FOREST ECOLOGY

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

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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.

One of the most prominent and ubiquitous patterns of life on Earth is the systematic increase in species diversity from temperate to tropical latitudes (*1*). For nearly half a century, ecologists have hypothesized that higher species diversity 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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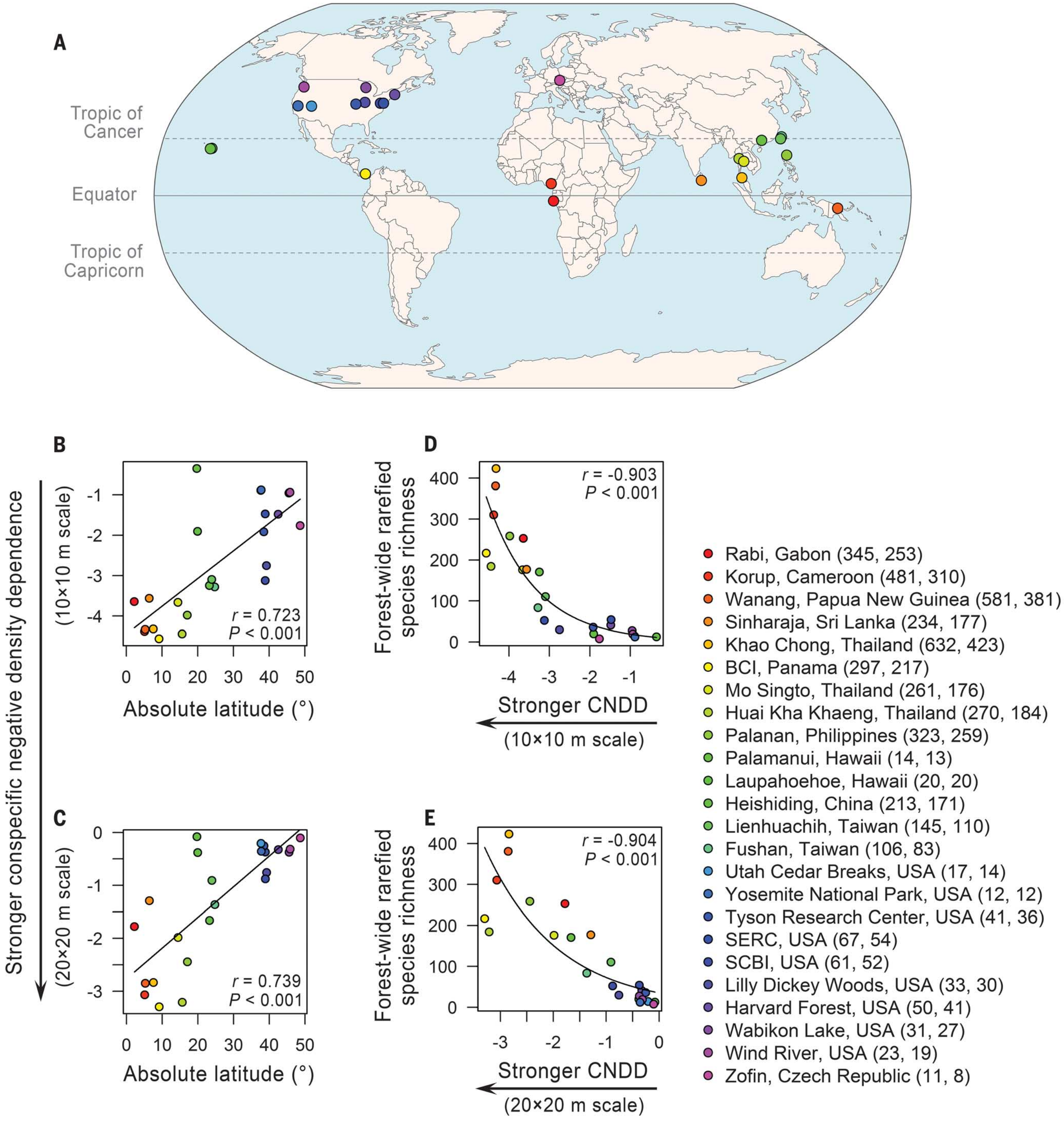

Fig. 1. Species richness increased with the strength of conspecific negative density dependence (CNDD) across tropical and temperate forests. (**A**) World map of stem-mapped forest plots (*n* = 24 forest plots) examined, which are part of the Smithsonian Center for Tropical Forest Science–Forest Global 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.

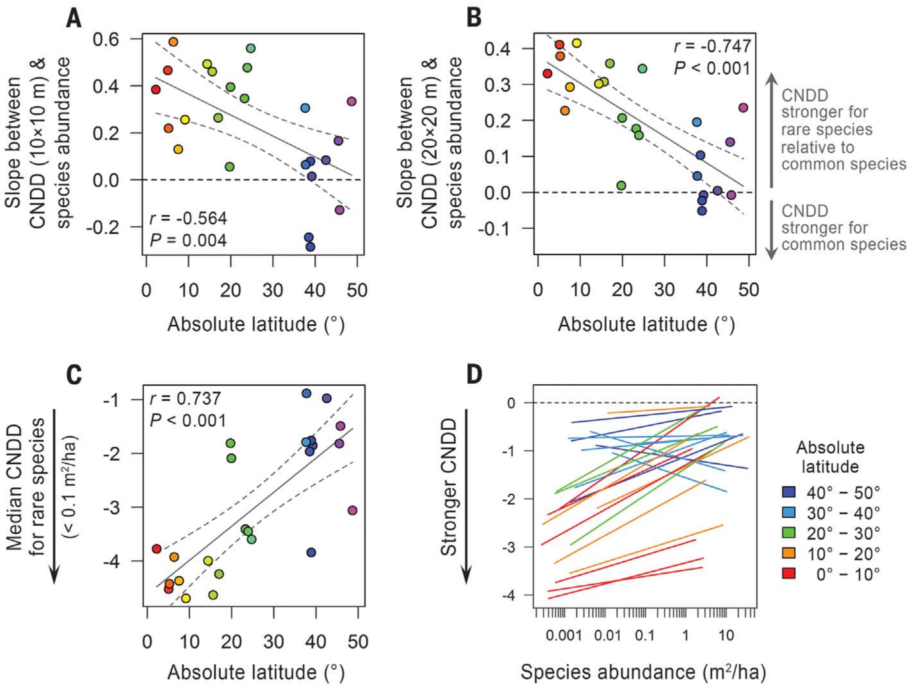

Fig. 2. Latitudinal shift in the strength of CNDD among common and rare species. Slopes and best-fit linear regression lines (±95% confidence interval) between species abundance [measured by basal area (square meters per hectare)] and CNDD measured at the (**A**) 10-m–by–10-m and (**B**) 20-m–by–20-m scales across species within each forest plot (n = 24 forest plots). Because lower values of CNDD reflect stronger CNDD, positive slopes indicate stronger CNDD for rare as compared with common species, and negative slopes indicate stronger CNDD for common versus rare species. (**C**) The median strength of CNDD for rare species (species with basal area less than 0.1 m^2/ha) was stronger at tropical than at temperate latitudes. CNDD for rare species is shown at the 10-m–by–10-m scale, but results were similar at the 20-m–by–20-m scale. For (A) to (C), plots are colored as in Fig. 1. (**D**) Best-fit linear regression relationships between the strength of CNDD (measured at the 10-m–by–10-m scale) and species abundance (square meters per hectare) within each forest plot (n = 24 forest plots) (table S8). Colors in (D) represent the latitudinal band a forest plot occupies, from tropical (red) to temperate (blue) latitudes. Species abundance is shown on a log scale. Density dependence was estimated with the Ricker model, but qualitatively similar results were found using another functional form (*25*) (fig. S7). Test statistics in (A) and (B) are Pearson correlation coefficients (r) from linear regression models, and the statistic in (C) is from a Spearman-rank test.

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 heterospecific adult and sapling densities in our models, we explicitly measured the influence of increasing heterospecific 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 from the effects of heterospecific densities (*25*). Thus, we isolated conspecific density effects (CNDD) relative to heterospecific 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 heterospecifics 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 (*5*, *28*). However, our results from tropical forests suggest that even stronger density-dependent regulation of rare species may cause their rarity and/or maintain diversity by stabilizing their population dynamics (*9*, *10*, *18*, *21*, *22*). Two previous studies from one of the tropical forest plots in our analysis (Barro Colorado Island, Panama) have shown that species abundance decreases with the strength of CNDD (*9*, *10*). Strong CNDD could also promote the persistence of rare species and reduce their risk of local extinction from demographic stochasticity by allowing them to recover from low densities (e.g., by escaping their specialized enemies) (*17*, *18*, *23*). Thus, stronger CNDD resulting from local biotic interactions may prevent erosion of biodiversity in tropical forests by limiting populations of common species and more strongly stabilizing populations of rare species. In contrast, our results from temperate forests suggest that CNDD maintains diversity by limiting populations of common species, 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*). Relationships between measures of species diversity and CNDD, as well as between species abundance and CNDD, across latitudes did not qualitatively change with the use of standardized effect sizes from this neutral model (table S9 and fig. S3 and S4).

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.

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7. Note that CNDD here refers to a per-neighbor or per-capita effect (the negative effect of an increase in the number of conspecific neighbors) that is species-specific and may be due to life-history differences among species. This is different from a community compensatory trend, where all species may have equivalent per-neighbor CNDD, but common species experience lower recruitment or survival on average because they encounter higher densities of conspecific neighbors.
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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/356/6345/1389/suppl/DC1
Materials and Methods
Figs. S1 to S12
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References (*33*–*73*)

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