover from low population density (23). These types of specialized interactions may not only explain why so many species are rare in the tropics (9, 10) but also why large numbers of rare species persist in tropical communities. In contrast, weak (or nonexistent) CNDD for rare species will not favor their recovery from very low densities, making these species more prone to local extinction from interspecific competition, generalist natural enemies, or demographic stochasticity (16, 18, 20) and potentially resulting in the erosion of diversity. Individual studies in either temperate or tropical latitudes have found evidence for stronger CNDD in either common or rare species (9, 10, 13, 14, 24). A global test of these alternatives would advance our understanding of the extent to and mechanisms by which CNDD contributes to the latitudinal-diversity gradient.

We tested the contribution of CNDD to changes in tree species diversity across temperate and tropical latitudes by using 24 globally distributed forest plots (Fig. 1A and tables S1 and S2) that are part of the Smithsonian Center for Tropical Forest Science–Forest Global Earth Observatory (CTFS-ForestGEO) network (25). In each large plot (mean size ± SD = 27.5 ± 13.7 ha, range = 4 to 50 ha), all stems ≥1 cm in diameter at breast height have been mapped, measured, and identified using standardized protocols (table S1) (25). For each plot, we measured species richness and diversity (Shannon diversity index), as well as rarefied species richness (species richness given a standardized number of individuals) to account for differences in plot size and total numbers of individuals (25). We measured the effects of CNDD and HNDD on sapling recruitment at both the 10-m–by–10-m and 20-m–by–20-m scales because effects of adult trees on younger trees decline with distance (14, 25, 26). By including heterspecific adult and sapling densities in our models, we explicitly measured the influence of increasing heterspecific densities on local sapling recruitment. Then, to quantify CNDD for each species in each plot, we measured the degree to which increasing adult conspecific densities suppress local recruitment of saplings, independent of the effects of heterspecific densities (25). Thus, we isolated conspecific density effects (CNDD) relative to heterspecific effects (HNDD) (14, 25). We compared the relative magnitude of CNDD to HNDD to evaluate the extent to which CNDD is caused by species-specific mechanisms and the degree to which it is expected to maintain diversity (17). In addition, differences in tree densities, measurement error, and dispersal rates across forest plots might bias estimates of CNDD (27). Although simulation tests indicated that our results are generally robust to these potential biases (25), we used nonparametric Spearman-rank correlation tests to accommodate potential biases in our estimates of CNDD across latitudes.

The strength of CNDD declined with increasing distance from the equator (Fig. 1, B and C). Moreover, rarefied species richness (Figs. 1, D and E, and tables S3 to S6), nonrarefied species richness (figs. S1 and S2), and Shannon diversity (figs. S1 and S2) all increased with the strength of CNDD across temperate and tropical forests. The relationship between rarefied species richness and CNDD was equally strong whether CNDD was measured at the 10-m–by–10-m (Fig. 1D) or 20-m–by–20-m scale (Fig. 1E), indicating that CNDD operating at the scale of local tree neighborhoods can strongly contribute to large-scale diversity gradients. In contrast, density dependence from heterspecifics was relatively weak, nonexistent (i.e., HNDD ≈ 0), or slightly positive (tables S3 and S4). Consequently, species richness and diversity also increased with the relative strength of CNDD to HNDD (table S7). Although differences in CNDD between eastern and western hemispheres might influence our results (25), a simple linear-regression model including both latitude and a binary variable for eastern and western hemispheres showed that the strength of
CNDD still significantly decreased with latitude (at the 10-m–by–10-m scale: $F_{1,22} = 16.16$, $P < 0.001$; at the 20-m–by–20-m scale: $F_{1,22} = 25.28$, $P < 0.001$) but did not differ between eastern and western hemispheres (at the 10-m–by–10-m scale: $F_{1,22} = 0.013$, $P = 0.910$; at the 20-m–by–20-m scale: $F_{1,22} = 0.90$, $P = 0.354$).

These results support the hypothesis that stronger CNDD caused by species-specific mechanisms—such as intraspecific competition or specialized host–enemy interactions—contributes to higher diversity in the tropics than at temperate latitudes (2, 3).

The strength of CNDD was also associated with species abundance within forest communities, but the slope of this relationship changed systematically across latitudes. As compared with common species, rare species had stronger CNDD in the tropics (Fig. 2, A and B, and table S8). At temperate latitudes, in contrast, rare species had similar—and in some cases weaker—CNDD relative to common species (Figs. 2, A and B, and table S8). This latitudinal shift in the relationship between species abundance and CNDD was largely driven by a strong increase in the mean strength of CNDD for rare species (species with basal area < 0.1 m$^2$/ha) at tropical latitudes (Figs. 2, C and D). Because HNDD was relatively weak compared with CNDD across latitudes and species (tables S3 and S4), the latitudinal shift in the relationship between species abundance and CNDD was qualitatively similar if the relative strength of CNDD to HNDD was evaluated instead (at the 10-m–by–10-m scale: $r = -0.560$, $P = 0.004$; at the 20-m–by–20-m scale: $r = -0.742$, $P < 0.001$) (25).

Our global analysis is consistent with, and resolves apparent contradictions among, previous studies conducted within temperate or tropical latitudes documenting either stronger CNDD for rare versus common species or vice versa (9, 10, 14, 24). Common species exhibited CNDD in both tropical and temperate forests (Fig. 2D), satisfying a basic condition for CNDD to maintain diversity in temperate and tropical communities, but not by strongly stabilizing populations of rare species. These apparent differences in the ways in which local biotic interactions maintain diversity in temperate and tropical communities may contribute to the persistence of greater numbers of species in the tropics (1).

To confirm that these patterns were not influenced by differences in total numbers of individuals and/or species across forest plots, we used a neutral model to simulate the expected patterns of CNDD in the absence of density dependence. In this model, the observed total numbers of individuals and species were retained for each plot, but spatial patterns determined by recruitment, mortality, and dispersal limitation were all neutral with respect to species identity (25).

Several mechanisms could explain shifts in CNDD across species and latitudes. First, stronger CNDD relative to HNDD at tropical versus temperate latitudes suggests that species-specific mechanisms, such as intraspecific competition for limiting resources or pressure from specialized enemies, might be stronger in the tropics (29, 30). Second, strong dispersal limitation for both trees and their specialized enemies can lead to more intense host–enemy interactions or intraspecific competition and might explain stronger CNDD for rare species in the tropics (22, 31). Third, stronger CNDD for rare as compared with common species at tropical latitudes may reflect greater susceptibility of rare tropical species to their specialized enemies (e.g., weaker defenses or immune responses relative to common tropical species) (32). Finally, differences in biogeographic history, climate, and speciation across latitudes likely have a direct influence on global patterns of species diversity (1, 15), but these factors may also influence diversity indirectly by altering the composition of enemy communities, the ways in which enemies interact with their hosts, and the strength of intraspecific competition (1, 29, 30).

These examples illustrate that global patterns of biodiversity cannot be understood without simultaneously considering local biotic interactions and regional processes (1, 15). Our results suggest that regional processes interface with local biotic interactions to determine the strength of CNDD across species and the maintenance of biodiversity across tropical and temperate latitudes.
Plant diversity increases with the strength of negative density dependence at the global scale

Sandra Yap and Jonathan A. Myers


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Maintaining tree diversity

Negative interaction among plant species is known as conspecific negative density dependence (CNDD). This ecological pattern is thought to maintain higher species diversity in the tropics. LaManna et al. tested this hypothesis by comparing how tree species diversity changes with the intensity of local biotic interactions in tropical and temperate latitudes (see the Perspective by Comita). Stronger local specialized biotic interactions seem to prevent erosion of biodiversity in tropical forests, not only by limiting populations of common species, but also by strongly stabilizing populations of rare species, which tend to show higher CNDD in the tropics.

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