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Drought tolerance and species abundance mediate dry season negative density dependence in a tropical forest

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Abstract

Conspecific negative density dependence (CNDD) is thought to be a key process in maintaining plant diversity. However, the strength of CNDD is highly variable in space and time as well as among species, and correlates of this variation that might help to understand and explain it remain largely unquantified. Using Bayesian hierarchical models, we took advantage of 10-year seedling monitoring data that were collected annually in every dry and rainy season in a seasonal tropical forest. We quantified the interspecific variation in the strength of CNDD and its temporal variation. We also examined potential correlates of this interspecific and temporal variation, including species functional traits (such as drought-tolerant traits, defense-related traits, and recourse acquisition traits) and species abundances. In the dry season, we found a negative relationship between the density of neighboring conspecific seedlings on seedling survival, while in the rainy season, there was a negative relationship between the density of neighboring conspecific adults on seedling survival. In addition, we found that interspecific variation in CNDD was related to drought-tolerant traits in the dry season but not in the rainy season. Across years, we found that drought-intolerant species suffer less CNDD during the dry seasons that have higher rainfall, whereas drought-tolerant species suffer less CNDD when the dry season has lower rainfall. We also found that rare species suffered stronger CNDD in the dry season. Overall, our study highlights that CNDD is highly variable among species and through time, necessitating a deeper appreciation of the environmental and functional contexts of CNDD and their interactions.

Xiaoyang Song and Masatoshi Katabuchi contributed equally to this work.

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conspecific negative density dependence, functional traits, intraspecific interaction, Janzen–Connell hypothesis, plant–plant interaction, seasonality, species diversity

INTRODUCTION

In any local community, the number of species that can coexist is influenced by several interacting mechanisms, including stabilizing forces that require species to have stronger negative interactions with their own species than with other species in order to counteract competitive exclusion and drift (Chesson, 2000). Such stabilizing factors can include interspecific differences in traits that influence a species' ability to acquire resources, fitness difference, or interact with enemies or mutualists (i.e., niche differences; Kraft et al., 2008). For example, spatial variation in the density of individuals within a species can lead to variation in their intensity of conspecific negative density dependence (CNDD), which in turn can allow several species to coexist even in the absence of explicit niche differences (Chesson, 2000; Wright, 2002). CNDD could reduce plant performance (growth, survival, and recruitment) under higher densities of conspecific neighbors. This was originally envisioned by the Janzen–Connell hypothesis (Connell, 1971; Janzen, 1970), which posits that spatial variations in species density influence the capacity of specialized natural enemies to locate and subsequently reduce the fitness of their target species. However, this concept has been expanded to include any form of spatial variation in fitness that arises from the consequences of CNDD (Hülsmann et al., 2021).

There is considerable evidence for CNDD in many types of systems, especially forests (Comita et al., 2014; Dirzo & Boege, 2008; Johnson et al., 2012; LaManna et al., 2017). However, just how important this CNDD is for the maintenance of diversity is more controversial (Cannon et al., 2021; Detto et al., 2019; Hülsmann et al., 2021; LaManna et al., 2021; May et al., 2020; Terborgh, 2020). Part of the reason for this controversy is that the strength of CNDD can vary dramatically among species and life stages (Comita et al., 2014; Song et al., 2021), as well as across environmental conditions that vary in space or time (Bachelot et al., 2015; Comita et al., 2009; Connell & Green, 2000; Kuang et al., 2017; LaManna et al., 2016; Metz et al., 2010; Suzuki et al., 2003).

Previous studies suggested that the interspecific variation in the strength of CNDD can either enhance or inhibit the maintenance of diversity in communities (Comita & Stump, 2020; Stump & Comita, 2018; Yenni et al., 2012). Several factors could contribute to the variation of CNDD among species in a community. First, the relative commonness or rarity of species can influence the strength of CNDD they experience (Comita et al., 2010; Zhu, Woodall, et al., 2015). Species that are inherently rarer at a given site may experience weaker CNDD than common species (Zhu, Woodall, et al., 2015), for example, if rarer species have fewer specialist enemies (Bachelot et al., 2016; Novotny et al., 2007), or are less likely to encounter conspecifics (Jiang et al., 2022). Alternatively, rarer species can suffer stronger CNDD than common species if they are more susceptible to enemies or intraspecific effects (Comita et al., 2010; Mangan et al., 2010). Second, differences among species in their functional traits can play an important role in driving interspecific variation in CNDD. If natural enemies mediate patterns of CNDD, traits associated with plant susceptibility such as nutritional quality (C:N), wood density, and secondary metabolites may help to explain interspecific variation in CNDD (Forrister et al., 2019; Umaña et al., 2018). Alternatively, if competitive processes mediate CNDD, resource acquisition traits that influence competitive ability might be more associated with the variation in CNDD among species. For example, drought tolerance traits, such as organic dry matter content, leaf thickness (LT), water use efficiency, leaf turgor loss point, and/or leaf water potential, may influence variation in CNDD when there is strong interspecific competition for water (O'Brien et al., 2017).

The strength of CNDD and its variation among species can also strongly vary with background environmental conditions that vary through time, such as the level of precipitation (Martini et al., 2021; Uriarte et al., 2018; Zambrano et al., 2017). In monsoon climates, seasonally variable precipitation could cause intra-annual variation in the strength of natural enemy damage and competition (Aide, 1992; Lin et al., 2012). For example, CNDD caused by natural enemies may occur mainly during the rainy season because the abundance and activity of herbivores and pathogens are positively correlated with temperature and humidity (Zheng et al., 2001). If CNDD results from the mechanism envisioned by Janzen (1970) that enemies of older individuals spill over to impact seedlings, we might expect a strong negative effect of neighboring adults on seedlings in the rainy season (Milici et al., 2020). Conspecific water competition, on the other hand, may increase in the dry season, leading to stronger CNDD from conspecific seedling neighbors with similar rooting depths (O'Brien et al., 2017), but potentially weaker CNDD effects from adult neighbors that harvest water from different soil depths (Song et al., 2022). Thus, we might expect CNDD to occur in rainy and dry seasons, but for different reasons.

Negative density dependence may also happen among phylogenetically related species (Paine et al., 2012). This is because phylogenetically related plant species often share more natural enemies that are not strictly host-specific and have similar recourse to acquisition strategies, resulting in stronger interspecific competition (Lebrija-Trejos et al., 2014; Liu et al., 2012; Paine et al., 2012). As a result, it is possible that patterns of heterospecific interactions could be better explained by metrics that incorporate phylogenetic similarity among neighbors rather than only species identity (Pu & Jin, 2018; Webb et al., 2006).

In this study, we took advantage of a long-term study on tree seedling dynamics in a permanent forest plot in a hyper-diverse seasonal tropical rainforest in Xishuangbanna, southwestern China (Cao et al., 2008). We investigate temporal and interspecific CNDD variation and examine whether this variation could be explained by plant functional traits and abundance. We hypothesize that CNDD mediated by natural enemies would have stronger effects in wetter years and wet seasons, and defense-related traits might influence variation in CNDD among species. In addition, we expect that CNDD mediated by intraspecific competition (water competition) might be stronger in drier years and in dry seasons, and the variation in CNDD among species might be explained by water acquisition traits. We also examine whether density-dependent patterns are influenced more by phylogenetically related neighbors. We expect that the phylogenetic relatedness of neighbors could better predict seedling demography than the effects of heterospecific neighbors, since related species often share natural enemies (Gilbert & Webb, 2007; Novotny et al., 2002) and have similar resource requirements (Gomez et al., 2010).

MATERIALS AND METHODS

Study site

Our study was conducted in the rainforest of Xishuangbanna, southwestern China (101°34′ E, 21°36′ N; Figure 1). This area is at the northern edge of the tropics with a mean annual temperature of 21.8°C and a strong monsoonal climate, with a rainy season from May to October and a dry season from November to April. In 2007, a 20-ha permanent plot was established at a protected site to monitor the spatial and temporal dynamics of the forest as part of a global network of forest plots using similar protocols (Feng et al., 2016). The plot was established following a standardized protocol (Condit, 1998) where all free-standing trees with ≥1 cm dbh were tagged and identified to the species level and monitored.

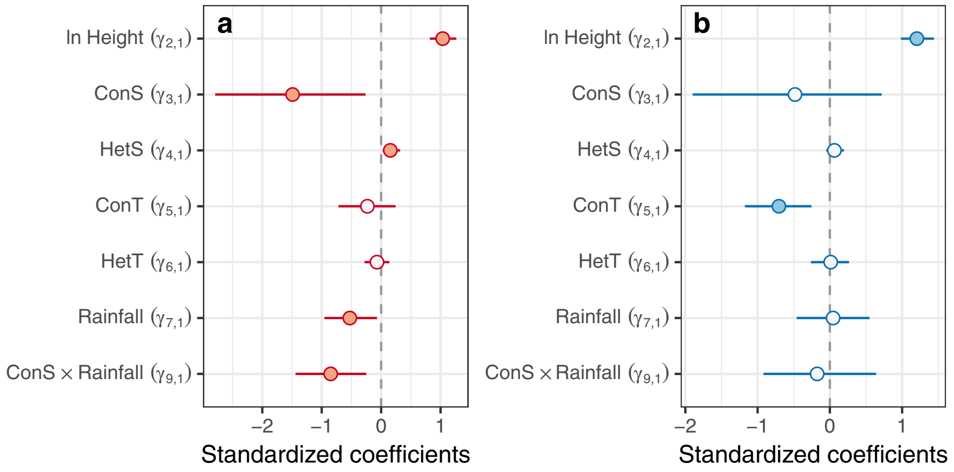

FIGURE 1 Standardized regression coefficients at the individual level ($\gamma_{k,1}$) modeling the effects of the best model in the dry (a) and rainy (b) seasons, reflecting community-level effects. Predictors included log of individual height (ln Height), conspecific seedling density (ConS), conspecific tree density (ConT), heterospecific seedling density (HetS), heterospecific tree density (HetT), rainfall, and interactions between densities and rainfall. Lines indicate 95% credible intervals and circles show posterior medians of coefficients. Filled circles indicate significant effects and open circles indicate non-significant effects. Positive $\gamma_{k,1}$ values indicate higher survival rates with increasing values of the predictors, while negative $\gamma_{k,1}$ values indicate lower survival rates with increasing values of the predictors. Note that predictors are scaled to a mean of 0 and a standard deviation of 1 within each season.

Measuring seedling dynamics

We monitored seed rain and seedling dynamics across the plot starting in November 2007 by establishing a total of 150 seed-trap and seedling monitoring stations using a stratified random design (avoiding streams and large rocks; Appendix S1: Figure S1). Each station consisted of a seed-trap (data not used here) and three 1 m × 1 m seedling plots that were positioned 2 m away from the seed trap in a triangle. In each seedling plot, we defined woody plants <1 cm dbh as seedlings which were then tagged, identified to the species level, and measured for height (from the ground to the highest apical bud). In each census period, we counted missing seedlings as dead and identified, counted, and tagged any new seedlings. Each year, we conducted seedling surveys at the end of the dry season (May) and at the end of the rainy season (November) for each of the 10 years included in this study (i.e., 20 census intervals from 2007 to 2017). All seedlings were included in our analyses. Seedlings that were monitored from May to October were defined as the survival status in the rainy season, and seedlings monitored from November to April of the next year were defined as the survival status in the dry season. The alive and dead individuals were recorded as 1 and 0, respectively.

Seasonal rainfall measurement

The monthly rainfall data from 2007 to 2018 were obtained from the Mengla County Meteorological Bureau (approximately 14 km from the plot). For each year, we calculated the total rainfall in each season, where May to October was defined as the rainy season and November to April of the next year was defined as the dry season (Appendix S1: Figure S2).

Functional traits of tree seedlings

We quantified several functional traits for all species encountered in this study in November 2019 using standard methodologies for plant trait measurements (Poorter & Markesteijn, 2008). For each species, we searched the area surrounding the forest plot and selected three seedlings <50 cm in height, excluding cotyledons, to harvest the aboveground parts for trait measurements. We measured LT with a micrometer. We divided harvested seedlings into stem and leaves and weighed the fresh mass of each. We scanned all leaves using a digital scanner (Canon 5600F Canon Inc., Tokyo, Japan), and determined individual leaf area (LA; in square centimeters) using the R package *LeafArea* (Katabuchi, 2017). Next, we dried stems and leaves from each seedling for 48 h at 65°C and then weighed each component to calculate the leaf and stem dry matter content (LDMC and SDMC 100 × dry mass per unit fresh mass; in percentage). We calculated stem density (SD; in grams per cubic centimeter) as the ratio of wood dry mass to fresh volume using the water displacement method (Perez et al., 2020), as well as the specific leaf area (SLA; LA/unit dry leaf mass; in square meters per kilogram). We measured stable carbon isotope composition (δC_{13}; in per-mille) with an isotope ratio mass spectrometer (DELTA V Advantage, Thermo Fisher Scientific, Inc., Bremen). We measured osmotic potential (π_{osm}; in micromoles per liter) with a VAPRO 5560 vapor pressure osmometer (Wescor, Logan, UT) from which we calculated the leaf turgor loss point (π_{tlp}; in micromoles per liter) following Bartlett et al. (2012). We measured carbon (C) and nitrogen (N) concentration (in milligrams per gram) with a Dumas-type combustion C–N elemental analyzer (Vario MAX CN, Elementar Analysensysteme GmbH, Hanau, Germany) from which we also calculated the carbon-to-nitrogen ratio (C:N). We only kept the functional traits that had correlation coefficients less than 0.7 in the subsequent models. Because we found that SDMC and SD were highly correlated, as were N and CN (Appendix S1: Figure S3), we only included SDMC and N in the following analyses. We averaged all trait data at the species level for analyses. We also conducted principal components analysis (PCA), selecting the first and second PCA components to represent the variation of functional traits.

Phylogeny and phylogenetic similarity

We used the R package *V.PhyloMaker* (Jin & Qian, 2019) to generate phylogenetic trees (PhyT) for the species list in our plot. Following the BLADJ algorithm approach, we constructed the PhyT after assigning species to the appropriate family or genus (see more detail in *V.PhyloMaker* package; Jin & Qian, 2019). From this PhyT, we calculated the phylogenetic relatedness of each pair of species (Garland & Ives, 2000) using the R package *ape* (Paradis et al., 2004).

Abundance calculations

We calculated two different abundance indices: the total individual number of each tree species and the total basal area of each tree species in the whole plot (Comita et al., 2010; LaManna et al., 2016).

Neighbor density calculations

We calculated six density parameters to quantify aspects of the local neighborhood. For seedlings, we calculated the densities of conspecific seedlings (ConS) and heterospecific seedlings (HetS) in each of the 1-m^2 seedling plots (Figure 1). We calculated the phylogenetic relatedness weighted densities of HetS neighbors as the phylogenetic seedlingneighborhood density. We also calculated the neighborhood density of larger conspecific trees (ConT) and heterospecific trees (HetT) (i.e., individuals with a diameter >1 cm) as the total distance-weighted basal area of conspecific and HetT that were found within a 20-m radius of each seed trap. We selected a 20-m radius based on previous neighborhood modeling studies in the same plot (Song et al., 2020; Wu et al., 2016). We divided the basal area of each tree by the distance between the tree and the center of the seed trap (Canham et al., 2004). We also calculated the PhyT neighborhood density by including the phylogenetic relatedness of each HetT to the focal individuals (Pu & Jin, 2018).

$$\mathrm{ConT} = \sum_{i}^{N} \left(\mathrm{conspecificBA}_i / \mathrm{Distance}_i\right) \tag{1}$$

$$\mathrm{HetT} = \sum_{i}^{N} \left(\mathrm{heterospecificBA}_i / \mathrm{Distance}_i\right) \tag{2}$$

$$\mathrm{PhyT} = \sum_{i}^{N} \left(\mathrm{phylogeneticrelatedness} \times \mathrm{heterospecificBA}_i / \mathrm{Distance}_i\right) \tag{3}$$

where i is a ConT or HetT individual found within the 20-m radius.

We excluded data collected from seedling plots that were within 20 m of the edge of the plot (66 of the 450 seedling plots). For analyses, we only included species that had more than 50 records during the study period. We also calculated the correlation between phylogenetic and non-phylogenetic-weighted neighbor densities.

Survival models

We first modeled seedling survival at the individual level to assess whether neighbor densities have different effects between the dry and rainy seasons and whether phylogenetic-weighted neighbor densities affect seedling survival differently compared with the heterospecific neighbor densities. We found strong positive correlations between heterospecific neighbor densities and phylogenetic-weighted neighbor densities (Appendix S1: Figure S5). Thus, the effects of phylogenetic-weighted neighbor densities and heterospecific neighbors on seedling survival were comparable (Appendix S1: Table S1). We also detected seasonal interactions with neighbor densities (Appendix S1: Table S1). Based on these findings, we will focus on heterospecific neighbor density in our subsequent trait-mediated survival models for each season separately to maintain model simplicity. These preliminary models also incorporated a scaling parameter c to account for nonlinear effects on a logistic scale (see *Traits and abundance-mediated survival models*).

Trait- and abundance-mediated survival models

Since the effect of tree neighbors on seedling survival is nonlinear on a logistic scale (Detto et al., 2019), we performed a grid search for the scaling parameter c between 0 and 1 in 0.01 increments that maximized the likelihood of the following survival model,

$$\mathrm{logit}(p_i) = b_0 + b_1 Z_{1i}^c + b_2 Z_{2i}^c \tag{4}$$

where p_i is the survival probability of the ith individual, and Z_1 and Z_2 are distance-weighted sums of the basal areas of conspecifics and heterospecifics (or phylogenetic neighbors), respectively (Appendix S1: Figure S4). We found the best estimates of c to be 0.27 for the dry season, 0.24 for the rainy season, and 0.26 for the combined analysis of both seasons (Appendix S1: Figure S1).

We built Bayesian hierarchical models to estimate the effect of functional traits and abundance on interspecific CNDD. Survival (s) of seedling record i of individual m for species j in census t in plot p in seedling station s was modeled using the Bernoulli distribution ($\mathcal{B}$):

$$s_{i,j,m,s,t,p} \sim \mathcal{B}\left(p_{i,j,m,s,t,p}\right) \tag{5}$$

$$\mathrm{logit}\left(p_{i,j,m,s,t,p}\right) = \boldsymbol{x_i} \cdot \boldsymbol{\beta_j} + \eta_m + \phi_s + \psi_p + \xi_t \tag{6}$$

where $\boldsymbol{\beta_j} = \left[\beta_{1,j}, \beta_{2,j}, \ldots, \beta_{K,j}\right]$ is the coefficient row K-vector for species j, K is the number of predictors for an individual seedling, $\boldsymbol{x_i} = \left[x_{i,1}, x_{i,2}, \ldots, x_{i,K}\right]$ is the vector of predictors of size K for an individual seedling, η_m is the random effect for seedling individual, ϕ_s is the random effect for seedling plots, ψ_p is the random effect for seedling stations, and ξ_t is the random effect for different censuses (note that · denotes dot product). The set of predictor variables ($\boldsymbol{x_i}$) includes intercepts, log of seedling heights, rainfall, densities of HetA trees that are scaled by 0.27 for the dry season or 0.24 for the rainy season, and the interactions of rains with ConS, with HetS, with ConA, and with HetA. We also considered models with phylogenetic density effects instead of heterospecific density effects.

In the species-level regression, the coefficients ($\boldsymbol{\beta_{1-K}}$) of each species j were assumed to have a multivariate normal distribution (MVN),

$$\boldsymbol{\beta_j} \sim \mathrm{MVN}\left(\boldsymbol{\gamma_k} \times \boldsymbol{u_j}, \boldsymbol{\Sigma}\right) \tag{7}$$

where $\boldsymbol{u_j} = \left[u_{1,j}, u_{2,j}, \ldots, u_{L,j}\right]$ is the row vector of predictors of size L for species j, L is the number of predictors for each species (i.e., the number of traits including an intercept), $\boldsymbol{\gamma_k} = \left[\gamma_{k,1}, \gamma_{k,2}, \ldots, \gamma_{k,L}\right]$ is the coefficient L-vector for the kth predictor in the individual-level regression, and $\boldsymbol{\Sigma}$ is the covariance matrix of the multivariate normal distribution. We modeled four different sets of species-level predictors separately. The set of species-level predictor variables ($\boldsymbol{u_j}$) includes (1) LDMC, SDMC, LA, SLA, LT, δC_{13}, C, N, and π_{tlp}, (2) principal components of the traits (PC1 and PC2), (3) abundance (number of individuals), or (4) basal area. The row vector $\gamma_{k,1}$ represents the average effects of each individual-level predictor (e.g., ConS) across species (i.e., community-level effects), whereas $\gamma_{k,l}$ ($l \neq 1$) represents the effects of the l-th individual-level predictor (e.g., SLA) on the variation in the strength of each individual-level predictor (e.g., variation in the strength of ConS among species). To allow comparisons among parameter estimates, the individual-level predictors ($\boldsymbol{x_i}$) and the species-level predictors ($\boldsymbol{u_j}$) were scaled to a mean of 0 and a standard deviation of 1 within each season and across species, respectively. We compute approximate leave-one-out cross-validation information criterion and expected log-predictive density for the models (Vehtari et al., 2017) to determine whether including the interaction with rainfall could provide a better predictive performance. The complete model details, including the Cholesky factorization and prior information, are provided in Appendix S1.

We estimated posterior distributions of all parameters using the Hamiltonian Monte Carlo (HMC) algorithm implemented in Stan (Carpenter et al., 2017) with weakly informative priors (Gelman et al., 2008). The HMC algorithm uses gradient information to propose new states in the Markov chain, leading to a more efficient exploration of the target distribution than traditional Markov chain Monte Carlo (MCMC) methods that rely on random proposals (Carpenter et al., 2017). This efficiency allows us to achieve convergence with fewer iterations than traditional MCMC methods. Four independent chains were run for 2000 iterations for each model with a warm-up of 1000 iterations. Convergence of the posterior distribution was assessed using the Gelman–Rubin statistic with a convergence threshold of 1.1 (Gelman et al., 2013), ensuring effective sample sizes greater than 400 (Vehtari et al., 2021), and by monitoring divergent transitions (Betancourt, 2016) for all parameters.

All statistical analyses were conducted in R version 4.3.1 (R Core Team, 2022) using the R package *targets* version 1.3.2 for workflow management (Landau, 2021).

RESULTS

We analyzed data from 9949 individuals across 73 species, totaling 54,280 observations. The abundance of seedlings was 2831.4 ± 990.9 (mean ± SD) in the dry season and 2596 ± 644.7 in the rainy season, excluding new recruitments. The survival rate was 0.872 ± 0.050 in the dry season and 0.878 ± 0.038 in the rainy season. There was no significant difference in seedling survival rate between the seasons ($F = 0.085$, $p = 0.774$).

We found a significant interaction between conspecific neighbor densities and seasons (Appendix S1: Table S1). Specifically, the strength of the CNDD effect caused by conspecific seedling density in the dry season was significantly stronger than in the rainy season. Moreover, the effect size of heterospecific neighbor densities is similar to the phylogenetic-weighted neighbor densities (Appendix S1: Table S1).

We evaluated four distinct models to determine the influence of rainfall and species-level predictors on the strength of CNDD effects. The best PCA model included all interactions with rainfall (Appendix S1: Tables S2 and S3). In contrast, the best multiple traits model included only the interaction between conspecific seedling density and rainfall for both the dry and rainy seasons (Appendix S1: Tables S2 and S3). The best models for both abundance and basal area models consistently included all interactions between neighbor densities and rainfall for both seasons (Appendix S1: Tables S4 and S5).

Overall, seedling height had a positive effect on seedling survival in both the dry and rainy seasons. On the other hand, the neighborhood factors that correlated with seedling survival changed between the dry and rainy seasons (Figure 1). In the dry season, we found a negative effect of conspecific seedling density on the survival of focal seedlings but no effect of conspecific tree density on focal seedling survival (Figure 1a). We also found a positive effect of HetS density on seedling survival and a significant negative effect of rainfall and the interaction between conspecific seedling density and rainfall

(Figure 1a). During the rainy season, seedling survival was not influenced by conspecific seedling density, but was negatively affected by conspecific tree density (Figure 1b).

When we used PCA values as species-level predictors, we found that PC values had less predictive capacity for the species-specific coefficient of conspecific neighbor densities in both the dry and rainy seasons (Appendix S1: Tables S6 and S7).

When we used traits as species-level predictors, we found that SDMC was positively correlated with the species-specific coefficient of conspecific seedling density in the dry season (Figure 2a, Appendix S1: Table S8). Furthermore, several functional traits were correlated with the interaction between conspecific seedling density and temporal variation in rainfall during the dry season. Specifically, LDMC, LT, and δC_{13} were negatively, and π_{tlp} was positively, correlated with the species-specific interaction coefficient between conspecific tree density and rainfall (Appendix S1: Table S8). That is, compared with the lower densities of conspecifics, when surrounding higher densities of conspecifics, species with lower LDMC, LT, and δC_{13} values, and higher π_{tlp} values, had higher survival when rainfall increased in the dry season (Figure 3a,c,e,g). By comparison, the survival of species with opposite traits had lower survival when rainfall increased in the dry season (Figure 3b,d,f,h). Furthermore, we found that LDMC, LT, SLA, and δC_{13} were significantly negatively correlated with the species-specific coefficient of rainfall in the dry season (Appendix S1: Table S8). That is, species with lower LDMC, LT, SLA, and δC_{13} values had increased survival at high rainfall levels (Figure 3a,c,e,g), but species with higher LDMC, LT, SLA, and δC_{13} values had decreased survival at high rainfall levels (Figure 3b,d,f,h). A positive correlation was also found between SDMC and the species-specific coefficient of rainfall in the dry season (Appendix S1: Table S8). However, we found no relationships between functional traits and conspecific densities in the rainy season (Appendix S1: Table S9). Leaf nitrogen content and π_{tlp} were positively correlated with the species-specific interaction coefficient between conspecific tree density and rainfall (Appendix S1: Figure S7 and Table S9).

We found that species abundance was positively correlated with the species-specific coefficients of conspecific seedling density (Figure 2b), and negatively correlated with the interaction between conspecific tree density and rainfall during the dry season (Appendix S1: Table S10). We did not find any significant correlation between species abundance and conspecific neighbor densities in the rainy season (Appendix S1: Table S11).

DISCUSSION

CNDD is a frequently observed phenomenon in plant communities that has long been implicated as an important mechanism underlying the maintenance of species diversity, particularly in highly diverse communities.

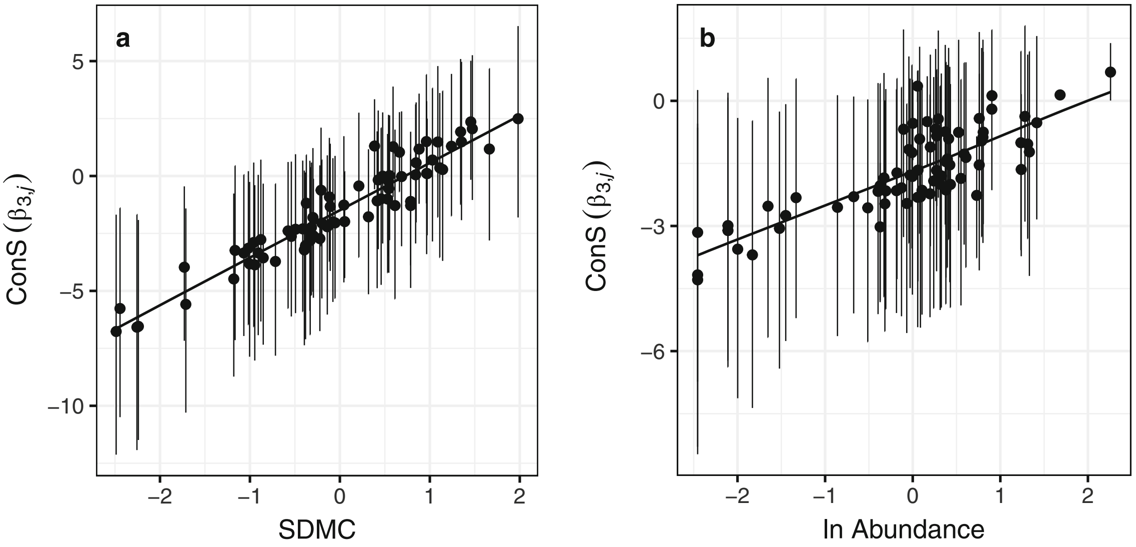

FIGURE 2 Predicted relationships during the dry seasons between the effects of conspecific seedling density (ConS) on seedling survival and (a) stem dry matter content (SDMC); (b) logarithm of abundance. The strength of the conspecific negative density dependence (CNDD) effect caused by conspecific seedling density declined significantly with increased SDMC and abundance (with positive ConS values indicating weaker CNDD). The line represents the predicted median of the relationship, the points show partial residuals of ConS for each species, and the vertical bars indicate 95% CIs (for detailed parameter estimates, see Appendix S1: Tables S8 and S10).

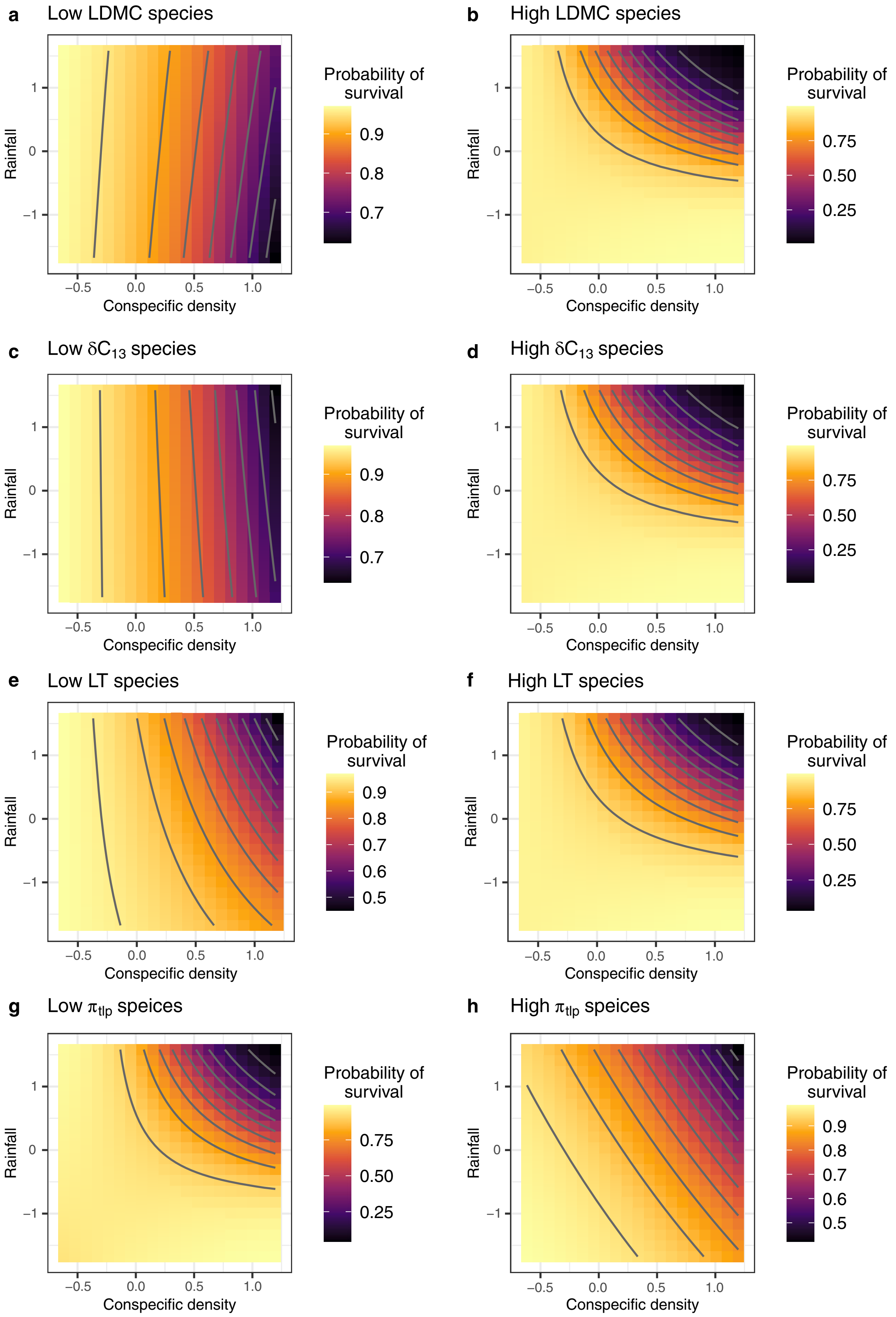

FIGURE 3 Legend on next page.

However, the strengths of CNDD can be highly variable among species, specifically those differing in traits and relative abundances, as well as through time as environmental conditions vary. Here, we took advantage of a long-term study on tree seedling survival in a hyper-diverse tropical forest to quantify the variation in the strength of CNDD across species with a wide range of functional traits related to enemy defense and resource acquisition, as well as through time within and among years. We found that when water resources are scarce (i.e., during the dry season), the reduced survival rates for seedlings are largely because of neighboring conspecific seedlings, and the degree of CNDD is reduced in species with higher stem dry mass. However, when resources are abundant (i.e., the rainy season), CNDD experienced by seedlings is largely due to neighboring adults rather than seedlings, and is less strongly related to species traits. Lastly, we found that interannual variation in rainfall influenced how species with different drought-related traits experienced CNDD, particularly in the dry season.

Seasonal variation in the strengths of CNDD

Overall, we found a negative correlation between conspecific neighbor density and seedling survival, indicating that CNDD is common in this forest community and consistent with studies in other systems (Comita et al., 2010; Hülsmann et al., 2021; LaManna et al., 2021). However, we propose that the mechanisms that drive CNDD may be different between the dry and rainy seasons. In the dry season, seedling survival was related to neighboring conspecific seedlings but not adult densities. We suspect that this pattern might arise because intraspecific competition among seedlings with similar resource requirements and acquisition strategies is expected to be high (Meinzer et al., 1999; O'Brien et al., 2017), whereas larger trees have access to deeper water sources so that they compete less with seedlings for water and other resources (Song et al., 2022). In the rainy season, however, the density of larger conspecifics was more important for CNDD in seedlings, possibly coinciding with seasonal variation in natural enemy pressure. Dry seasons in tropical forests tend to have lower herbivory (Aide, 1992; Coley & Barone, 1996; Wright, 1996) and pathogen infection rate and pathogenicity (Liu & He, 2019; Milici et al., 2020) compared with wetter seasons. This is consistent with the Janzen–Connell (Connell, 1971; Janzen, 1970) perspective on CNDD, where natural enemies on larger adult trees have negative impacts on neighboring seedlings during the rainy season. Thus, this change from seedling- to adult-induced CNDD from dry to rainy seasons may indicate a shift in the mechanism driving CNDD from intraspecific competition to natural enemy pressure.

We also found evidence for heterospecific positive density dependence for seedling survival in the dry season but not in the rainy season. A possible reason for the positive associations between heterospecific densities and seedling survival in the dry season could be explained by hydraulic niche partitioning among species (Fichtner et al., 2020). In addition, consistent with previous studies in this forest and similar forests, the survival model based on heterospecific density alone and the survival model incorporating phylogenetic information yielded very similar results, indicating that replacing heterospecific densities with phylogenetic densities does not improve survival models (Wu et al., 2016; Zhu, Comita, et al., 2015). While phylogenetically related species may have more distinct defenses and natural enemies than expected (Forrister et al., 2019; Sedio et al., 2018), the strong correlations between phylogenetic and non-phylogenetic-weighted neighbor densities (Appendix S1: Table S1) lead to less phylogenetic negative density dependence in these tropical forests.

Functional traits and interspecific CNDD

A strong correlation between SDMC and interspecific variation in CNDD strength (Figure 2a) is likely related to how SDMC and related traits influence both drought tolerance and pathogen resistance. Specifically, species with high SDMC have dense tissues with smaller vessel lumen area and lower xylem conductance (Chave et al., 2009), which is associated with conservative functional economies and higher drought tolerance (Markesteijn &

FIGURE 3 Contour plots illustrating interactions between conspecific seedling densities and rainfall on seedling survival rates in the dry seasons and their association with functional traits: (a, b) leaf dry matter content (LDMC), (c, d) leaf thickness (LT), (e, f) stable carbon isotope composition (δC_{13}), and (g, h) leaf turgor loss point (π_{tlp}). The predicted result was generated from the best model in the dry season. Color scales show marginal estimated median predictions for each response variable across the full range of rainfall and upper 90% quantiles of conspecific seedling density (the distributions of conspecific seedling densities are positively skewed). All other variables were set at their mean value for marginal predictions. Low and high trait values indicate 25% and 75% quantiles of the trait distribution in the observed dataset, respectively. Only variables with credible intervals not overlapping 0 are plotted.

Poorter, 2009; Poorter & Markesteijn, 2008), as well as potentially higher resistance to stem rot and pathogens (Augspurger, 1984). As a result, we suspect that high SDMC species were less susceptible to CNDD because they were less susceptible to water competition and enemies.

We also found variation in the strength of CNDD in response to changes in precipitation within the dry seasons (Figure 1a, Appendix S1: Table S8). Specifically, when there was less rainfall during the dry season, drought-intolerant species with acquisitive functional strategies (i.e., those with low δC_{13}, LDMC, LT, and high π_{tlp} values) tended to experience stronger CNDD. In contrast, drought-tolerant species with the opposite traits tended to experience less CNDD. The stronger CNDD for drought-intolerant species in the drier dry seasons was likely because less water availability during the drier dry season led to an increase in mortality caused by intraspecific competition (O'Brien et al., 2017), which would favor drought-tolerant species. In addition, when conditions were drier during the dry season, this can lead to lower resistance to natural enemies of drought-intolerant species (Desprez-Loustau et al., 2006; Jactel et al., 2012), which could also increase CNDD mortality for drought-intolerant species. These results underscore the importance of considering both seasonal and long-term variations to gain a more comprehensive understanding of the relationship between species traits and the strengths of CNDD.

Drought-intolerant species had lower seedling survival than more drought-tolerant species during the drier dry seasons. Additionally, interspecific CNDD varied with rainfall levels. These findings suggest that fluctuations in rainfall, both within and between years, likely play an important role in promoting species coexistence and biodiversity in this forest. Furthermore, given the potential for many such forests to experience higher levels of drought and precipitation variation in future climate scenarios (Brodribb et al., 2020), we might speculate that drought-tolerant species may benefit not only because of their drought resistance but also because they are less sensitive to CNDD.

None of the traits we analyzed showed associations with CNDD in the rainy season (Appendix S1: Table S9). There are at least two likely reasons for this. First, as we showed in this study and a previous study (Lin et al., 2012), the interspecific variation in CNDD in the rainy season is too small to detect associations with traits. Second, we did not include traits associated with chemical defenses that may be more likely to deter enemies in the rainy season (Aide, 1992; Milici et al., 2020). Future research focusing on plant defense traits, for example, by measuring ecometabolomics (Walker et al., 2022), may be useful for better understanding the role of chemical defense traits in moderating patterns of CNDD.

Abundance and interspecific CNDD

Our findings also contribute to accumulating evidence regarding the correlations between CNDD and species abundances. We found a significant positive correlation between the CNDD and the abundances of species in the dry season (Figure 2b), consistent with studies that found stronger CNDD effects in rare species (Comita et al., 2010; Johnson et al., 2012; LaManna et al., 2017; Mangan et al., 2010). However, our results are inconsistent with studies from other forests that showed no relationships between CNDD and species abundance (Chen et al., 2019; Metz et al., 2010; Murphy et al., 2017), or stronger CNDD effects in common species (Bagchi et al., 2014; Zhu, Woodall, et al., 2015). Our result was also in line with a previous study in our system, which reported a negative correlation between the strength of CNDD effect and species abundance in a 2-year study interval (Lin et al., 2012). Although conspecific tree densities alone did not significantly reduce seedling survival rates, rare species experienced higher mortality rates when surrounded by more conspecific tree neighbors during the drier dry seasons (Appendix S1: Table S10). These results suggest that rare species may experience more disadvantages during drought. A recent study also suggested that rare and less common species suffered stronger CNDD effects in tropical forests worldwide, which could lead to greater stabilization of tropical tree communities through more robust regulation of species abundances and help maintain the high local diversity in tropical forests (Hülsmann et al., 2024).

CONCLUSION

We have demonstrated that CNDD, a mechanism proposed to be critical for species coexistence and the maintenance of diversity, varies considerably among species with different water-acquisition-related traits and in response to within- and among-year variations in precipitation. Specifically, we have shown that neighboring seedlings drive CNDD during the dry season while neighboring adults drive CNDD during the rainy season. This result suggests that patterns of CNDD cannot be attributed to a single mechanism or driver over time. Furthermore, we found that interspecific variation in CNDD and their variation with rainfall was related to differences in drought tolerance traits among species. Rare species suffered a stronger CNDD effect than common species, particularly during the dry season. In summary, while CNDD likely plays an important role in regulating populations and promoting coexistence in tropical rainforests, the drivers of this mechanism depend on background climate (e.g., precipitation) and the traits that determine how species respond to drought. Such interactions will likely become increasingly important as variable rainfall regimes and extreme drought threaten global forests with ongoing climate change (Brodribb et al., 2020).

AUTHOR CONTRIBUTIONS

Xiaoyang Song, Min Cao, and Jie Yang designed the study. Xiaoyang Song, Wenfu Zhang, and Xiaobao Deng collected data. Xiaoyang Song and Masatoshi Katabuchi performed the analyses. Xiaoyang Song, Masatoshi Katabuchi, Jonathan M. Chase, Daniel J. Johnson, and Jie Yang led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Song et al. 2024) are available in Science Data Bank at https://doi.org/10.57760/sciencedb.02276.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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