Neighborhood effects explain increasing asynchronous seedling survival in a subtropical forest

LEI CHEN,1,2 YUNQUAN WANG,1,3 XIANGCHENG MI,1 XIAOJUAN LIU,1 HAIBAO REN,1 JIANHUA CHEN,4 KEPing MA,1,5 AND NATHAN J. B. KRAFT2

1State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093 China
2Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California 90095 USA
3Key Laboratory for Biodiversity Science and Ecological Engineering of Ministry of Education, College of Life Sciences, Beijing Normal University, Beijing 100875 China
4College of Chemistry and Life Sciences, Zhejiang Normal University, Jinhua 321004 China

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Abstract. Biotic interactions play a critical role in mediating community responses to temporal environmental variation, but the importance of these effects relative to the direct effects of environmental change remains poorly understood, particularly in diverse forest communities. Here we combine a neighborhood modeling approach with insights from coexistence theory to assess the effects of temporal variation in species interactions and environmental conditions (e.g., precipitation, temperature, and understory light availability) on seedling survival over nine census years in a subtropical forest. We find significant temporal shifts in the magnitude of neighborhood effects on both community-wide and species-level seedling survival (statistically significant random effects of neighborhood × year and neighborhood × species × year interactions). These results are consistent with the idea that environmental change will play a fundamental role on forest regeneration dynamics by altering biotic interactions at the neighborhood scale. Moreover, differences among species in response to neighbors over time contribute to a pattern of temporal decoupling of seedling survival between species, which can help to promote diversity in certain contexts. In separate analyses of multiple regression on distance matrices (MRM), altered interactions with neighbors are much stronger predictors of asynchronous seedling survival among species than the pure effects of climate and plant functional traits, explaining twice as much variation (43.9% vs. 22.2%). In sum, these results reveal that divergent species responses to interannual environmental variability detected are driven primarily by indirect effects mediated by changing biotic environments. This highlights the importance of including indirect effects from local biotic (neighborhood) interactions in forecasts of forest community responses to global change.

Key words: demographic decoupling between species; direct and indirect effects; forest dynamics plot; neighborhood effects; seedling survival; subtropical forest; temporal environmental variation.

INTRODUCTION

The global environment has undergone unprecedented changes in recent decades (Jones and Mann 2004, Cai et al. 2015). The effects of these changes on population dynamics, species distribution, community structure, and the stability of ecosystem functioning have received much attention recently, and together these insights have improved our ability to predict biotic responses to future environmental regimes (Easterling et al. 2000, Walther 2010, Thornton et al. 2014). Environmental change can alter community assembly and species diversity directly by influencing species’ physiology and demography, or indirectly by shifting the fitness, abundance and identity of competitors (Gilman et al. 2010, Alexander et al. 2015, Gunderson et al. 2017). While direct links between climate and the autecology of individual species have been well documented (e.g., Parmesan and Yohe 2003, Moritz et al. 2008, Wolkovich et al. 2012), few studies have examined the extent to which environmental change will impact diverse communities by altering biotic interactions indirectly relative to the direct effects (Davis et al. 1998, Adler et al. 2009, Blois et al. 2013).

Ecological communities are strongly shaped by important lateral (e.g., competition and facilitation) and vertical (e.g., mutualism, predation, and herbivory) species interactions (Hutchinson 1957, Connell 1961, Chase and Leibold 2003). A recent review found that many kinds of biotic interactions are sensitive to environmental...
conditions, and that this sensitivity can lead to unpredictable impacts on community structure (Tylianakis et al. 2008). In fact, these biotic interactions can overwhelm direct effects on particular species’ responses to climate change (Suttle et al. 2007, Alexander et al. 2015, but see Chu et al. 2016). However, it is challenging to extrapolate from these results to diverse forest communities that can have hundreds of long-lived species and we still lack an understanding of the abiotic and biotic factors that mediate forest responses to temporal environmental change (Uriarte et al. 2018). This is because most empirical studies to date typically focus on relatively small spatial scales that are too small for optimal detection of the drivers of ecological processes and on a small subset of interacting species within a larger community, which limits the ability to make inference on whole community responses to environmental change (reviewed by Fayle et al. 2015).

Subtropical evergreen broad-leaved forests of China are among the most species-rich areas in the world, containing more than 10,000 vascular plant species in an area from 23° to 33° N and 98° to 123° E (Song 2013). The El Niño–Southern Oscillation (ENSO) has produced at least 11 La Niña events in this region since 1960 and contributes to a pattern of highly variable annual rainfall and frequent winter storms (Fig. 1; Yuan and Yan 2013, Jiang et al. 2014). In January and February 2008, repeated snow and ice storms afflicted the area as a result of an extreme La Niña event (hereafter termed “the 2008 winter storm”); these were the only ice storms observed in the last 50 years (Zhou et al. 2011). Here, we document nine years of seedling dynamics (2006–2014) in 24 ha of diverse subtropical forest (Gutianshan Forest Dynamics Plot, GTS FDP) spanning this time period of recent interannual climate variability (precipitation and temperature) and the 2008 winter storm disturbance, and test how environmental change impacts species interactions and demography. The spatially explicit, standard seedling censuses (Harms et al. 2000) and forest structure data from FDPs (Anderson-Teixeira et al. 2015) allow for the unique opportunity to study the fate of focal seedlings in relation to changes in the abiotic environment and in local biotic (neighborhood) interactions.

A considerable body of theory and empirical research have emphasized the profound impacts of increasing environmental variability on diversity maintenance in natural communities through the storage effect (Chesson 2000). Among other factors, the diversity of species observed in nature can be maintained when species differ in their responses to temporal variation in environmental conditions, which may manifest as demographic decoupling between species (Chesson and Warner 1981, Chesson 1994, 2000). In this study, we combine a neighborhood modeling approach (Uriarte et al. 2004, Comita et al. 2010) with perspectives from recent applications of species coexistence theory (Angert et al. 2009, Adler et al. 2013) to explore the relative importance of indirect effects from biotic interactions vs. species’ direct responses to environmental fluctuations in driving forest regeneration dynamics (Fig. 2). We use the phrase “demographic decoupling” to refer to the aggregate environmental effect, including both direct and indirect effects, on the observed degree of asynchrony in seedling survival between species over time. Under the storage effect, a demographic decoupling might be observed when environments of different years, operating through autecological differences in functional or other physiological traits, can contribute to variation in species performance directly, with larger functional differences in response to environment between species corresponding to stronger demographic decoupling (Angert et al. 2009). On the other hand, demographic decoupling can also arise from environmentally driven changes to the

![Fig. 1. Snow-ice storm and La Niña events in the climatic data from southern China (south of 35° N, China). Bars indicate days of snow-ice storm during winter, with continuous low temperature and snow-ice storms of > 5 d (left axis), whereas gray dots and black circles represent the occurrence of eastern Pacific (EP) and central Pacific (CP) La Niña events, respectively, from 1960 to 2009. Gray lines represent annual variability of total precipitation in dry season (August–November) in Gutian, Kaihua County, since 1958 (right axis) and the gray area is the study period from 2006 to 2014.](image)
density and identity of competitors and the strength of per-capita interactions between species indirectly, with increasing asynchronous population dynamics when there are larger differences among species in their responses to neighbors/neighborhood (i.e., the density and identity of neighboring plants) over time (Pake and Venable 1995).

Given the limited knowledge about the relative importance of the direct and indirect pathways driving seedling dynamics in a changing environment, the primary goal of our study is to assess to what extent are the demographic decoupling among species a function of the direct environmental effects as well as the indirect effects mediated by neighborhood interactions (e.g., abiotic conditions alter plant sensitivity to competitors, Callaway et al. 2002). Specifically, we investigated two questions: (Q1) Do neighborhood interactions mediate seedling demographic response to interannual environmental variation? (Q2) Is species seedling survival temporally decoupled, and if so, whether the decoupling of seedling survival between species can be predicted by plant functional traits and altered neighborhood interactions? To address Q1, we look for significant interactive effects of neighborhood, year, and species on focal seedling survival by including interactions among these variables in mixed-effects models. To answer Q2, we first quantify the magnitude of demographic decoupling between species, as measured by the statistical interaction between species and year for seedling survival. We then calculate (1) species’ differences in response to temporally varying physical environment. (d) The direct environmental effect can be assessed by testing the role of interspecific variation (absolute differences) in plant functions (climate sensitivity and traits): demographic decoupling between species is expected to increase with functional differences between species. Each point for panels c and d represents the square root of the average pairwise squared difference between two species.

**MATERIALS AND METHODS**

**Study site and seedling plots**

The study was conducted in the predominantly old growth, subtropical forest of the GTS National Nature Reserve 24-ha Forest Dynamics Plot (FDP), China.
(118.12°E, 29.25°N). All woody stems with DBH (diameter at breast height, 1.3 m) ≥ 1 cm were tagged, mapped, and identified to species at 5-yr intervals beginning in 2005. Detailed descriptions of community composition, climate, and topography of GTS FDP can be found in Legendre et al. (2009). In May 2006, a seed rain and seedling-monitoring network was initiated along trails, with 130 seed traps following CTFS-ForestGEO protocol (Harms et al. 2000). Each seed trap was accompanied by three adjacent 1-m² seedling plots placed 2 m from each seed trap on three sides away from the trail. All woody plants <1 cm DBH were tagged, measured (height and number of leaves) and identified to species in the plots three times a year before 2008 (May, August and December) and twice a year afterwards (May and August) to document new recruits and survivors (Chen et al. 2010). Not all individuals could be identified to the species level, and < 0.1% recruits that were ultimately recorded as unknown were excluded from the analyses. We selected the May census date (from 2006 to 2014) as the annual point of comparison for seedling status (alive or dead).

Statistical analyses

Neighborhood models of seedling survival.—To assess neighborhood mediated environmental effects on seedling survival, we examined random effects of neighborhood × species × year and neighborhood × year interactions in a generalized linear mixed model by using the following equations:

\[
s_{ijk} = \text{Bernoulli}(p_{ijk})
\]

\[
\text{logit}(p_{ijk}) = \beta_0 + \beta_1 \times \log(\text{Height}_{ijk}) + (\gamma_0 + \pi_j + \pi_k + \pi_{jk})
\times \text{Neigh}_{ijk} + \phi_j + \phi_k + \phi_{jk} + v_{pt} + v_t.
\]

(1)

(2)

In this model, \(p_{ijk}\) is the probability of seedling survival of individual \((i)\) from species \((j)\) and census year \((k)\); \(\beta_0\) and \(\beta_1\) are overall mean intercept and the effect of log-transformed initial seedling height (Height); \(\gamma_0\) is the main fixed effect of neighborhood (i.e., the density and identity of neighboring plants); \(\pi_j, \pi_k,\) and \(\pi_{jk}\) denote random neighborhood effects at species, year, and species × year interaction level; and \(\phi_j, \phi_k,\) and \(\phi_{jk}\) represent random effects of species, year, and species × year interaction on focal seedling survival. As seedling survival is likely to exhibit some degree of spatial dependence, the effects of seedling plot and census trap station were incorporated as spatial random terms (\(v_{pt}\) and \(v_t\)) in the model to control for potential spatial autocorrelation (Chen et al. 2010). Significant random neighborhood effects depending on year (\(\pi_s,\) the neighborhood × year interaction) and species × year interaction (\(\pi_{sk},\) the neighborhood × species × year interaction) indicate community-level and species-level seedling response to yearly variation are modulated by neighborhood effects, respectively.

Our analysis of the neighborhood effects relies on the traditional analyses of competition, in which seedling survival is regressed as a function of the density and identity of neighboring seedlings and adult trees in the vicinity (<20 m; Uriarte et al. 2004, Comita et al. 2010). Seedling neighborhood variables included the numbers of conspecific and heterospecific seedlings and the Simpson index of diversity of all seedlings that existed in the same 1 × 1 m seedling plot during the census in which the focal seedling was recorded (Metz et al. 2010). As basal area performed better than tree number, adult neighborhood variables were quantified as the sum of the basal area of conspecific or heterospecific tree and the Simpson diversity of all trees ≥ 1 cm DBH within 20 m from the center of the seed trap station (Comita et al. 2009). These biotic variables were selected because they are expected to be most strongly reflecting lateral and vertical biotic interactions in forest communities (Uriarte et al. 2018). As the 2008 winter storm changed the forest tree composition and canopy openness, we used the 2005 FDP census data to calculate adult neighborhood variables for seedling cohorts before 2008, and 2010 tree census data was used for seedling cohorts after 2008. Each neighborhood variable (Neigh) was standardized to a mean of zero and unit variance and then included one variable at a time in order to manage model complexity. Seedling species with fewer than five individuals in each of at least four years were excluded as focal species (see Appendix S1: Table S1).

Quantifying demographic decoupling among species 2

We used the concept of demographic decoupling to quantify species’ differences in response to yearly variation. For seedling survival dataset, we tested for a significant interaction between species and year on seedling survival after controlling for the main effects of year, species, log-transformed seedling height, and seedling plot nested within each census station by using a mixed model. We decomposed the random effect of species × year interaction on seedling survival into an effect for each species in each year using the ranef function (lme4 package in R) and then calculated pairwise demographic dissimilarity (\(D\)) of seedling survival between all species pairs. The ranef function is a generic function to extract the conditional modes of the random effects from a fitted mixed model object (Bates et al. 2015). In our application, demographic dissimilarity was calculated as the square root of the mean squared differences in the interaction effects (\(x\)) at each census year \((k)\) for species pair \(i\) and \(j\), and is defined as

\[
D_{ij} = \sqrt{\frac{\sum (s_{ik} - s_{jk})^2}{M_{ij}}}
\]

(3)

where we summed the squares of the differences in each year (excluding years in which any one of the species was absent) and then dividing by the number of years in which both species were observed (\(M = 4-8\) yr; Angert
et al. 2009). Species that have similar response to yearly variation will have smaller differences compared to species that respond dissimilarly to yearly variation.

**Calculation of species’ differences in response to neighbors over time, demographic sensitivity to climatic variables and functional traits**

We created neighborhood-effect distance matrices to describe species’ differences in response to neighborhood interactions across years. We used the ranef function mentioned above to extract the significant random effects of neighborhood on seedling survival depending on species-by-year interaction for each species in each year ($\pi_{ik}$ in Eq. 2) and then calculated the neighborhood-effect dissimilarity between all species pairs by using the same approach as mentioned in Eq. 3.

To quantify species demographic sensitivity to interannual environmental variability, we modeled seedling survival using annual censuses from 2006 to 2014 against interannual variation in seasonal temperature and ln(seasonal precipitation) after removing seedling height effect by using a mixed-effects approach. This model allows climatic effects on seedling survival varying across species by adding a species-level random slope. Random intercepts were species and seedling plot nested within each seedling census station. Species-specific slopes were used as estimates of species’ demographic sensitivity to climate variables. Daily temperature and precipitation data were obtained from the GTS National Nature Reserve weather station (<5 km from GTS FDP) for each year and used to calculate total cumulative precipitation and average minimum and maximum temperatures during three seasons: growing season (May–July), dry season (August–November), and cold season (December–February).

Light is usually considered to be an important factor in regulating seedling recruitment and survival after the 2008 winter storm disturbance. We hypothesize that differential species response to changing light conditions is a potential contributor to demographic dissimilarity among species. However, as the interannual variation in understory light condition was not measured directly, we used seven field measured functional traits (i.e., leaf area, specific leaf area, wood density, seed mass, maximum height, leaf nitrogen content, and leaf phosphorus content) that were measured as a part of previous research (Liu et al. 2016) to infer the potential effects of changing light availability. These traits were selected as they were usually regarded as continuous indexes of the species regeneration light requirements (Poorter and Kitajima 2007, Poorter 2009). A principal components analysis (PCA) was adopted to evaluate relationships among these traits and we extracted PCA axes 1 (PC 1) to represent tradeoffs in light partitioning among species, which explained 40.9% of variation among traits (Appendix S1: Table S2). The first component had large negative loadings for wood density and positive loadings for specific leaf area, leaf nitrogen content, and leaf phosphorus content (Appendix S1: Table S2).

**Correlates of seedling demographic dissimilarity**

We used multiple regression on distance matrices (MRM) to analyze the correlates of seedling demographic dissimilarity (Lichstein 2007). MRM is an extension of partial Mantel analysis and can be used to estimate the explanatory power of multiple explanatory variables on one response variable. We explored the influence of neighborhood-effect distance matrices and plant autecological difference matrices (i.e., species absolute differences in climate sensitivity and functional traits) for their abilities to explain demographic dissimilarity among species. As species are not phylogenetic independent, we calculated phylogenetic (cophenetic) distance among species by using a well-resolved molecular phylogenetic tree (Erickson et al. 2014). We adopted phylogenetic relatedness as a predictor for the effects of phylogenetic history among species on seedling demographic dissimilarity, though no significant effect was found (Mantel test, $r = 0.035$, $P = 0.368$). In addition, we also used Mantel tests to evaluate the relationship between the pairwise differences among species for each trait and difference in average seedling survival as some of the traits used might be also related to other aspects of species biology. For multitrait comparisons, we identified the combination of trait differences that best described average seedling survival difference and $P$ values were adjusted for multiple comparisons using the Benjamini-Hochberg correction. Finally, we estimated the importance for each of the explanatory variables relative to the others by using the calc.relimp function in the R package relaimpo (Groemping 2006) and partition the variation of seedling demographic dissimilarity to pure neighborhood effects, pure environmental effect (i.e., direct effects of climate sensitivity and functional traits), and shared factors by comparison of $R^2$ values between the three models (combined, neighborhood effect only, and environmental effect only; Lichstein 2007).

All analyses were conducted in R 3.5.0 (R Development Core Team 2018). Mixed models were fitted using the glmer function in the lme4 package (Bates et al. 2015). The significance of the fixed and random terms was determined by Wald’s $z$ test, and likelihood ratio tests (LRTs) performed by comparing each model with the correspondingly reduced model (Bolker et al. 2009). All MRM models were implemented using the MRM function in the R package ecolodist (Goslee and Urban 2007).

**Results**

**Interactions between neighborhood variables and yearly variation on seedling survival**

Climate was highly variable during the study period (Fig. 1) and the impacts of 2008 winter storm and annual environmental variability on seedling community composition was marked (Appendix S1: Fig. S1). By analyzing annual seedling survival for 58 woody species over the nine census years of the study, we tested how yearly
environmental variation affects local biotic interactions among tree seedlings and nearby larger trees. Collectively, these species represented 95.8% of 25,404 seedling observations we monitored (Appendix S1: Table S1).

Pertinent to our first research question, we modeled focal seedling survival across years as a function of intra- and interspecific interactions within the neighborhood. Neighborhood models were preferred compared to neighborhood independent model based on the Akaike Information Criterion (AIC), suggesting pervasive neighborhood dependent interactions (Table 1). The estimated main fixed effects of most predictor variables were not significant after controlling for the random effects at species, year and their interaction level, except for heterospecific seedling density (Table 1). Seedlings surrounded by more heterospecific neighbors generally had enhanced survival rates, whereas conspecific neighbors tended to have a negative effect. Furthermore, we found a significant interaction between year and heterospecific tree basal area on seedling survival, indicating that the impact of competition with larger trees varied from year to year (variance = 0.012, likelihood ratio test \( P = 0.008 \); Table 1). Importantly, the effects of conspecific and heterospecific seedling density, as well as tree neighborhood diversity on seedling survival all varied significantly across species-by-year interaction term (variance = 0.023–0.112, likelihood ratio test \( P < 0.020 \); Table 1). Thus, there is ample evidence that at the individual species level, species differed in their response to neighbors over time.

*The relative importance of factors contributing to temporally decoupled seedling survival among species*

Measurements of the demographic decoupling across species show that species respond to years (corresponding to differences in environmental conditions, among other factors) in different ways, a key prerequisite for the temporal storage effect to operate in this community (variance = 0.250, likelihood ratio test \( P < 0.001 \) for the species \( \times \) year interaction). We quantified demographic dissimilarity among species and then explored the factors driving the observed asynchronous seedling survival.

Combined MRM models, which examine correlations between seedling demographic dissimilarity, and neighborhood-effect distance matrices and tree autecological difference matrices, explained 66.1% of the variation in the data (Table 2). The best predictors of asynchronous seedling survival, in order of importance, were species differences in response to neighborhood tree diversity, and differences among species in sensitivity to precipitation in dry season and average maximum temperature in growing season (Fig. 3). Most of this explanatory power came from interspecific variation in the effect of neighborhood tree diversity, which was significantly and positively correlated with temporally decoupled seedling survival (Table 2). Specifically, species pairs with more different responses to neighborhood tree diversity also had more different patterns of seedling survival (Fig. 4). After accounting for other environmental and biotic factors, species differences in tree diversity effect explained 20.3% of the variation in among-year synchrony of seedling survival (Fig. 3). In variation partitioning analyses, 43.9% \((a + b)\) of the interspecific variation \(R^2\) in seedling survival over time was explained by species differences in neighborhood effects and nearly half of that was jointly explained by environmental effects \(b = 23.6\%\), compared to 22.2\% \((c)\) for the pure environmental effects (i.e., direct effects of climate sensitivity and functional traits; Table 2).

**DISCUSSION**

To explore the relative importance of direct and indirect environmental effects on community dynamics, we

Table 1. Summary of statistical analyses of neighborhood effects on seedling survival.

<table>
<thead>
<tr>
<th>Neighborhood variable</th>
<th>Main fixed neighborhood effect†</th>
<th>Random neighborhood effect‡</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seedlings within 1-m² plot</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conspecific seedling density</td>
<td>−0.004</td>
<td>0.005</td>
<td>0.047</td>
</tr>
<tr>
<td>Heterospecific seedling density</td>
<td>0.114*</td>
<td>0.003</td>
<td>0.027*</td>
</tr>
<tr>
<td>Seeding Simpson diversity</td>
<td>0.067</td>
<td>0.006</td>
<td>0.099**</td>
</tr>
<tr>
<td>Trees ≥ 1 cm DBH within 20 m radius</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conspecific tree basal area</td>
<td>−0.277</td>
<td>0.005</td>
<td>0.075*</td>
</tr>
<tr>
<td>Heterospecific tree basal area</td>
<td>0.077</td>
<td>0.012**</td>
<td>0.033**</td>
</tr>
<tr>
<td>Tree Simpson diversity</td>
<td>−0.029</td>
<td>0.003</td>
<td>0.020†</td>
</tr>
<tr>
<td>Without neighborhood variable</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: Each of the six neighborhood variables was included in a generalized linear mixed model separately and the strength of neighborhood effect on seedling survival was modeled to vary among species (the random effect of neighborhood \( \times \) species interaction), census year (the random effect of neighborhood \( \times \) year interaction) and species-by-year interaction term (the random effect of neighborhood \( \times \) species \( \times \) year interaction). AIC, the Akaike information criterion value from each mixed model.

† Parameter estimate and \( Pr(>|z|) \) statistic for \( z \) value.
‡ Variance estimate and likelihood-ratio test \( P \) value.

\( * P < 0.05; ** P < 0.1; *** P < 0.001. \)
examined interspecific variation in species responses to interannual environmental variation and tested how altered neighborhood interactions and tradeoffs in plant functional strategies underlie the demographic decoupling of seedling survival among species. Our results support the importance of both processes but also provide compelling evidence that demographic decoupling between species is primarily driven by temporal shifts in the direction and magnitude of neighborhood interactions. These results reinforce the idea that environment-mediated changes in local biotic interactions are essential to account for when forecasting forest community shifts in a changing world.

For sessile organisms like trees, individuals interact most intensely with immediate physical neighbors (Janzén 1970, Connell 1971, Terborgh 2012, Chen et al. 2018). A comparison between mixed models with and without neighborhood effects reveals that seedling survival depends on feature of the neighborhood (Table 1). In keeping with a recent study (Uriarte et al. 2018), neighborhood interactions modulate the impacts of inter-annual environmental variation on seedling survival.

### Table 2. Results of the multiple regression on matrices analysis.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Combined model ((a + b + c))</th>
<th>Neighbor effect model ((a + b))</th>
<th>Environmental effect model ((b + c))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Difference among species in neighborhood effects over time</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conspecific seedling neighbor</td>
<td>0.0126</td>
<td>0.0063</td>
<td>0.0574</td>
</tr>
<tr>
<td>Heterospecific seedling neighbor</td>
<td>0.0104</td>
<td>0.0173</td>
<td>0.0937</td>
</tr>
<tr>
<td>Tree diversity</td>
<td><strong>0.0574</strong></td>
<td><strong>0.0817</strong></td>
<td><strong>0.0001</strong></td>
</tr>
<tr>
<td>Difference among species in response to yearly environmental variation</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total precipitation (growing season, May–July)</td>
<td>0.0148</td>
<td>0.0137</td>
<td>0.1217</td>
</tr>
<tr>
<td>Average maximum temperature, Max T (growing season, May–July)</td>
<td>0.0310</td>
<td><strong>0.0364</strong></td>
<td><strong>0.0002</strong></td>
</tr>
<tr>
<td>Total precipitation (dry season, August–November)</td>
<td>0.0226</td>
<td>0.0312</td>
<td>0.0021</td>
</tr>
<tr>
<td>Average maximum temperature, Max T (dry season, August–November)</td>
<td>0.0261</td>
<td><strong>0.0336</strong></td>
<td><strong>0.0003</strong></td>
</tr>
<tr>
<td>Average minimum temperature, Min T (cold season, December–February)</td>
<td>0.0172</td>
<td><strong>0.0363</strong></td>
<td><strong>0.0003</strong></td>
</tr>
<tr>
<td>Difference on PC1(7 key traits)</td>
<td>0.0041</td>
<td>0.0100</td>
<td>0.1387</td>
</tr>
<tr>
<td>Difference in wood density</td>
<td>0.0099</td>
<td>0.0132</td>
<td>0.0981</td>
</tr>
</tbody>
</table>

Notes: Relative contributions of neighborhood and environmental effects for explaining variation among species in seedling survival over time (demographic dissimilarity) are presented in Fig. 3. \(R^2\) represents the explained variation in decoupled seedling dynamics. Fractions \(a-c\) are as follows: \(a\) is the pure neighborhood effect \(R^2 = 0.203\); \(c\) is the pure environmental effect \(R^2 = 0.222\); \(b\) is the variation jointly explained by neighborhood and environmental effects \(R^2 = 0.236\). Variables that are significant at \(\alpha = 0.05\) following Bonferroni correction for multiple comparisons are shown in boldface type.

\(\dagger\) Model \(R^2 = 0.661\).
\(\ddagger\) Model \(R^2 = 0.439\).
\(\S\) Model \(R^2 = 0.458\).

FIG. 3. Estimated relative contribution of factors in explaining asynchronous seedling survival among species. Overall model: \(R^2 = 0.661\). Full model outputs and descriptions of predictors are provided in Table 2.
Specifically, heterospecific tree basal area affected the community-wide seedling response to yearly variation (the statistically significant random effect of heterospecific tree basal area × year interaction; Table 1). While at the species level, our analyses also provide statistical evidence that species response to neighbors (i.e., conspecific and heterospecific seedling density, and tree neighborhood diversity) depended on the census year, which differed markedly in climatic conditions of different years (the statistically significant random effects of neighborhood × species × year interaction; Table 1). Overall, these results highlight a critical role of local biotic interactions in mediating species responses to changing environments, especially in early life stages (Ettinger and HilleRisLambers 2013).

Species demographic responses could be driven either by direct physiological responses to the environment or by abiotic-driven changes in biotic interactions, such as competition, herbivory, or predation (Ibanez et al. 2013). To understand the relative importance of the direct and indirect effects of environmental change on seedling dynamics, we made two predictions about seedling performance with regard to species responses to the density and identity of neighboring plants and plant functional tradeoffs (Fig. 2c, d). By using multiple regression on distance matrices (MRM), a significant portion of temporally decoupled seedling survival can be explained by differences in demographic sensitivity to interannual climate (e.g., seasonal precipitation and temperature) (Table 2). These findings are congruent with the results of study on demographic decoupling through reproduction in an annual plant community in the Sonoran desert, which demonstrate that functional tradeoffs in the timing of favorable conditions are major drivers of the magnitude of demographic decoupling (Angert et al. 2009). Additionally, we found altered interactions with neighbors are much stronger predictors of asynchronous seedling survival among species than the direct effects of climate and plant functional traits (43.9% vs. 22.2%), indicating a strong environment-dependent biotic effect on community dynamics (Suttle et al. 2007, Alexander et al. 2015, Uriarte et al. 2018). Our study provides some of the first empirical evidence from diverse forests that neighborhood-mediated environmental effects can outweigh or even reverse the direct effects of changing abiotic conditions.

The average survival difference among species was positively related to species’ differences in response to conspecific and heterospecific seedling density and neighborhood tree diversity (Appendix S1: Table S3). The positive relationships might be detected because species interactions with their neighbors are environment dependent and can vary across time via changes in interactions with pathogens and insect herbivores (Augspurger 1984, Comita et al. 2009) or via shifts in the competitive environment (Adler et al. 2009, Alexander et al. 2015). In diverse forests, the conspecific neighbor effect and heterospecific and diversity effects are commonly attributed to the role of host specific natural enemies (Janzen 1970, Connell 1971, Peters 2003). Several studies suggest that changes in abundance of herbivores and pathogens could result in temporal differentiation in enemy-mediated distance and density dependence (Lin et al. 2012, Comita et al. 2014) and asynchronous seedling survival among species might primarily be driven by differences in susceptibility to natural enemies. Second, altered species’ competitive environments could also contribute to asynchronous seedling survival. A recent experimental study, which looked at monocultures vs. mixed seedlings exposed to drought, suggested that competition for water in drought environment was reduced in more diverse neighborhoods (O’Brien et al. 2017). However, this probably cannot be used to explain the patterns we found as competition for limiting resources has been considered to be weak to nonexistent in diverse forests (Paine et al. 2008, Forrister et al. 2019). A third possibility is that the effects of the surrounding neighborhoods tell more about local habitat heterogeneity than biotic interactions (Comita and Hubbell 2009). Seedling survival of species with differential

![Fig. 4. Seedling demographic dissimilarity is correlated with species differences in response to (a) neighborhood interaction (Mantel r = 0.651; P < 0.001; tree neighborhood diversity) and (b) interannual environmental variation (Mantel r = 0.52; P < 0.001; total precipitation in dry season).](image)
habitat preferences would be expected to be quite differently linked to the neighboring seedling and tree community. These explanations are not mutually exclusive, and manipulative studies elucidating the mechanisms that drive temporal variation in neighborhood effects will be crucial for understanding future responses of forests to environmental change.

Environmental fluctuations can help to maintain diversity in communities when species differ in their demographic responses to that variation (Chesson 2000, Adler et al. 2013, Usinowicz et al. 2017). The full quantification of the strength of the storage effect requires estimating the covariance between species per capita growth responses to the environment in the absence of competition with the impacts of competition, which has proved challenging in many plant communities (reviewed in Adler et al. 2013). As a first step toward exploring the potential for the temporal storage effect to promote diversity in this system, we quantified demographic decoupling between species, which is an important prerequisite for the storage effect to operate. Variation in seedling survival was sensitive to annual environmental variation. Specifically, seedling survival depended significantly on the interaction between species and year after controlling for the main effects of year and species. It is therefore important to consider temporal environmental variation along with other fundamental axes of niche differentiation in future investigations of the drivers of species coexistence in diverse forest communities (Wright 2002, Valladares et al. 2015).

Light is usually considered one of the most important resource gradient driving seedling dynamics after disturbance events in forest communities (Comita et al. 2009, Jin et al. 2018). The 2008 winter storm in the site caused extensive damage to the forest canopy and changes in understory light conditions. Species differences on PC1 scores (seven key traits) (Appendix S1: Table S2) quantified species light acquisitive trade-off between rapid growth and resource capture under favorable conditions (e.g., light-demanding species: low wood density, large specific leaf area, and high leaf nitrogen, and phosphorus content) and the ability to survive under high crowding and stress conditions (e.g., shade-tolerant species, high wood density; Wright et al. 2004, Lasky et al. 2014). Surprisingly, the degree of seedling demographic decoupling was statistically unrelated to difference on PC1 (Table 2). This may be because increases in light availability following disturbance in diverse forests are often short lived, which likely contributed to decreased interannual variation in understory light availability (Walker 1991). Additionally, we indeed found wood density, related to allocation to growth vs. plant resistance to pathogens (Chave et al. 2006), was significantly related to the species-by-year interactions for seedling survival, but this relationship disappeared after accounting for other factors (Table 2 and Appendix S1: Table S3). Conversely, species’ demographic sensitivity to average maximum temperature in growing and dry season, and total precipitation in the dry season were significantly related to the demographic decoupling between species (Table 2). The relative lower predictive power of functional traits might be attributed to the fact that easily measured traits included might not be the most relevant to species demographic responses to environmental change (e.g., water use, resistance to drought and natural enemies; Yang et al. 2018).

Although our study suggests indirect environmental effects mediated by neighborhood interactions outweigh the direct effects, our conclusions are tempered by the relatively short time period of the study compared to the life span of trees. If species interactions are not dependent on environmental change at later life stages, results restricted to seedling stage might overestimate the importance of the indirect effects on the entire community. Further study employing multiple tree stages is needed to provide a detailed insight. Nevertheless, it is worth noting that seedling dynamics are central to achieve an understanding of the long-term response of a forest to environmental change as the seedling stage has thought to be the bottleneck of forest regeneration, and overall forest dynamics are largely determined by biotic and abiotic processes that operate most intensely at the seedling stage (Green et al. 2014).

Our results reported here demonstrate that partially decoupled seedling survival across years is explained by a complex combination of variation among species in altered neighborhood interactions as well as interspecific variation in the physiological and demographic responses to annual environmental variation. Environmental change can alter interactions among co-occurring plants and in turn alter species’ responses over time. Therefore, our study emphasize the critical role of neighborhood interactions in predicting the impacts of environmental change and predictions based solely on the autecology of plant species may fail to forecast future shifts in the diversity and composition of complex communities.

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