COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Conspecific negative density dependence in rainy season enhanced seedling diversity across habitats in a tropical forest

Xiaoyang Song[1,2] · Wenfu Zhang[1] · Daniel J. Johnson[3] · Jie Yang[1,4] · Mengesha Asefa[1] · Xiaobao Deng[1] · Xiaofei Yang[1] · Min Cao[1]

Abstract

Conspecific negative density dependence (CNDD) could be one of the most important local-scale mechanisms shaping plant species coexistence. However, the spatial and temporal changes in the strength CNDD and the implications for the plant diversity remain unknown. We used 10 years of seedling data, in a seasonal tropical rainforest, to discover how CNDD influences tree seedling survival across habitats and seasons. We also evaluated the relation between CNDD and species diversity. We found the strength of CNDD in the valley habitat was significantly stronger than in ridge habitat in rainy season, but not significantly different in dry season. Corresponding to expectations of CNDD as mechanism of diversity maintenance, seedling species diversity was significantly higher in valley habitat than in ridge habitat and significantly correlated with CNDD. Additionally, conspecific and heterospecific seedling neighbour densities positively affected the survival of tree seedlings, but heterospecific adult neighbour density had a weak effect. Our study finds that CNDD varied significantly across habitats and was correlated with local seedling diversity. Our results highlight the importance of CNDD in driving species diversity at the local scale. Recognizing the spatial and temporal variation in the strength of CNDD will aid efforts to model and understand species coexistence.

Keywords Intraspecific · Janzen–Connell hypothesis · Plant–soil feedback · Plant–plant interaction · Species diversity

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✉ Jie Yang
  yangjie@xtbg.org.cn

1 CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, Yunnan, China

2 Center of Conservation Biology, Core Botanical Gardens, Chinese Academy of Sciences, Mengla 666303, China

3 School of Forest Resources and Conservation, University of Florida, Gainesville, FL, USA

4 Center of Plant Ecology, Core Botanical Gardens, Chinese Academy of Sciences, Mengla 666303, China

Introduction

Conspecific negative density dependence is a key mechanism that drives community assembly in tropical forests (Wright 2002; Comita et al. 2010; Forrister et al. 2019). Seedling survival tends to be lower under higher densities of conspecific neighbours, but greater when further away from conspecific trees which provide opportunities for other species to establish near species experiencing strong negative density-dependent mortality (Janzen 1970; Connell 1971). Many studies have demonstrated the existence of CNDD at both community and species level (Carson et al. 2008; Comita et al. 2014), while few studies explicitly link the CNDD to community structure (Comita et al. 2010) and plant diversity (Harms et al. 2000; Johnson et al. 2012; LaManna et al. 2017).

Conspecific negative density dependence (CNDD) can be driven by two important mechanisms: intraspecific competition or/and natural enemies. Strong intraspecific competition for limited resources could result in density-dependent patterns, especially the asymmetric competition

from conspecific adults (Chesson 2000). Meanwhile, dense conspecific neighbours could cause high damage/mortality by attracting more host-specific herbivores and pathogens (Janzen 1970; Connell 1971; Forrister et al. 2019). Both mechanisms could be influenced by abiotic factors, such as seasonality, temperature and soil moisture (Dirzo and Boege 2008; O'Brien et al. 2017; Song et al. 2018b), and the changing of abiotic factors may either enhance or diminish the strength of CNDD (Wu et al. 2016). For example, a global meta-analysis found that the strength of CNDD in experimental conditions increased with precipitation, suggesting that humidity or water availability positively related to the strength of CNDD (Comita et al. 2014). The variation in abiotic conditions may change the strength of CNDD effect significantly by altering the intraspecific competition and natural enemy abundance; thus, it is important to study the spatial and temporal variation of CNDD effect to better understand the community assembly and species coexistence under climate change.

The spatial variance in strength of CNDD could be found with the changing of abiotic habitat (LaManna et al. 2016; Johnson et al. 2017). As the activity of natural enemies is stronger under humid conditions, plants in the wetter habitat may suffer stronger CNDD effect (Spear et al. 2015; LaManna et al. 2016). For instance, an irrigation experiment suggested host-specific pathogens caused more virulent disease in wet than in dry conditions (Hossain et al. 2019). In contrast, another manipulated experiment suggested drought-stimulated stronger intraspecific competition among plants (O'Brien et al. 2017), which suggests that CNDD from intraspecific competition could be stronger in dry conditions. This complexity highlights the need to assess how a rigorously calculated the strength of CNDD interacts with abiotic factors and the implications for community assembly and plant diversity. At a local scale, topography integrates multiple environmental gradients including water availability and edaphic characteristics into one general categorical variable providing a grouping variable to study the response CNDD effect to abiotic factors.

In monsoonal climates, the strength of CNDD could be either higher in rainy season or in dry season according to different situations. Population size and activity of species-specific herbivores and pathogens can be positively correlated to higher temperature and humidity in the rainy season (Aide 1992; Coley 1998; Leigh et al. 2004; Brenes-Arguedas et al. 2009; Swinfield et al. 2012). The fluctuations in populations of natural enemies (such as specialized herbivores and pathogens) between seasons could lead to strong temporal variability in the strength of CNDD mortality. In contrast, extreme climatic events, such as drought, may increase intraspecific competition for water and associated soil nutrients (Sterck et al. 2011; O'Brien et al. 2017). For instance, conspecific seedling neighbours caused higher

density-dependent mortality in dry season than in the rainy season in a two-year interval study in a Chinese seasonal tropical rainforest (Lin et al. 2012). However, the temporal variance of CNDD remains relatively unexamined. Moreover, issues of methodological bias have been raised with studies of density dependence (Detto et al. 2019), resulting in questions about the strength and importance CNDD in natural communities which we address in our methodology.

In this study, using a long-term dataset spanning 10 years, we aim to address the uncertainty of spatial and temporal variation in CNDD in a tropical forest and the spatial pattern of species diversity at local scale in southwest China. Particularly, we focus on two questions: (Q1) whether conspecific negative density dependence affects seedling survival of woody species, if so, does the strength of CNDD change among habitat and season? (Q2) How does the strength of CNDD relate to the local species diversity patterns? We hypothesize that (H1), the survival of seedlings, will be significantly affected by CNDD, and topography and season will interact to significantly alter the strength of conspecific neighbour density on seedling survival, and (H2), the species diversity, would vary among topographic position and would increase with the strength of CNDD effect.

Materials and methods

Study site

The study was conducted in a seasonal tropical rainforest in Xishuangbanna, southwestern China (101° 34′ E, 21° 36′ N). This area is situated in the northern edge of tropics with mean annual temperature 21.8 °C, and a strong monsoonal climate, with a rainy season from May to October and a dry season from November to April (Cao et al. 2006). Based on the record at the National Forest Ecosystem Research Station in Xishuangbanna, during the study period (2007–2017), annual precipitation averaged 1275.2 ± 75.99 mm with about 80% occurring during the rainy season (Fig. S1). The rainfall during our census years was relatively uniform and there was no obvious extremely dry or wet seasons.

A 20 ha permanent plot was established in 2007 in Xishuangbanna to monitor the spatial and temporal dynamics of the forest based on a standardized protocol (Condit 1998). All free-standing trees with ≥ 1 cm diameter at breast height (DBH), were tagged and identified to species level. In November 2007, a total of 150 seed-trap stations were established in the plot in a stratified random arrangement to monitor the seed rain and seedlings in time and space, streams and boulders were avoided (Fig. 1). Each seed-trap station consisted of a seed-trap and three 1-m² seedling plots positioned 2 m away from the sides of the seed trap. In each seedling plot, free-standing woody plants < 1 cm DBH
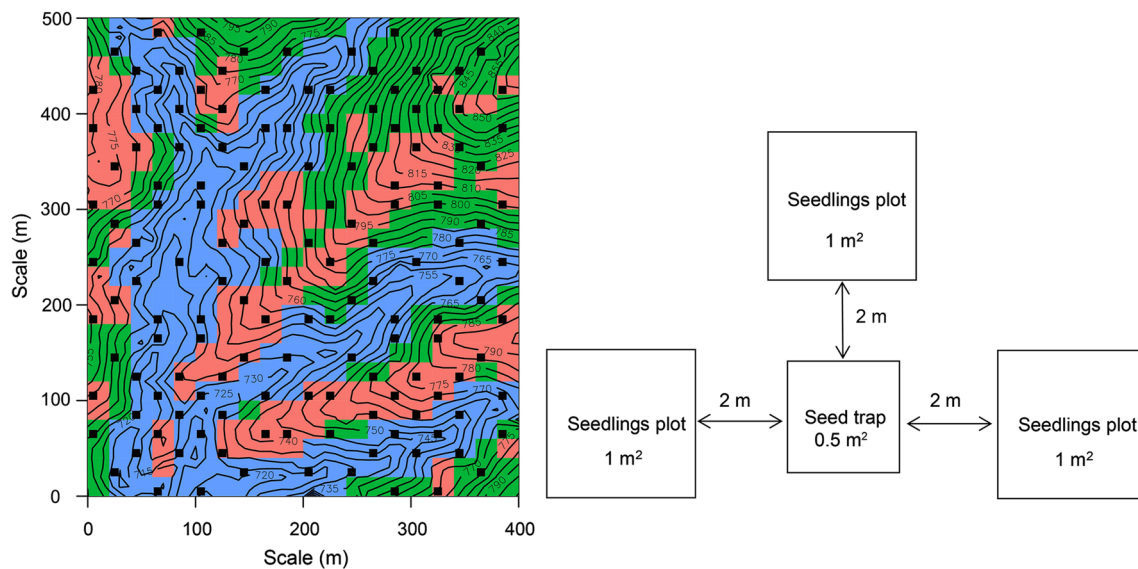
Fig. 1 Distribution and layout of seed traps in the 20 ha plot. The left panel is the topographic map of the 20-ha plot and right panel is the components of a census station. The numbers in the contour map are elevation (m) and the squares represent the locations of the 150 seed traps. Red, green and blue represent ridge (47 seed traps with 138 seedling plots), slope (39 seed traps with 117 seedling plots) and valley (64 seed traps with 192 seedling plots) habitat types, respectively. Each of the three 1-m² seedling plots is 2 m away from the central seed trap

were defined as seedlings and were tagged and identified to species level. Height of each seedling was measured from the ground to the apical bud. The first seedling survey was carried out in November 2007. We conducted subsequent surveys at the end of dry season (May) and at the end of rainy season (November) of the following years (20 census intervals). In this study, we analysed the seedling data collected from November 2007 to November 2017. We defined the data obtained in May as the dry season data, and the data obtained in November as the rainy season data.

Topography habitats division

The 20 ha plot was divided into 500 quadrats, 20 m × 20 m. For each 400 m² quadrat, elevation was calculated as the mean of the elevation at its four corners. Slope was the mean angular deviation from the horizontal of each of the four triangular planes formed by connecting three corners at a time. Convexity was calculated as the difference between the mean elevation of the focal quadrat and the mean elevation of the eight surrounding quadrats. For edge quadrats, convexity was calculated as the difference between the elevation of the focal quadrat center and the mean elevation of the four corners. Each quadrat was assigned to a habitat category based on its topographic attributes, elevation, slope and convexity from a previous study of the site (Zhang et al. 2017). Using thresholds of 779.8 m for elevation, 27.14° for slope (the median value of elevation and slope in the plot) and zero for convexity,

the 500 quadrats, were classified in three topographic habitats (ridge, slope and valley; Fig. 1 and Table S1).

Neighbour density calculations

We calculated four density parameters to quantify various aspects of local neighbourhood effects. We treated heterospecific species as equivalent because previous studies have suggested the effect of phylogenetic-related neighbour density on seedling survival is limited (Zhu et al. 2015; Wu et al. 2016). For seedlings, we calculated the densities of conspecific (*ConS*) and heterospecific (*HetS*) seedlings in each of the 1-m² seedling plots (Fig. 1).

We calculated conspecific adult neighbour density (*ConA*) and heterospecific adult neighbour density (*HetA*) as the total distance-weighted basal area of conspecific and heterospecific trees that were found within a 20 m radius of each seed trap. A 20-m radius was selected as it had lowest Akaike's information criterion (AIC) value based on preliminary analyses comparing models with 5-, 10-, 15- and 20-m radius (Table S2). This 20-m radius was also used by a previous study in the same plot (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 (*DISTANCE*). To simulate the non-linearity function of local biotic interaction, we introduced the exponent *c* suggested by Detto et al. 2019:

$$ConA \text{ or } hetA = \sum_{i}^{N} \left(BA_i / \mathrm{DISTANCE}_i \right)^c,$$

where i was a conspecific (*ConA*) or heterospecific (*HetA*) tree individual found within the 20 m radius. As a result, data from 66 of the 450 seedling plots were excluded from the following analyses because these seedling plots were within 20 m of the edge of the plot (222 species with 10,773 individuals and 62,258 records were included in the further data analysis). We fitted models with different values of c (from 0 to 1) and c value with maximum likelihood value was selected (Fig. S3). That is $c = 0.26$ in dry season and $c = 0.24$ in rainy season.

Seedling survival models in dry and rainy seasons

The survival probability of individual seedlings was modelled using generalized linear mixed-effect models (GLMMs) with binominal error distribution.

We first tested whether neighbour densities affect the survival of tree seedlings and whether the effect varied between seasons. The response variable was the state of the focal seedling, assigned 1 (alive) or 0 (dead). The explanatory variables included seedling height (log-transformed) and neighbour factors (*ConA*, *HetA*, *ConS* and *HetS*). Seedling height was included as a covariate because it showed significant correlation with its survivorship in previous studies (Lin et al. 2012; Wu et al. 2016). Individual and census were added as random effects to account for the observations of survival from multiple censuses and temporal variation in community-wide survival probabilities (Zhu et al. 2015). We treated every seedling plot and the corresponding seed-trap station as a nested random factor to account for the spatial autocorrelation (Chen et al. 2010). Species identity was added to the model as a random factor to account for the inherent differences in survival probabilities of each species. We also considered species-specific CNDD effect by adding *ConA* as a random slope term. We add season (two levels: dry season and rainy season) as an interaction term with conspecific adult neighbour density to test if the relative effect strength of CNDD varied significantly between dry and rainy seasons overall and in each habitat.

We then tested whether the CNDD effect varied among topographic habitat in the dry and rainy season, respectively. We compared the relative effect strength of CNDD among different topographic habitats (three level: ridge slope and valley) by adding habitat as an interaction term with conspecific adult neighbour density. All values of continuous explanatory variables, including log-transformed seedling height, were standardized by subtracting the mean value of the variable and dividing by one standard deviation before all analyses.

Correlation between seedling species diversity and CNDD among habitats

Shannon diversity index was used to calculate the species diversity of surviving seedlings in each seed-trap station for each census. We calculate the mean value of species diversity of survival seedlings for each seed-trap station among censuses in dry season and rainy season, respectively. ANOVA with post hoc Tukey's test was conducted to test whether species diversity varied among habitats. Pairwise t tests were conducted to test whether species diversity varied between dry and rainy seasons. A linear model was used to investigate if there was significant correlation between species diversity of tree seedlings and the strength of CNDD among topographic habitats. In addition, we calculated the species diversity of adult trees (dbh ≥ 1 cm) within 20 m from the seed trap as the potential specie pool. We tested the correlation between adult tree diversity and seedling diversity using linear model and also tested the different adult tree species diversity among habitat using ANOVA.

All analyses were conducted in R 3.0.3 (R Core Team 2018). Mixed-effect models were fitted using the *glmer* function of the *lme4* package (Bates et al. 2014).

Results

We found the survival of seedlings varied with neighbour factors. We found significant CNDD effect, that is, the density of conspecific adult neighbours (*ConA*) significantly decreased the probability of seedling survival in both dry and rainy season (Fig. 2). We found positive effect of conspecific seedling neighbour density on seedling survival in rainy season and positive effect of heterospecific seedling neighbour density on seedling survival in dry season. The effect of heterospecific adult density was not significant in either season. We did not find a significant difference in CNDD among topographic habitats in the dry season (Fig. 2a). However, we found the strength of CNDD varied significantly among topographic habitats in rainy season (Fig. 2b) with the valley habitat having significantly stronger CNDD than in ridge habitat. However, the strength of CNDD did not significantly differ between dry and rainy seasons overall, and within each topographic habitat (Table S3).

The Shannon diversity index was 1.67 ± 0.43 in ridge, 1.83 ± 0.34 in slope and 1.86 ± 0.36 in valley habitat in dry season and 1.66 ± 0.43 in ridge, 1.83 ± 0.35 in slope and 1.89 ± 0.35 in valley habitat in rainy season, respectively. There is a non-significant difference in diversity between rainy and dry seasons (t value $= -0.31$; P value $= 0.76$). Shannon diversity index showed significant difference among topographic habitats in dry season (F value $= 3.15$; P value $= 0.04$) and rainy season (F value $= 4.44$; P

Fig. 2 The relative influence of neighbour density variables on the survival of seedlings (mean ± 2 SE) at community level in the **a** dry and **b** rainy seasons, the interaction between *ConA* and topographic habitat was considered. *ConA*$_{Valley}$, *ConA*$_{Slope}$ and *ConA*$_{Ridge}$ indicate the variance of *ConA* coefficient among topographic habitats. Filled points indicate parameter estimates significantly different from zero at the alpha = 0.05 level. ** (*P* value < 0.01) indicates significant differences of Conspecific negative density dependence (CNDD) effect between topographic habitats. *ConA* conspecific adult density, *HetA* heterospecific adult density, *ConS* conspecific seedling density and *HetS* heterospecific seedling density
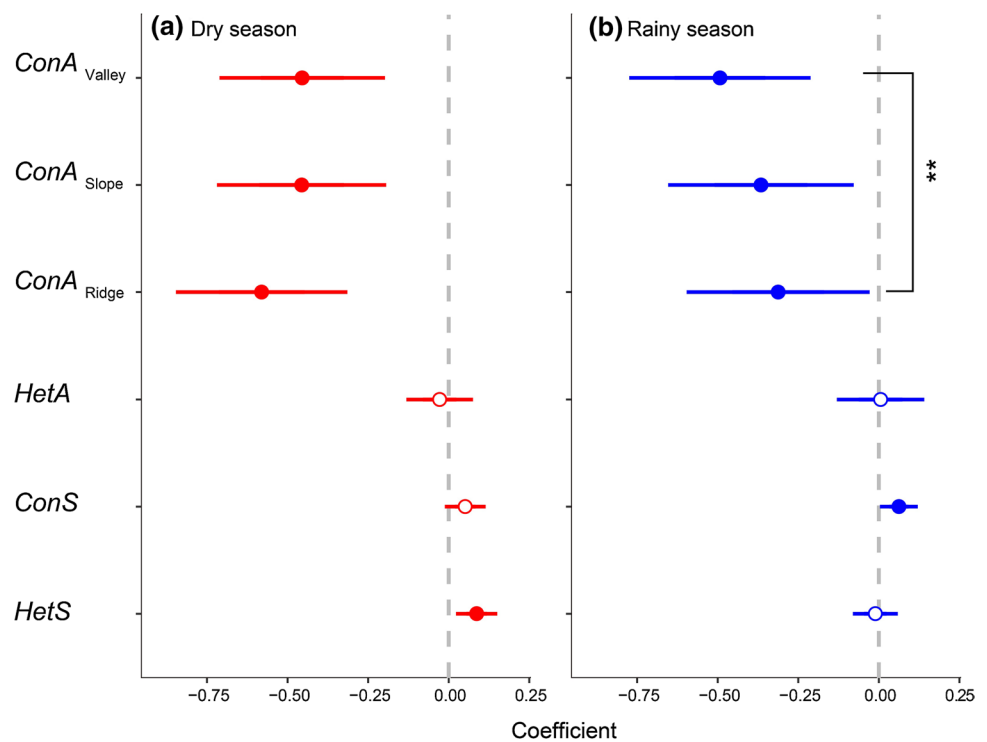
value = 0.01). Shannon diversity index was significantly higher in slope and valley habitat than in ridge habitat, but was not different between slope and valley habitat (Fig. 3a,

b). In the dry season, the variation of CNDD effect among topographic habitats was significantly positively correlated to Shannon diversity index of tree seedlings (Fig. 3a).
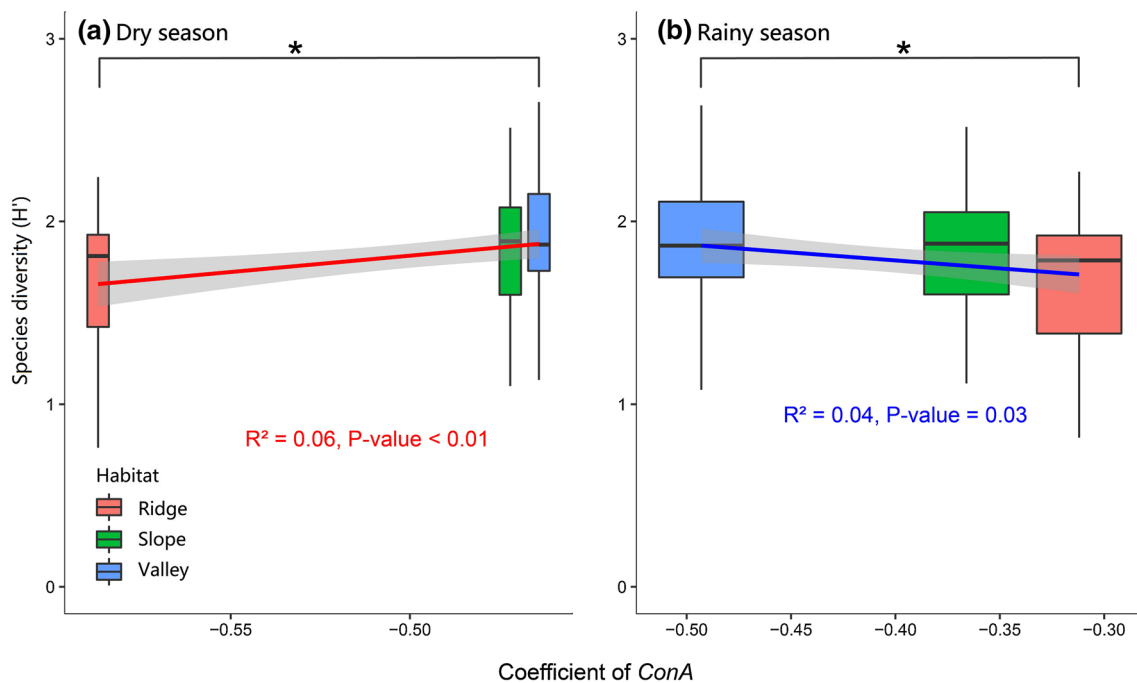
Fig. 3 The correlation between CNDD and species diversity (H', Shannon diversity index) of tree seedlings in **a** dry and **b** rainy seasons during the census period (from 2007 to 2017). * (*P* value < 0.05)

indicates significant differences in species diversity between topographic habitats. Note: the horizontal scale differs between **a** and **b**

In the rainy season, the variation of CNDD effect among topographic habitats was significantly negatively correlated to Shannon diversity index of tree seedlings (Fig. 3b). We found that there was a weak positive correlation between adult tree diversity and seedling diversity (coefficient = 0.193, R^2 = 0.04, P value = 0.022), and the tree species diversity was not significantly different among habitat types (F value = 0.816, P value = 0.444).

Discussion

We investigated the influence of conspecific neighbour density on seedling survival through 10 years of seedling monitoring work in a tropical forest, whether CNDD can interact with topography and can potentially affect species diversity at local scale. We found conspecific adult neighbour densities had significant negative effects on the survival of seedlings, and the strength varied with season and topography. In rainy season, CNDD was significantly stronger in valley habitat than in ridge habitat, and was negatively related with seedling species diversity among topographic habitat which indicated that CNDD could have important impacts on species diversity and coexistence at the local scale.

We found conspecific adult neighbour density significantly negatively correlated with seedling survival in this tropical forest (Fig. 2). This result is consistent with evidence from our previous study (Lin et al. 2012; Wu et al. 2016) and other tropical forests (Queenborough et al. 2007; Comita and Hubbell 2009; Comita et al. 2010; Johnson et al. 2017; Murphy et al. 2017; Zhu et al. 2018). The negative effects of conspecific adult neighbours on seedling survival could be caused by asymmetric intraspecific competition for resources (He and Duncan 2000; Martinkova and Honek 2011) and/or increased damage by natural enemies (Janzen–Connell hypothesis, Janzen 1970; Connell 1971), such as specialized herbivores and/or host-specific pathogens (Bell et al. 2006; Bagchi et al. 2014; Gilbert and Parker 2016; Liang et al. 2016). We found conspecific seedling neighbour densities have positive relation on the survival of seedlings (Fig. 2), there are at least two reasons why this might be the case. On the one hand, in tropical forest, conspecific seedling neighbours tend to have weaker negative interactions, presumably because of the small size and relatively low density (Paine et al. 2008; Svenning et al. 2008) resulting in weak competition among seedlings. On the other hand, the negative effect of conspecific seedling neighbours may be masked by habitat effects, for instance, tree species in their preferred habitats may increase the seedling abundance and promote the seedling survival (Johnson et al. 2017). The positive relation between seedling survival and heterospecific seedling neighbor density (Fig. 2) has also been found in other tropical forests (Lu et al. 2015; Zhu et al.

2015) and temperate forests (Johnson et al. 2014; Pu et al. 2017). This could be explained by the "species herd protection hypothesis" (Peters 2003). This hypothesis assumes a host may have lower probability to be damaged by its specialized herbivores and pathogens when more heterospecific neighbours are nearby. As a result, seedling survival is likely to be higher in an area with high heterospecific seedling neighbours. Alternatively, the increased survival in denser areas of heterospecifics may also indicate a habitat effect (Comita and Hubbell 2009), for instance, a resource-rich location where seedling survival is not limited by resource limitation (e.g. canopy gaps).

We found CNDD was strong in the valley habitat, but weak in the ridge habitat in rainy season (Fig. 2b), but CNDD strength was not significantly different among habitat in dry season (Fig. 2a). Multiple mechanisms may lead to this pattern. First, the soil moisture in rainy season is higher in the valley habitat, compared to the ridge habitat (Song et al. 2013 and Fig. S2). Thus, moisture availability in the valley habitat could increase natural enemies populations and virulence (Coley and Barone 1996) and intensify the spread of plant disease (Brenes-Arguedas et al. 2009; Swinfield et al. 2012; Spear et al. 2015) resulting in higher conspecific seedling mortality. Moreover, soil nutrients in valley habitats in this plot were richer than in ridge habitat (Hu 2010), which may lead to stronger intra-specific competition (LaManna et al. 2016) and/or activity of specific pests or pathogens (Bever et al. 2012; Terborgh 2012), resulting in much stronger negative plant–soil feedback (LaManna et al. 2016; Crawford et al. 2019). In addition or alternatively, seedlings may suffer less attraction by natural enemy, but stronger asymmetric intra-specific competition for water resource from conspecific adult neighbours in the dry season and result in similar CNDD among habitats (Fig. 2a). The spatial variation of CNDD has long-term implications to species coexistence either through enhancement by a storage effect (Chesson 1994) or through reduction of coexistence by weakening CNDD, and thereby affecting the spatial pattern of species diversity at local scale.

Janzen (1970) and Connell (1971) originally hypothesized that CNDD could help maintain the high species diversity in tropical forests. However, most work has demonstrated the existence of CNDD (Comita et al. 2014), but few of them linked CNDD with species diversity pattern (Johnson et al. 2012; Bagchi et al. 2014; LaManna et al. 2017). And a recent work by Detto et al. (2019) suggested some previous works studying CNDD could have reached biased conclusions. Our analysis is not subject to the majority of the biases outlined because we are not using static data. We are using analysis of survival with a neighbourhood model, and we used categorical habitat variables but not continuous variables to minimize the potential measure errors inherent in using precipitation or soils variables

which are highly variable spatially. We have followed the advice given and allowed our neighbourhood metric to be modified by a fit exponent to allow for a functional form that best describes the data relations (Detto et al. 2019). In our study, the strength of conspecific density dependence among topographic habitat showed significant negative correlation with seedling species diversity in the rainy season (Fig. 3b). The stronger CNDD in the valley habitat related to higher species diversity. In contrast to the prevailing explanations of the species diversity, variation at local scale is primarily attributed to physical aspects of the environment, such as soil nutrients and light condition (Martinez-Camilo et al. 2018; Song et al. 2018a). Our results support local variation of species diversity patterns being driven by local species-specific ecological interactions and the variation in CNDD could be related to the local variation in species diversity (Harms et al. 2000). Our results are consistent with the idea that stronger CNDD could maintain higher species diversity in tropical forest at the local scale. Additionally, the studies at continental and global scales have suggested local interactions can help describe the latitudinal patterns of diversity (Johnson et al. 2012; LaManna et al. 2017). The positive correlation between CNDD effect and species diversity in dry season (Fig. 3a), however, may not be a causal relation, as the CNDD effect was not significantly different among habitats in dry season (Fig. 2a). Thus, our results highlighted that the difference in CNDD effect among topographic habitat during the rainy season could be an important driver in determine differences in seedling diversity among habitats. For a given habitat, other mechanisms may also drive the species diversity simultaneously. The species pool may determine the maximum number of species that a habitat could have through dispersal limitation. The species diversity of adult trees could have positive affect on the species diversity of seedlings in the understory by supplying more species propagules. Then, habitat filtering and interspecific interactions may decrease the species diversity by filtering the maladapted species that fail in seed germination and seedling establishment by suffering higher abiotic stress or predation rate (HilleRisLambers et al. 2012).

We found non-significant seasonal differences in the strength of CNDD on the survival of tree seedlings in this seasonal tropical forest (Table S3). Alternately, a previous study found that the CNDD effect was higher in dry season. (Lin et al. 2012), which only focused on the seasonal variation of CNDD caused by conspecific seedling neighbour and did not account for tree neighborhoods. One possible reason could be the differential response of the strength of conspecific competition and populations of specialized pests and pathogens to moisture availability. Declining precipitation can cause high conspecific competition for water resource (O'Brien et al. 2017) since conspecifics access water in similar ways (Meinzer et al. 1999). But declining precipitation

to drought conditions could create unsuitable conditions for herbivore and pathogen populations (Aide 1992; Coley and Barone 1996), thus decreasing the strength of CNDD. The strength of CNDD might be determined by the combined effect of these processes. Similar effects of CNDD, in both dry and rainy seasons, could occur if the seasonal variation of intraspecific competitions is balanced by the seasonal variance of natural enemy effects. An experimental drought in Panama showed that the strength of CNDD was lower in the severe dry season than typical dry season conditions and minimal wet season conditions (Bunker and Carson 2005). Hence, the temporal variation of CNDD in forests can have complex dynamics and requires more investigation to uncover the mechanisms.

Overall, we discovered that conspecific negative density dependence was stronger in valley habitat, but weaker in ridge habitat in rainy season. These variations have important implications for species coexistence and community diversity, where species diversity in valley habitat is significantly higher than in ridge habitat. Our results highlight the effect of CNDD on seeding survival and species diversity. The spatial variability CNDD could be a key process that determines species coexistence and plant diversity at local scale.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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