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The strength of density-dependent mortality is contingent on climate and seedling size

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Abstract

Questions

Density-dependent processes may promote species diversity in plant communities. Here, we tested whether seedling survival was density-dependent and varied by seedling size, species, and climatic factors.

Location

Tropical rainforest, Xishuangbanna, southwestern China.

Methods

Generalized linear mixed-effects models were used to examine seedling survival (232 tree species) across nine years of seedling census data from a 20-ha tropical forest dynamics plot. Our predictor variables included conspecific and heterospecific neighbor density, size of the seedling and annual variation in climatic factors.

Results

We found significant negative effects of conspecific tree density, but positive effects of heterospecific seedling density on the survival of tree seedlings in this plot. In general, conspecific negative density dependence (CNDD) was observed most frequently for large size classes of seedlings (≥20 cm in height), while heterospecific positive density dependence (HPDD) was similar at all size classes. CNDD for large seedlings was stronger during warm years, and HPDD for large seedlings was stronger during dry years.

Conclusions

Our study suggests that the strength of density dependence varied through time and the strength was influenced by water availability and temperature. Our results highlight the potential for changes in species composition and species coexistence that could result from increasing temperature strengthening conspecific negative density-dependent effects and decreasing precipitation strengthening heterospecific

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positive density-dependent effects.

Key words: competition; density dependence; Janzen-Connell hypothesis; mixed models; neighbor effect; precipitation; seedling; temperature.

Introduction

One of the most important mechanisms promoting species diversity is negative density-dependent mortality (Wright 2002; LaManna et al. 2016; LaManna et al. 2017). Such processes reduce seedling survival when higher densities of conspecific neighbors surrounding by. Conversely, the survival of individuals increases with declining density of conspecific trees, affording establishment opportunities for other species' seedlings near species experiencing strong density-dependent mortality (Janzen 1970; Connell 1978; Harms et al. 2000; Johnson et al. 2012). The fluctuations in weather can alter community assembly (Gornish & Tylianakis 2013) and inter- and inner-annual weather variability has been found to have some connection with the strength of density-dependent mortality (Yanar et al. 1997; Hersh et al. 2011; Lin et al. 2012; Bachelot et al. 2015).

Among the main mechanisms driving negative density-dependent (NDD) mortality at early ontogenetic stages are resource competition from conspecific neighbors (Stoll & Newberry 2005), and natural enemies and pathogen attacks (Clark & Clark 1985). Moreover, previous studies showed that the strength of CNDD showed significant seasonal and annual variability (Lin et al. 2012; Wu et al. 2016). For instance, in a tropical seasonal rainforest in southwest China, the dry season showed stronger CNDD mortality than the rainy season, which indicates that water availability might influence the CNDD processes (Lin et al. 2012). Another study, in Costa Rican tropical forest, showed that common species had higher CNDD than rare species in warmer and wetter years (Bachelot et al. 2015). To date, the factors that drive the temporal dynamics of CNDD effects are poorly understood. Especially in the context of global change, understanding the effects of changing climate on the mechanisms that influence species coexistence is critical to making informed forecasts of forest response in the future (Valladares et al. 2015).

Climatic conditions, in particular those associated with water availability, have

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potential to play a key role in driving community dynamics linked with NDD processes in tropical rainforests. It has been hypothesized that increased temperature and precipitation could enhance activities of pathogens and herbivore insects (Brenes-Arguedas et al. 2009; Swinfield et al. 2012), ultimately leading to stronger CNDD effects. Bunker & Carson (2005) suggested that declines in annual precipitation weaken NDD in a seasonal forest in Panama. However, Lin et al. (2012) suggested that dry periods may increase water limitation and enhance intraspecific competition which results in stronger CNDD effects during dry periods.

In addition to the negative effects on conspecifics, previous studies have shown that heterospecific neighbors tend to have positive density-dependent effects on seedling survival (Comita & Hubbell 2009; Johnson et al. 2014; Lu et al. 2015). This effect could be explained as a result of the "species herd protection hypothesis" that suggests that the increase of heterospecific density can decrease the encounters between pests and pathogens and their preferred (or most susceptible) hosts, which in turn increases the survival rate of rare host (Peters 2003). Moreover, the strength of protection may fluctuate with the density of pests and pathogens (Dobson 2004; Bagchi et al. 2014; Spear et al. 2015; Xu et al. 2015). The density of pests and pathogens is likely to rapidly increase and potential to outbreak levels when host density is high resulting in high rates of mortality and driving evolutionary selection (Clay et al. 2008; Bagchi et al. 2010). As masting events tend to be correlated with environmental conditions, density dependent process may link to weather patterns (Jia et al. 2011; Zhang et al. 2014). Interspecific interactions can also produce positive density-dependent effects by facilitating survival of heterospecific seedlings by alteration of the habitat (Bertness & Callaway 1994; Jia et al. 2011; Zhang et al. 2014).

Besides the effect of temperature and precipitation on the strength of NDD, seedling age (size) is an additional factor that impacts seedling demography (Metz et al.2010; Zhu et al. 2015; Record et al. 2016). NDD can be stronger in the earlier life stages of plants (Comita et al. 2014; Zhu et al. 2015), potentially because seedlings lack defenses and resistance capacities, thus, they are more easily attacked by natural

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enemies. On the other hand, CNDD may increase with seedling age because the accumulation of specific pathogen and increasing asymmetric conspecific resource competition from conspecific trees (Lin et al. 2012; Liu et al. 2012; Benitez et al. 2013). The increased NDD effect with size may promote diversity by enhancing the establishment of heterospecific species.

Here, we tested whether variation in density dependence was explained by environmental factors. In addition, we tested whether relationships exhibited size dependence. Particularly, we focus on the following questions: How does climate affect the strength of density-dependent processes on seedling survival? Does climate affect the strength of conspecific and heterospecific density dependence for seedlings? Does the role of climate in density-dependent responses vary with seedling size?

Methods

Study site

The study plot is located in Xishuangbanna, south-western China (101°34′E, 21°36′N) (Fig. 1). This region is strongly affected by monsoon climate, showing distinct rainy and dry seasons. Mean annual temperature and rainfall of this region are, respectively, 21.8℃ and 1493 mm. Majority of rainfall (about 80% of annual rainfall) occurs in the wet season between May and October (Cao et al. 2006). The 20 ha Xishuangbanna forest dynamics plot (400 m × 500 m) was established in 2007, following the protocol of Condit (1998), where all free-standing trees, ≥1 cm diameter at breast height (DBH), were tagged and identified into species (Condit 1998).

In November 2007, we established 150 seed-trap stations (a 0.5-m^2 seed trap with three 1-m^2 seedling plots) stratified randomly in the plot to monitor seed rain and seedling dynamics (Fig. 1). Three seedling plots were placed 2-m away from sides of the seed trap. In each seedling plot, woody plants < 1 cm DBH were defined as seedlings, and were tagged and identified. Height of the seedlings was measured from the ground to the apical bud. The first seedling survey was carried out in November 2007. We conducted subsequent surveys in November of the following years. In this study, we analyzed the seedling data collected from 2007 to 2015, excluding 25 unidentified seedlings (Table A1).

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Climate data

The monthly record of air temperature and precipitation was collected at the meteorological station of Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies of Xishuangbanna Tropical Botanical Garden. This station is 47.4 km away from the Xishaungbanna forest dynamic plot. We calculated average monthly temperature and total precipitation from November to October of the following year as the annual mean monthly temperature and annual precipitation.

Density calculations

Four density variables were calculated to estimate the neighborhood effects. We calculated the density of conspecific (Den_{con}) and heterospecific (Den_{het}) seedling neighbors for the focal seedling within the 1-m^2 seedling plots for each year (Fig.1).

We calculated the total basal area of conspecific (BA_{con}) and heterospecific (BA_{het}) trees that found within a 20 m radius of each seed trap. We divided the basal area of each tree by the distance between the tree and the center of the seed trap (*DISTANCE*):

$$BA_{con}\ or\ BA_{het} = \sum_{i}^{N} (BA_i / DISTANCE_i)$$

where *i* is a conspecific or heterospecific tree individual found within the 20 m radius. A 20-m radius was assigned following a previous study in this plot (Wu et al. 2016), which indicated that 20-m had stronger support than other scales (10-m and 30-m). 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.

Statistical analysis

We divided the response variable (the probability of seedling survival) into three size categories based on seedling height *i.e.* all seedlings, small seedlings (height < 20 cm) and large seedlings (height ≥ 20 cm) (Lin et al. 2014; Wu et al. 2016). The annual (from November to the November of the next year) survival probability of seedlings was modeled using generalized linear mixed models (GLMMs) with binominal error distribution. Binomial response variable was used to show whether individual

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seedlings were alive (given 1) or dead (0). The explanatory variables included seedling height (log-transformed) which showed significant correlation with its survivorship in previous studies (Lin et al. 2012; Wu et al. 2016), The density of conspecific (BA_{con}) and heterospecific (BA_{het}) adult neighbors, and the density of conspecific (Den_{con}) and heterospecific (Den_{het}) seedlings. We standardized continuous explanatory variables (including log-transformed seedling height) by subtracting their mean values and dividing by their standard deviations before analyses to allow for comparisons among parameter estimates. Three seedling plots nested within a sampling point, and we assigned this as a random effect in the GLMMs. Species identity was also incorporated to the model as a cross random effect to account for the inter-specific variations of survival probabilities.

Statistical models were developed with all density variables as fixed effects. Firstly, we estimated the relative effects of all factors on the survival of seedling at a community level. Then, we used linear regression models to test whether conspecific adult density-dependent effects and heterospecific seedling density-dependent effects of all seedlings, small seedlings and large seedlings correlated with annual mean temperature or annual precipitation. We also tested whether conspecific adult density-dependent effects and heterospecific seedling density-dependent effects vary between seedling size classes. We performed the Shapiro-Wilk test to test if the data is normally distributed and Bartlett's test to test if the variances in each of the groups are the same. Then, we used t-test to determine if the coefficient values of two density parameters had significant difference between size classes.

We conducted all analyses in R 3.0.3 (R Development Core Team 2015). We use glmer function with the recommended Laplace method (Bolker et al. 2009) of the lme4 package to fit the generalized linear mixed-effect models (Bates et al. 2014)

Results

Densities of conspecific and heterospecific neighbors showed both significant negative and positive impacts on seedling survival depending on size classes and years (Table 1). Conspecific seedling density showed both significant positive and

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negative effects on seedling survival in all seedlings pooled, as well as small (< 20 cm in height) and large seedlings (≥ 20 cm in height) and the effects varied year to year. Conspecific adult density showed significant negative effects on survival of seedlings in all seedlings (3 of 8 years) and large seedlings (5 of 8 years). We found positive density-dependent survival related to heterospecific seedling density in all size classes (5 of 8 years for all seedlings, 1 of 8 years for large seedlings and 4 of 8 years for small seedlings). We found no significant effect of heterospecific tree density on seedling survival in any size class (all seedlings, large seedlings and small seedlings).

Both conspecific and heterospecific density effects were found to be correlated with climatic factors. Conspecific adult density-dependent effects on survival of large seedlings were significantly correlated with annual mean temperature ($R^2 = 0.59$, $P = 0.02$); however, conspecific adult density-dependent effects on survival of all seedlings and small seedlings were not significantly correlated with annual mean temperature (Fig. 2). Effects of heterospecific seedling density on seedling survival of all seedling size classes were correlated with annual precipitation ($R^2 = 0.54$, $P = 0.04$), as well as large seedlings ($R^2 = 0.40$, $P = 0.09$), but heterospecific seedling density-dependent effects of small seedlings were not significant correlated with annual precipitation (Fig. 3).

We found large variation in conspecific adult density-dependent effects, but small variation in heterospecific seedling density-dependent effects among seedling size classes (Table 1). Large seedlings tended to suffer more seedling mortality due to conspecific negative density-dependence from adult tree neighbor than small seedlings ($t = 3.10$, $P = 0.01$; Fig. 4). Alternately, the strength of heterospecific seedling density-dependent mortality did not differ between seedlings size classes (Fig. 5).

Discussion

Density dependence effects help drive seedling survival dynamics in tropical forest communities. In this study, we were interested in examining the role of temporal climatic variation (temperature and precipitation) and seedling size on the strength of density dependence survival. Our results show that the strength of CNDD

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of large seedlings (≥ 20 cm in height) is strongly dependent on annual variation in temperature. Furthermore, we found that the strength of heterospecific density dependence also varies with climatic conditions, specifically precipitation, indicating that neighboring tree identity influences community dynamics depending on weather conditions. Further, we found that the strength of density dependence is size-dependent.

Conspecific negative density-dependent variation and climatic condition

Seeding mortality was both positively and negatively related to conspecific seedling density depending on the year (Table 1). Negative density-dependent mortality is common during the seedling stage of tree species (Comita et al. 2014). A previous study indicated that CNDD related to seedling density was easily detected when large recruitment events happened (Metz et al. 2012) which are often related to climatic cues. However, previous studies indicated that the negative effects of conspecific seedling density may be overwhelmed by the habitat effect (Comita & Hubbell 2009). Thus, the positive effect of conspecific seedling density could be an indication that seedlings survival may benefit from habitat preference (Valencia et al. 2004).

To date, few studies have found clear relationships between the strength of negative density dependence and temporal variability in climatic conditions (Lin et al. 2012; Bachelot et al. 2015). Compared to other studies, our study used a long term time-series dataset which may have increased our ability to detect this correlation. We found evidence that the CNDD was strongly related to mean annual temperature (Fig. 2). The increasing temperature generally accelerates the metabolisms of seedlings, and larger seedlings tend to have greater demands for resources during warm periods which may increase mortality by intraspecific competition. Alternately, warmer years may benefit pathogen populations and the result would be similar. This is an area that should receive greater research attention in the future.

In a Costa Rica tropical wet forest, the strength of CNDD was enhanced by both increasing temperature and precipitation (Bachelot et al. 2015). However, in our study, precipitation was not correlated to CNDD. Declining precipitation can cause high

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conspecific competition for water resource because conspecifics access water in similar ways (Meinzer et al. 1999), which could result in increasing CNDD. But declining precipitation can result in drought and creating unsuitable conditions for pests and pathogens (Coley & Barone 1996), which could result in decreasing CNDD. Thus, increased competition from conspecific tree neighbors may be balanced by decreased natural enemy attacks. Future studies could focus on disentangling the effects of climate on competition and natural enemy populations to advance our understanding of the controls on forest community composition.

Heterospecific positive density-dependent variation and climate

We found positive density dependence of heterospecific seedling neighbors (Fig. 5), the survival of target seedlings was higher when surrounded by higher number of heterospecific neighbors. This maybe because the high proportion of heterospecific neighbors decreased the intraspecific competition. Our result was also consistent with studies in another tropical forest (Comita & Hubbell 2009), which could be explained by the "species herd protection hypothesis" (Peters 2003). This hypothesis assumes increased heterospecific crowding decreased the probability of a host encountering its pests and pathogens. As a result, seedling survival is likely to be lower in an area of high conspecific tree neighbor density and higher in an area with many heterospecific tree neighbors. The HPDD could also be caused by the niche partitioning among species that reduced the competition exclusion compared to conspecifics (Vandermeer 1972). Moreover, heterospecific neighbors may have positive effects on the performance of seedlings by facilitating beneficial microenvironments (Bruno et al. 2003).

The positive heterospecific density-dependent effects may also indicate that conditions of the site, such as light resource, water availability and soil characters, have a positive influence on seedling survivorship (Comita & Engelbrecht 2009; Comita & Hubbell 2009; Bai et al. 2012; Piao et al. 2013). A previous study in this region has also shown that the edaphic and topographic variables had important effects on seedling survival (Wu et al. 2016). In this study, we found that positive heterospecific density dependence was consistent between seedling size classes (Fig.

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296 5), and the effect was increased with decreasing precipitation (Fig. 3). Positive
297 interactions among different plant species can increase with abiotic stress (Callaway
298 et al. 2002). Our study suggests that water limiting conditions could increase the
299 facilitation process among individuals of different species and might enhance the
300 positive effect caused by the herd protection process.

301 ***Size dependent density dependence***

302 We found that conspecific negative density-dependent effects were stronger in
303 large seedlings than small seedlings (Fig. 4). The strength of CNDD changed across
304 size classes in other forests (Comita et al. 2014; Zhu et al. 2015). Our result, however,
305 showed that the larger seedlings suffered stronger CNDD from trees than smaller
306 seedlings. The increased negative density-dependent effect with seedling sizes might
307 be driven by the accumulation of specific pathogen or increasing asymmetric
308 conspecific resource competition (Lin et al. 2012; Liu et al. 2012; Benitez et al. 2013).
309 However, small seedlings were easily damaged by changed environmental conditions
310 during a study in Panama (Engelbrecht et al. 2005). A study in lowland Amazonian
311 rain forest showed opposite results, the density of conspecific seedlings showed
312 strong negative effects on the survival of first-year seedlings (Metz et al. 2010). Our
313 results suggested that the seedling-seedling interaction might be weak in this tropical
314 forest. Further studies could examine different mechanisms (e.g. intraspecific
315 competition or negative plant soil feedback) on the generality of these processes.

316 ***Implications for predicting the response of seedlings to climate change***

317 In the context of global climate change, the effect of climate on the mechanisms
318 promoting species diversity should be given more attention (Valladares et al. 2015),
319 since changing climatic conditions may alter competition and facilitation processes
320 and ultimately affect the patterns of species richness and diversity (Gornish &
321 Tylianakis 2013). Previous studies suggested that high species diversity loss may
322 happen in tropical areas, if drought conditions increase because most tropical tree
323 species are drought sensitive (Slik 2004; Slot & Poorter 2007). In our study region,
324 during the last 40 years, annual temperatures increased, while evapotranspiration rates
325 and relative humidity decreased (Fan et al. 2011; Fan & Thomas 2013). Based on our

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findings, we suggest that increased temperature and drought may increase the strength of both negative conspecific and positive heterospecific density-dependent effects, which may promote species coexistence to a certain extent.

In summary, we found strong evidence that density-dependent seedling survival is strongly influenced by climatic variables. The strength of these effects is size-dependent and strongly influenced by annual precipitation and annual mean temperature. Our results highlight the importance of evaluating long-term data in the framework of climatic changes.

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Appendix

Table A1 The sample size of each GLMM model

Tables

Table 1. Effect of seedling height, density of conspecific and heterospecific seedling neighbors, total basal area of conspecific and heterospecific trees neighbors on seedling survivals for eight census intervals (*Hgt*, seedling height; Den_{con}, the density of conspecific seedlings and Den_{het}, the density of heterospecific seedlings; BA_{con}, total basal area of conspecific trees; BA_{het}, total basal area of heterospecific trees; #P< 0.1; *P < 0.05).

	All seedling size					Seedling ≥ 20 cm					Seedling < 20 cm				
	Hgt	Den_{con}	Den_{het}	BA_{con}	BA_{het}	*Hgt*	Den_{con}	Den_{het}	BA_{con}	BA_{het}	*Hgt*	Den_{con}	Den_{het}	BA_{con}	BA_{het}
2007-2008	1.17*	-0.11	0.07	-0.11	-0.02	0.52*	-0.03	0.04	-0.30#	-0.25	1.53*	-0.13	0.09	-0.11	0.01
2008-2009	1.27*	0.27*	0.24*	-0.19#	-0.07	1.50*	0.36*	0.13	-0.66*	0.07	1.40*	0.23*	0.26*	-0.08	-0.06

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2009-2010	1.15*	0.23*	0.21*	-0.37*	-0.11	1.15*	0.29*	0.08	-0.70*	-0.16	1.20*	0.14	0.27*	-0.16	-0.09
2010-2011	1.25*	0.20#	0.21*	-0.31*	-0.02	1.33*	0.23	0.16	-0.44*	-0.06	1.14*	0.16	0.14	-0.19	0.01
2011-2012	0.78*	-0.13	0.06	0.01	0.19#	0.60*	0.21	0.16	-0.31#	0.10	1.15*	-0.39*	-0.03	0.18	0.25
2012-2013	1.00*	-0.05	0.17	-0.20	-0.02	0.68*	0.05	0.17	-0.01	-0.15	1.34*	-0.04	0.16	-0.14	0.08
2013-2014	0.88*	0.07	0.27*	-0.12	-0.05	0.97*	0.13	0.31*	-0.23	-0.19	0.99*	-0.10	0.20#	0.07	0.06
2014-2015	1.50*	-0.21#	0.22*	-0.13	0.02	1.20*	-0.29#	0.22	-0.16	0.14	1.50*	-0.08	0.21#	-0.02	-0.11

Figures

Figure 1. Location and map of the 20-ha plot and the components of each seed-trap station. The locations of the 150 seed trap stations were represent by squares. The three 1-m^2 seedling plots were 2 m away from the seed trap.

Figure 2. Relation between estimates of adult conspecific adult density dependent (CNDD) and annual mean temperature (black points refer to all seedlings; red points and line refer to large seedlings; green points refer to small seedlings ; *P < 0.05).

Figure 3. Relation between estimates of heterospecific seedling density-dependence (HPDD) and annual precipitation (black points and line refer to all seedlings; red points and line refer to large seedlings; green points refer to small seedlings; #P< 0.1; *P < 0.05).

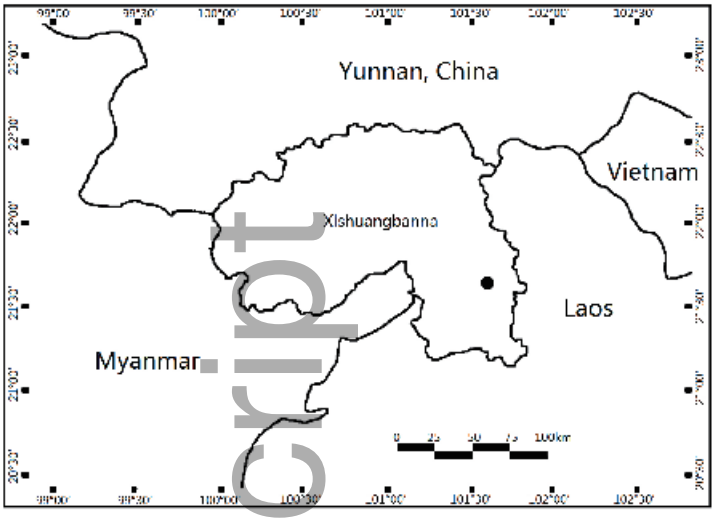
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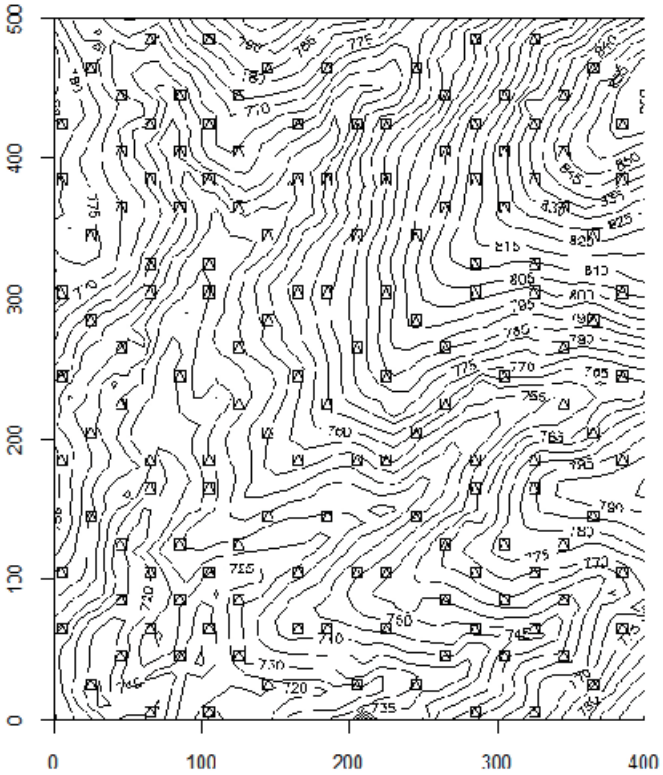
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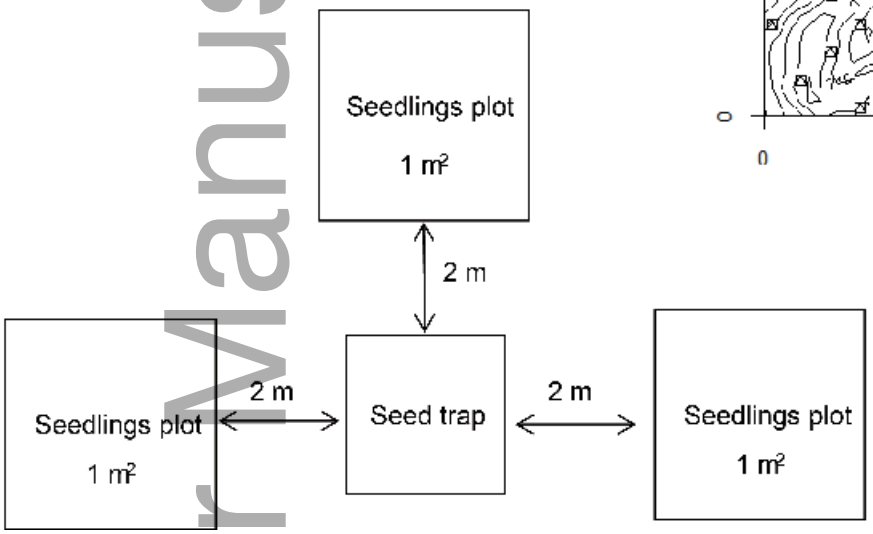
545 Figure 4. Estimates of conspecific adult density dependence for large seedlings (red)
546 and small seedlings (green). Error bars represent stand error (t = 3.10, $P = 0.01$).
547
548 Figure 5. Estimates of heterospecific seedling density dependence for large seedlings
549 (red) and small seedlings (green). Error bars represent stand error (t = 0.14, $P = 0.89$).

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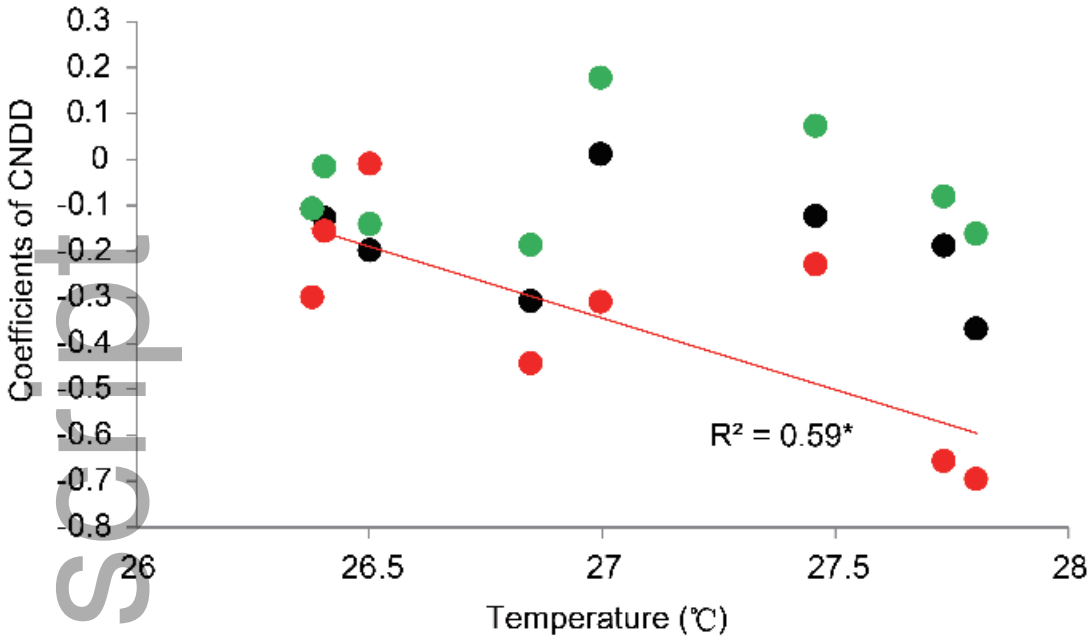




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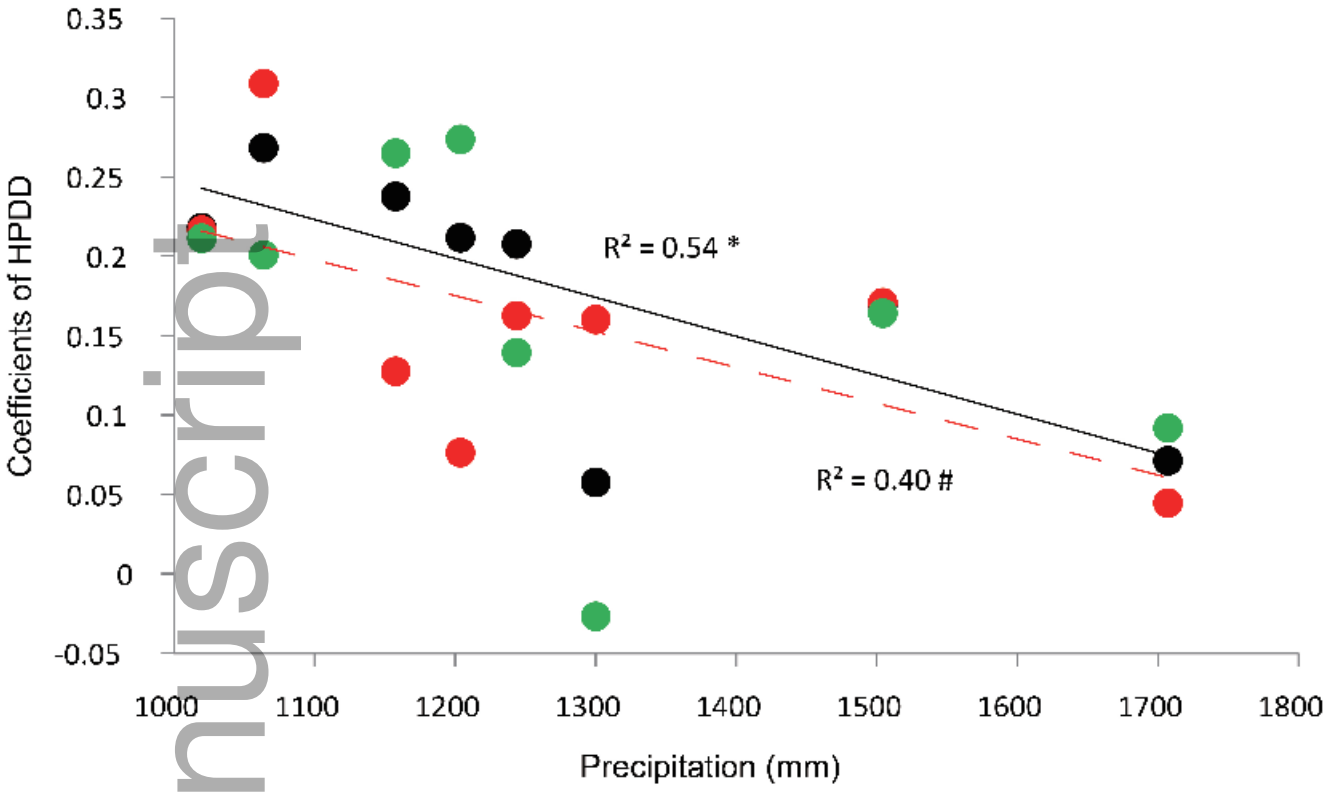
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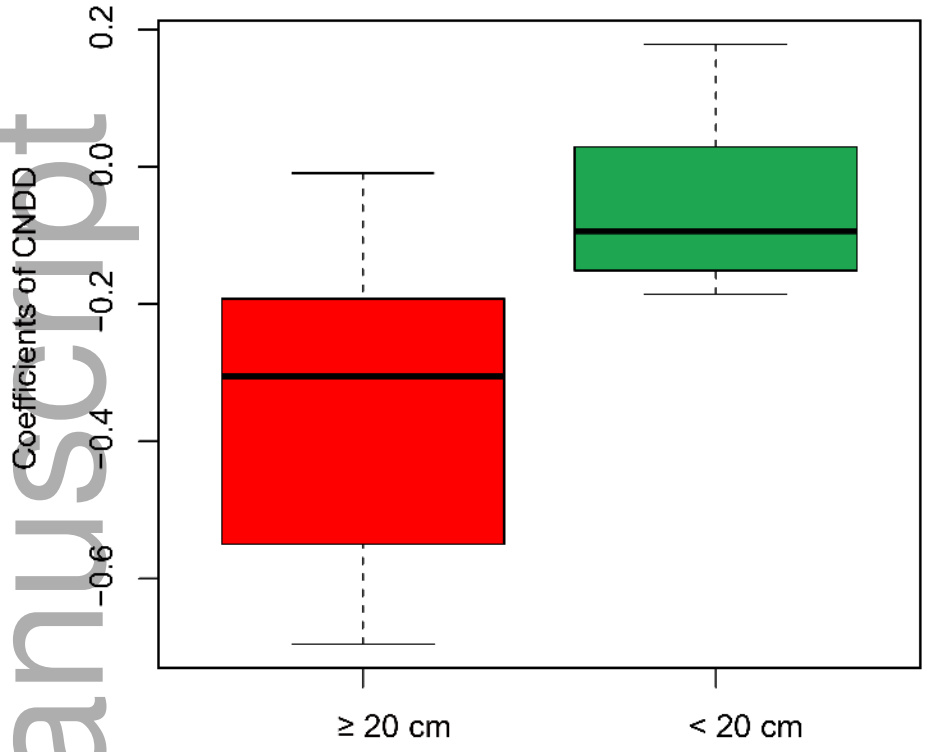


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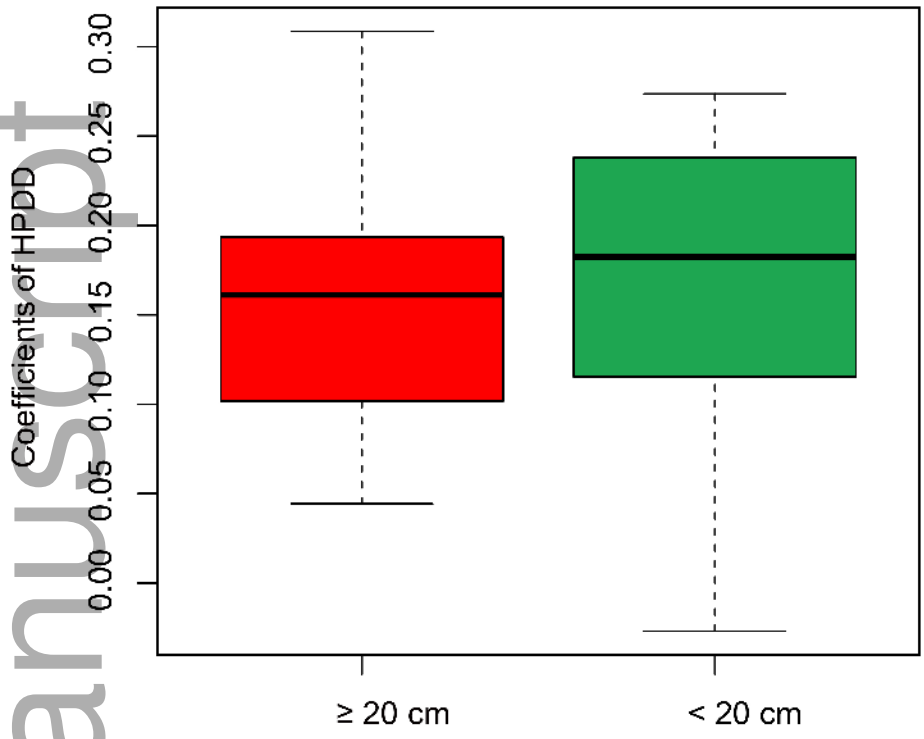
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