Received: 18 May 2021 | Revised: 27 September 2021 | Accepted: 10 November 2021

DOI: 10.1002/ecy.3643

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Interannual climate variability has predominant effects on seedling survival in a temperate forest

Zhichao Xu[1,2,3] | Daniel J. Johnson[4] | Kai Zhu[5] | Fei Lin[1,3] | Ji Ye[1,3] | Zuoqiang Yuan[1,3] | Zikun Mao[1,2,3] | Shuai Fang[1,3] | Zhanqing Hao[6] | Xugao Wang[1,3]

[1]CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China

[2]University of Chinese Academy of Sciences, Beijing, China

[3]Key Laboratory of Terrestrial Ecosystem Carbon Neutrality, Liaoning Province, China

[4]School of Forest, Fisheries, and Geomatics Sciences, University of Florida, Gainesville, Florida, USA

[5]Department of Environmental Studies, University of California, Santa Cruz, California, USA

[6]School of Ecology and Environment, Northwestern Polytechnical University, Xi'an, China

Correspondence
Xugao Wang
Email: wangxg@iae.ac.cn

Funding information
National Natural Science Foundation of China, Grant/Award Numbers: 31961133027, 31770666, 32001121; K.C. Wong Education Foundation; Key Research Program of Frontier Sciences, Chinese Academy of Sciences, Grant/Award Number: ZDBS-LY-DQC019; Strategic Priority Research Program of the Chinese Academy of Sciences, Grant/Award Number: XDB31030000; US National Science Foundation, Grant/Award Numbers: 1926438, 2045309

Handling Editor: Anthony W. D'Amato

Abstract

Mechanisms such as conspecific negative density dependence (CNDD) and niche partitioning have been proposed to explain species coexistence and community diversity. However, as a potentially important axis of niche partitioning, the role of interannual climate variability in driving local community dynamics remains largely unknown. Here we used a 15-year monitoring data set of more than 53,000 seedlings in a temperate forest to examine (1) what are the relative effects of interannual climate variability, biotic interactions, and habitat conditions on seedling survival; (2) how the effects of biotic interactions change with interannual climate variability, and habitat conditions; and (3) whether the impacts of interannual climate variability, biotic interactions, and habitat conditions differ with plant traits. Interannual climate variability accounted for the most variation in seedling survival at the community level, followed by biotic interactions, and habitat conditions. Increased snowpack and decreased minimum temperature during the non-growing season had positive effects on seedling survival. Effects of conspecific neighbor density were weakened in higher snowpack, effective accumulated temperature, elevation, and soil-resource gradient, but were intensified with increased ultraviolet radiation, maximum precipitation, minimum temperature, and soil moisture. In addition, the relative importance of interannual climate variability versus biotic interactions differed depending on species-trait groups. Specifically, biotic interactions for gravity-dispersed species had a larger effect size in affecting seedling survival than other trait groups. Also, gravity-dispersed species experienced a stronger CNDD than wind-dispersed, probably because wind-dispersed seedlings rarely had adult conspecifics nearby. We found that interannual climate variability was most strongly associated with seedling survival, but the magnitude of climatic effects varied among species-trait groups. Interannual climate variability may act as an inhibitor or accelerator to density-dependent interactions and should be accounted for in future studies, as both a potential direct and indirect factor in understanding the diversity of forest communities.

KEYWORDS
conspecific negative density dependence, interannual climate variability, relative contribution, species traits, survival variation

INTRODUCTION

Understanding how species can stably coexist in diverse communities is a fundamental question in ecology (Chesson, 2000; Wright, 2002). Mechanisms such as conspecific negative density dependence (CNDD) (Harms et al., 2000; Zhu et al., 2015) and niche partitioning (Johnson et al., 2017; Pasinelli, 2000) have been proposed and tested to explain the maintenance of biodiversity. CNDD can suppress the performance (i.e., survival and growth) of host offspring close to the parent host individual due to strong host-specific natural enemies and intraspecific competition (Connell, 1971; Janzen, 1970), which facilitates species coexistence and diversity maintenance (LaManna et al., 2017; Zhu et al., 2015). Considerable numbers of studies have found that the magnitude of CNDD at higher latitudes may be smaller compared with lower latitudes, leading to an explanation of the latitudinal gradient in species diversity (Johnson et al., 2012; LaManna et al., 2017; but also see Chisholm & Fung, 2018, Huelsmann & Hartig, 2018, and Detto et al., 2019). However, biotic interactions are probably similarly strong at all latitudes, but are partially offset by greater effects of abiotic conditions at higher latitudes (Comita, 2017). Therefore, the relative contribution of biotic and abiotic effects is important for understanding the maintenance of species diversity.

Niche partitioning allows each species to divide resource availability and therefore avoid competitive exclusion (Johnson et al., 2017). Niche partitioning may result from a few crucial abiotic variables, for example, light availability, soil water content, nutrient resource, and topographic conditions (Kobe & Vriesendorp, 2011). While numerous studies provide evidence for the significant effects of niche partitioning at early life stages (e.g., seedling of plant species) and diversity may be maintained by differences among species in resource use (Silvertown, 2004), niche partitioning alone is unlikely to explain the marked diversity of plant communities (Comita & Stump, 2020). The relative importance of niche partitioning resulting from habitat heterogeneity in terms of abiotic factors, such as light, soil moisture (SM), and elevation, is often less compared with CNDD (Johnson et al., 2014). However, as a potentially important axis of niche partitioning in plant communities, interannual climate variability was rarely included to test the role of abiotic factors in maintaining species diversity (Zuidema et al., 2013).

The seedling stage is the most vulnerable period in the whole life history of a plant, and the most sensitive to changes in the external environment (Clark & Clark, 1989). So, seedling establishment and survival play an important role in shaping community succession and diversity, and the distribution patterns of species (Kuang et al., 2017). Recent studies in subtropical and tropical forests have shown that interannual variation of climate variables (e.g., precipitation, solar radiation) have strong impacts on seedling survival and help to predict the responses of communities to the changing environment (Song et al., 2018; Uriarte et al., 2018). To our knowledge, little information is known about the role of interannual climate variability in driving community dynamics, specifically the importance of climate variables relative to edaphic and topographic factors, and biotic interactions in natural temperate forests (Ali et al., 2019).

In addition, forest propagules may suffer either increased or decreased CNDD mortality depending on habitat heterogeneity and changing climate (LaManna et al., 2016; Uriarte et al., 2018). The frequency, direction, and magnitude of biotic interactions are being strongly altered under climate warming, temperature instability, and extreme precipitation events (Romero et al., 2018). Studies in tropical forests have found that seedling survival had a positive response to increased solar radiation (Uriarte et al., 2018), and the negative effects of conspecifics on survival were intensified during high precipitation and increased temperatures (Song et al., 2018), which led us to question whether these effects were observable in temperate forests as well. Observations on such effects would increase our understanding of whether different coexistence mechanisms operate in temperate forests compared with tropical forests.

Species with different traits may inherently vary considerably in survival (McCarthy-Neumann & Kobe, 2008; Kobe & Vriesendorp, 2011). Some evidence has shown that shade-intolerant seedlings tend to dominate in the high light gaps and grow fast with leaves, which may be more vulnerable to enemies and experience greater resource competition than shade-tolerant species (Coley & Barone, 1996). Seedlings of gravity-dispersed species may be more affected by CNDD due to the higher seed density close to their parents (Howe & Miriti, 2004), resulting in severe predation from specialized predators (Janzen, 1970), in contrast wind-dispersed seedlings may escape from high mortality caused by CNDD through a greatly dispersed distance (Bai et al., 2012). Also, plant lifeforms (e.g., trees and shrubs) may determine the capability to defend against enemies and environmental stress (Howe & Miriti, 2004). Beyond quantifying the effects of species traits on survival, it is essential to understand the process in which climate influences plant performance mediated by species traits (Uriarte et al., 2016). Furthermore, identifying species traits that most closely correlate with the effects of climate stressors on tree performance is a key step toward testing differences in species responses to climate variability and forecasting forest dynamics in the future (Fisher et al., 2010).

Here, we used a 15-year monitoring data set of more than 53,000 seedlings in a temperate forest to evaluate the relative contribution of interannual climate variability, biotic interactions (CNDD), and habitat conditions on seedling survival in community and different species-trait groups. Specifically, we asked the following questions:

1. What are the effects of interannual climate variability, biotic interactions, and habitat conditions on seedling survival? We predict that all these factors contributed to seedling survival, but interannual climate variability would have stronger effects than biotic interactions (CNDD) and habitat conditions (Uriarte et al., 2018).
2. How does the strength of CNDD vary with climate and habitat conditions? We hypothesize that seedlings will experience stronger CNDD under higher SM and soil fertility due to strong host-specific natural enemies and intraspecific competition (LaManna et al., 2016). Conversely, lower minimum temperature will weaken the effects of CNDD, because cold weather could inhibit the activity and accumulation of pathogens and insects around conspecific neighborhoods.
3. How do species traits affect the contribution of interannual climate variability, biotic interactions, and habitat conditions? We expect species that are more susceptible to CNDD are shade intolerant and gravity dispersed, because shade-intolerant species tend to have shorter lived leaves, which may be more palatable to enemies (Coley & Barone, 1996). Gravity-dispersed species tend to produce high seedling densities close to the adults, which generates considerably negative effects from species-specific enemies drawn to conspecific neighbors.

MATERIALS AND METHODS

Study site and data collection

This research was conducted in a 25-ha (500 m × 500 m) Changbaishan (CBS) temperate forest dynamic plot (42°23′ N, 128°05′ E) in Northeast China. The CBS plot was established by the Chinese Academy of Science (CAS) in collaboration with the Forest Global Earth Observatory (ForestGEO, http://www.forestgeo.si.edu) (Davies et al., 2021). In 2004, 150 seed traps (0.5 m^2) were established to monitor seed rain and litterfall (Appendix S1: Figure S3). Three 1 m^2 seedling plots were placed 2 m away from three sides (west, north, east) of each seed trap. In each seedling plot, woody plants <1 cm diameter at breast height (DBH) were defined as seedlings, and they were tagged and identified. The height of each seedling was measured from the ground to the apical bud. For this study, we used annual seedling data collected from 2005 to 2019, which included 53,928 seedlings, representing 17 tree species and 28 shrub species.

Calculation of neighboring densities

Four neighborhood biotic variables were quantified: conspecific and heterospecific seedling densities (from this point forwards S.con and S.het), and conspecific and heterospecific tree densities (from this point forwards T.con and T.het). T.con and T.het were calculated based on basal area divided by the distance between conspecific and heterospecific neighbor and the focal seedling (Equation 1) (Kuang et al., 2017). Using 2004, 2009, 2014, and 2019 plot censuses data (trees and shrubs with DBH ≥1 cm), we determined the best combination for community-level analysis and each trait group separately (Appendix S1: Figure S1) (exponent [a, b] from 0 to 2 in increments of 0.25 for diameter [a] and distance [b]) (Johnson et al., 2017), by fitting survival models with covariate for seedling height, conspecific and heterospecific seedling densities, and conspecific and heterospecific tree neighborhoods at three distances (10, 20, and 30 m). The best combination (a, b) was indicated by the AIC score (Appendix S1: Figure S1):

$$\boldsymbol{A} = \sum_i^N \mathrm{BA}_i{}^a / \mathrm{DISTANCE}_i{}^b \qquad (1)$$

where i is an individual tree; $\boldsymbol{A}$ is T.con or T.het calculated based on basal area modified by the DISTANCE between conspecific and heterospecific neighbor and the focal seedling and BA is the basal area of conspecific or heterospecific individual tree.

Climate and habitat variables

We defined the interannual climate variability as the fluctuation of yearly meteorological factors collected at the meteorological station, which was located 4 km from the CBS plot. To assess the effects of interannual climate variability on seedling survival, we selected six climate factors (growing season ultraviolet radiation [UV], growing season solar radiation [RAD], growing season effective accumulated temperature [EAT], growing season maximum precipitation [RAIN], non-growing season minimum temperature (TEM), and non-growing season snow depth [SNOW]) through a correlation analysis (Appendix S1: Figure S5 and Table S5; Appendix S2).

Elevation was measured by a total station (https://www.jurovichsurveying.com.au/faq/what-is-a-total-station) at the four corners of a 20 × 20 m grid in the 25-ha plot. We calculated the elevation in a 1 × 1 m grid using kriging interpolation methods. Elevation was estimated at the center point of the seedling plot, and convexity was calculated for each seedling plot (Kuang et al., 2017). For the soil-resource gradient (Appendix S2), we interpolated the soil variables to 1 × 1 m grid by kriging, and converted the calculated values for each seedling plot. To reduce the multicollinearity of soil variables, we performed a principal component analysis (PCA) on soil variables. The first principal component (PCA1), which explained 55.24% of the total soil variation, was used to describe the total soil fertility of each seedling plot (Mao et al., 2019) (Appendix S1: Figure S2 and Table S2).

Statistical analyses

We modeled seedling survival from 2005 to 2019 as a function of three types of fixed effects, including (1) biotic neighborhoods, (2) climate variables, and (3) habitat conditions, using a generalized linear mixed-effects model (GLMM) (Appendix S1: Table S1). The GLMM was a binomial regression, with the response variable as a complementary log–log transformation of seedling state: 1 (survived) or 0 (died), and all continuous explanatory variables were standardized by subtracting the mean and dividing by the standard deviation. Seedling height was included as a covariate to account for the size-dependent survival (Johnson et al., 2017). Census year, species, and seedling plot were included as random effects within our models (Kuang et al., 2017; Appendix S1: Table S7). Each species-trait type was not used as a categorical predictor in the model; instead, we modeled these groups: Tree and Shrub species (Bai et al., 2012), Shade-tolerant and shade-intolerant species (Wang et al., 2012), Gravity- and Wind-dispersed species (Bai et al., 2012) separately, which allowed us to interpret the results separately (Appendix S1: Table S6). Because predictors were all Z-scored prior to analyses, the relative importance of each predictor could be simply calculated as the ratio between its parameter estimate and the sum of absolute values of the beta coefficients of all predictors, and expressed as a percentage (Le Bagousse-Pinguet et al., 2017). In addition, we conducted a sensitivity analysis to evaluate the influence of dominant species *Fraxinus mandschurica* on the community-wide estimates and correlates of interspecific variation results (Appendix S1: Figure S6).

All analyses were conducted in R 3.6.2 (R Development Core Team; http://r-project.org). We fit models using the "glmer" function in the *lme4* package in R (Bates et al., 2015).

RESULTS

Relative contribution of biotic and abiotic variables

The relative contribution of climate, biotic interactions, and habitat conditions in explaining seedling survival varied greatly at the community level (R^2 = 0.44, Appendix S1: Table S9). Climate factors had predominant effects on seedling survival (64.7%), followed by biotic interactions (8.3%) and habitat conditions (6.8%) (Appendix S1: Table S3). The initial size (Height; 20.2%) had a strongly positive effect on seedling survival (Figure 1). EAT and SNOW showed positive relationships with seedling survival, whereas UV, RAIN and TEM significantly decreased seedling survival (Figure 1). In addition, EAT (18.1%) and SNOW (15.6%) contributed the most among abiotic factors (Appendix S1: Table S4). Seedling survival showed a positive response to increases in SM and elevation (Figure 1). T.con (5.7%) had the most strongly negative effect within biotic interactions on seedling survival (Appendix S1: Table S4).

Effects of climate variability and habitat heterogeneity on CNDD

CNDD significantly varied with climate factors and habitat conditions at the community level (Figure 1; Appendix S1: Table S8). The negative effects of conspecifics on seedling survival were intensified with increased growing season UV radiation, RAIN, and non-growing season TEM (Figure 2a–c), but high EAT and SNOW could weaken the negative strength of T.con (Figure 2e, f). The effects of CNDD were slightly stronger under higher SM but weakened with increasing elevation (Figure 2d,g). Specifically, the strength of CNDD

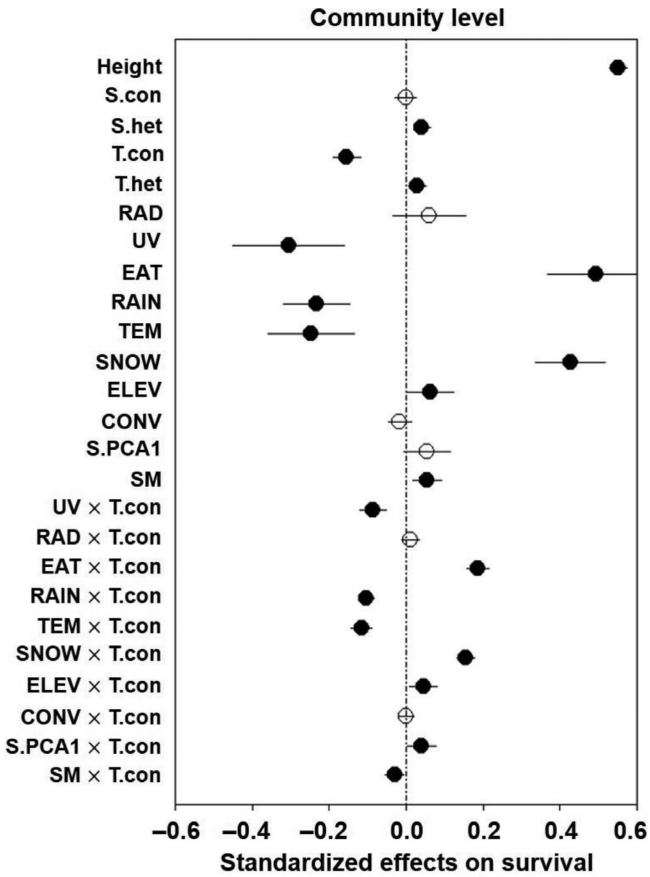

FIGURE 1 Community-wide estimates of interannual climate variability, habitat conditions, and biotic neighborhoods on seedling survival. Filled circles indicate significant effects ($p < 0.05$) and white circles mean no significance. CONV, convex degree, EAT, growing season effective accumulated temperature; ELEV, elevation; RAD, growing season radiation; RAIN, growing season maximum precipitation; S.con/S.het, conspecific/heterospecific seedling density; S.PCA1, soil-resource gradient; SM, soil moisture; SNOW, non-growing season snowpacks; T.con/T.het, conspecific/heterospecific adult density; TEM, non-growing season minimum temperature; UV, growing season ultraviolet radiation

decreased with increasing S.PCA1 (resource-rich environments) (Figure 2h).

Differences with species traits

The relative effects of climate, biotic interactions, and habitat conditions on seedling survival were significantly related to species traits (Appendix S1: Table S9). Climate factors had a high relative contribution (68.7%) to the variation on tree seedling survival ($R^2 = 0.45$), while biotic factors (9.4%) had only approximately one-ninth of the contribution of climate variables for tree seedlings (Appendix S1: Table S3). The relative contribution of climate variability was also higher than biotic interactions among shrub species (59.4% vs. 7%, $R^2 = 0.30$), shade-tolerant species (57.3% vs. 14.1%, $R^2 = 0.46$), shade-intolerant species (68.1% vs. 10.1%, $R^2 = 0.41$), and wind-dispersed species (66.4% vs. 7.5%, $R^2 = 0.42$) (Appendix S1: Table S3). Particularly, we found a relatively higher contribution for biotic interactions (25.7%, $R^2 = 0.50$) within gravity-dispersed species compared with the other trait groups (Figure 3h; Appendix S1: Table S3).

The top two abiotic variables in explaining survival variation were EAT and SNOW for each species-trait group (Figure 3; Appendix S1: Table S4). Comparatively, T.con was the strongest predictor of seedling survival within biotic interactions (Figure 3; Appendix S1: Table S4), especially for gravity-dispersed species (Figure 3h). As we predicted, gravity-dispersed and tree seedlings were more susceptible to CNDD than wind-dispersed and shrub seedlings, however, shade-tolerant and shade-intolerant species did not significantly differ (Figure 3g). In addition, increased UV significantly correlated with reduced seedling survival, except for the tree seedlings (Figure 3a,d,g).

DISCUSSION

In this study, we used a 15-year monitoring data set to assess the relative contribution of interannual climate variability, biotic interactions, and habitat conditions in explaining seedling survival in a temperate forest. Interannual climate variability is the most strongly associated with seedling survival compared with biotic variables and habitat conditions. Specifically, seedling survival responded positively to increased snowpack, decreased with minimum temperature during the non-growing season, and was negatively related to conspecific densities at the community level. Additionally, we found that seedlings would experience a stronger CNDD process when precipitation increased and snowpack decreased, both of which were projected outcomes of climate change in this region (Wang et al., 2021; Zhou et al., 2020). This study also revealed variations with species traits for the relative importance of biotic and abiotic variables and the impacts of climate variability and habitat conditions on biotic interactions, further supporting the potential role of species traits in shaping community structure and population regulation.

Seedling survival was most sensitive to climate variability

Previous studies have generally found that seedling survival is often more strongly affected by biotic

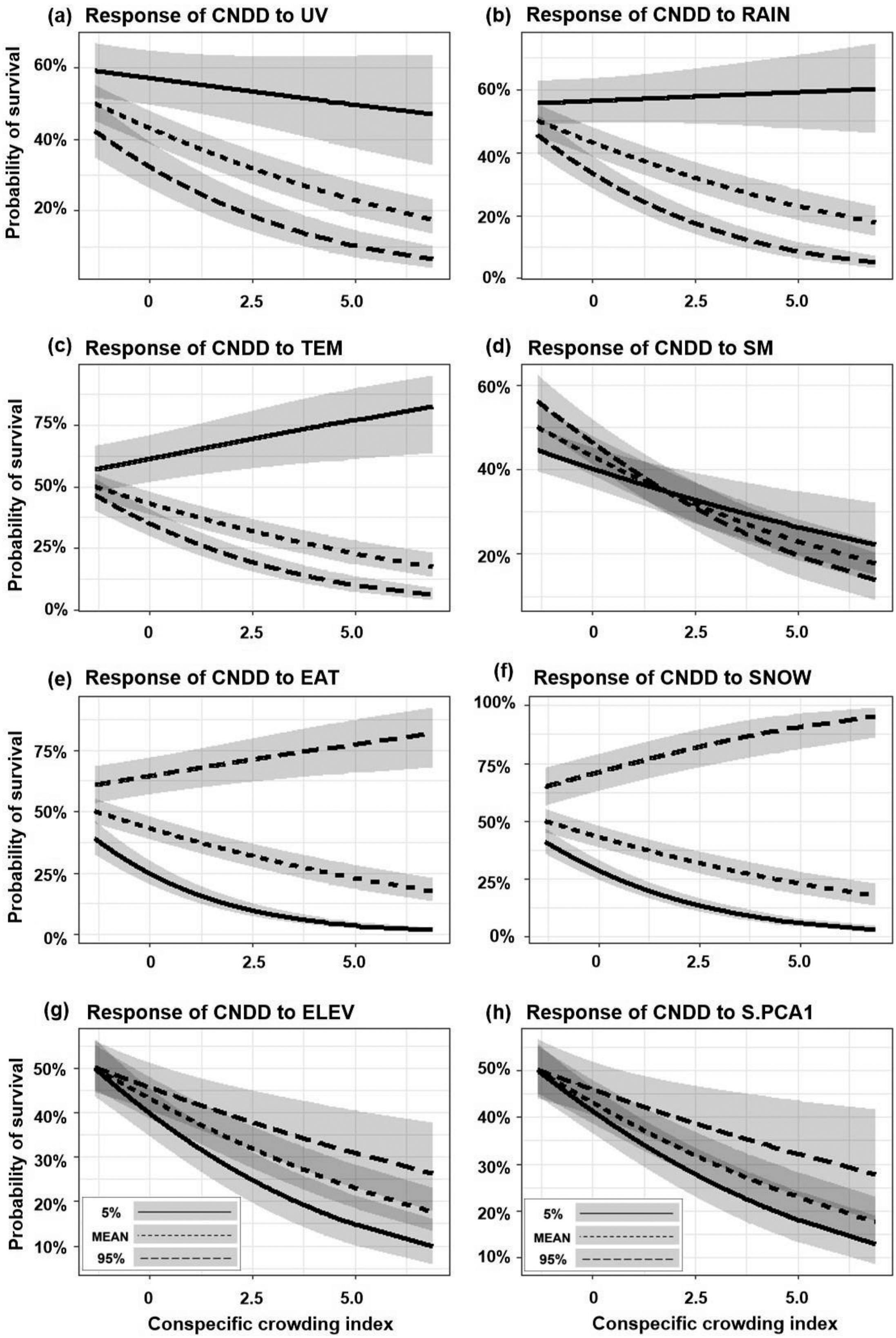

FIGURE 2 (a–h) Response of seedling survival to conspecific density for various climate and habitat variables. We calculated the 5% (solid lines), 95% (dashed lines) quantiles, and the mean values (dotted lines) of each variable to analyze the variation in the conspecific negative density dependence (CNDD) with different levels of climate and habitat variables (e.g., (a) the strength of CNDD at different levels is: 95% > MEAN > 5%). Abbreviations used are consistent with Figure 1

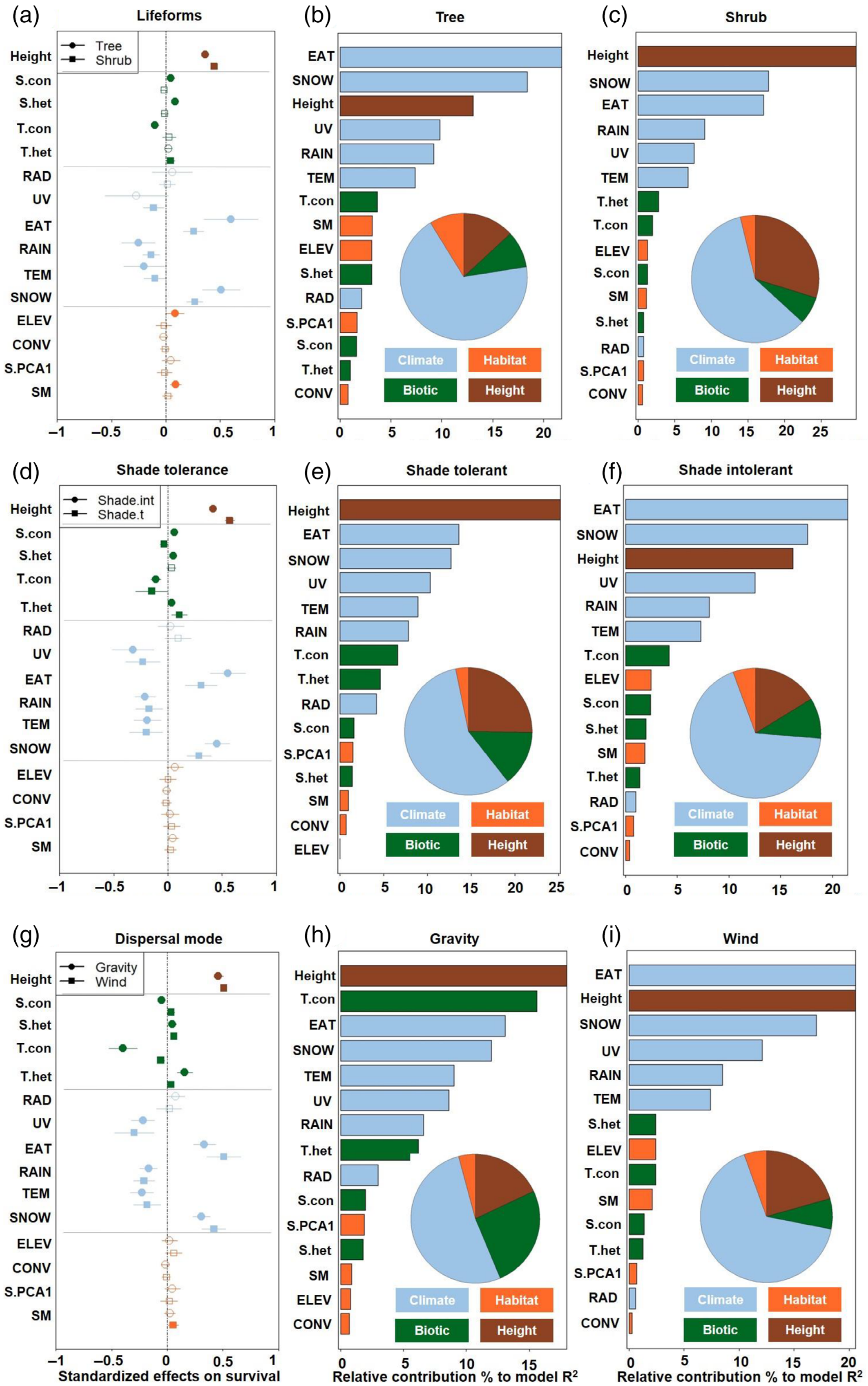

FIGURE 3 Legend on next page.

neighborhoods than abiotic conditions in temperate forests (Johnson et al., 2014; Yao et al., 2020). The seedling stage is particularly vulnerable to climatic fluctuations and efforts to predict the ongoing effects of a changing climate on forest community should consider climate and how its effects on regeneration dynamics play out in long-term development processes (Uriarte et al., 2018). Our results for abiotic factors including interannual climate variability demonstrated stronger effects on seedling survival than biotic neighborhoods, providing further evidence that temporal variation in climate if included could improve our ability to predict seedling survival dynamics in temperate forests.

Among these climate factors, EAT had the strongest impact on seedling survival at the community level. The significantly positive relationship between EAT and survival potentially supports the theory that resources and heat together could be used as the measure of available energy (Pausas & Austin, 2001). We also found a negative correlation between the maximum precipitation and survival rate, which was consistent with a recent study (Johnson et al., 2017) that stated that increased rainfall would accelerate the seedling mortality potentially due to a benefit for pathogen and herbivore populations (Swinfield et al., 2012). Additionally, heavy precipitation in a short time could cause severe water logging, leading to anoxic soil conditions and reductions in survival (Born et al., 2015). Unlike the positive effects of increased UV radiation on survival in which UV radiation may improve plant resistance to external interference and promote growth (Ballare et al., 2012; Uriarte et al., 2018), we found a negative relationship between seedling survival and UV radiation, which could be explained by the direct and indirect mechanisms. On the one hand, numerous studies have indicated that rising UV radiation may directly result in the decomposition of chlorophyll, destruction of protein structure, and decrease in photosynthesis for plants (Takeuchi et al., 1996). On the other hand, UV radiation can indirectly reduce litter decay rates through the inhibition of microbial decomposer activity (photoinhibition), and the destruction of UV on chemical content and nutrient release (Pancotto et al., 2003). However, it is unfortunate that we did not have the understory light availability (canopy cover) data for each seedling plot, which has been reported to have a large impact on seedling dynamics (Uriarte et al., 2018).

With an average of 5 months of winter conditions in the CBS forest site we found that decreased minimum temperature and increased snowpack during the non-growing season significantly contributed to a higher seedling survival. Low temperatures might induce dormancy in plants, which is a survival strategy for plants to resist risk from fluctuant environments (Rohde & Bhalerao, 2007), especially at the seed and seedling stages. Freezing temperature, conversely, is also a limiting factor for individual plant performance (Parker, 1963), which may result in injuries to roots, stems or bud tissue, further affecting plant survival and growth in the following growing season (Augspurger, 2013; Pescador et al., 2018). However, as a natural safeguard, thick snowpacks insulate soil and seedling from fluctuations in air temperature, and protect seedlings from the damage of more frequent freeze–thaw cycles and freezing to greater depths, and maintains the stability of nutrient cycling (Cline, 1997). In temperate regions, the transition from winter to spring is becoming increasingly unpredictable because of warming winter temperatures, leading to "false springs," which will weaken the cold hardiness for woody plants (Augspurger, 2013). Additionally, elevated temperatures reduce the depth and duration of non-growing season snowpacks (Stewart, 2009), making vegetation experience wider temperature fluctuations, greater exposure to herbivores, more frequent freeze–thaw cycles, and freezing to greater depths (Augspurger, 2013; Smull et al., 2019), potentially reducing the ability to grow and tolerate stem removal in the following growing season (Pescador et al., 2018). Specifically, we found soil and topographic variables had the least explainability for seedling survival. The lack of response may be that habitat data were estimated indirectly by kriging rather than directly estimated on a plot-by-plot or year-by-year basis.

Climate variability and habitat heterogeneity influence biotic interactions effects

We found a positive relation between seedling survival and heterospecific neighbor densities, which could be potentially explained by the "habitat effect" (Comita & Hubbell, 2009) and "species herd protection hypothesis" (Peters, 2003). The former indicated a resource-rich location where all seedling survival is not limited by resource

FIGURE 3 Parameter estimates of effects of climatic, habitat conditions and neighborhoods on seedling survival for plant-type guilds (top row), shade-intolerance guilds (middle row), and dispersal-mode guilds (bottom row). Filled circles indicate significant effects ($p < 0.05$) and open symbols indicate p-values >0.05. Pie charts represent the contribution of interannual climate variability, biotic interactions, habitat conditions, and initial size to model R^2. Bar charts represent the ratio between the beta coefficient of a given predictor and the sum of absolute values of the beta coefficients of all predictors, expressed in %. Abbreviations used are consistent with Figure 1 limitation, which generates a positive association between heterospecific density and survival; the latter assumes that a host may have lower probability to be damaged by its specialized herbivores and pathogens when more heterospecific neighbors are nearby. In fact, it is difficult to precisely assign covariates into discrete categories, and future works need to further explore which mechanism leads to the positive associations between seedling survival and heterospecific density. CNDD effects could drive seedling survival dynamics and promote species diversity in plant communities (Connell, 1971; Janzen, 1970). However, the CNDD impacts on community dynamics may be linked with habitat heterogeneity and the changing environment (Song et al., 2018; Uriarte et al., 2018). The linkage of CNDD and climate is important in the context of increasingly intense climate warming, temperature instability, and extreme precipitation events (Romero et al., 2018). Our results provide, to our knowledge, the first evidence that the interactions between CNDD and interannual climate variability can have large impacts on seedling survival in temperate forests.

The strength of CNDD was enhanced by both increased maximum precipitation and SM. Several studies in tropical forests have also shown that the strength of CNDD was enhanced under high rainfall and wet conditions (LaManna et al., 2016; Uriarte et al., 2018) partially because the capacity of pathogens or herbivores to drive density-dependent mortality was reduced in drier climates and when rainfall was less frequent (Swinfield et al., 2012). In addition, we found a positive relationship between CNDD magnitude and UV radiation. As UV radiation increased, beneficial fungi that infect plant roots and assist in absorption of nutrients (termed mycorrhizae) suffered severe inhibition, while fungi (e.g., powdery mildew pathogen) that can be pathogenic for plants had great proliferation and survivorship (Newsham et al., 2000). Also, UV radiation may facilitate some insects herbivory (e.g., moth larva) proceeding faster growth and accumulation around the neighboring plants (McLeod et al., 2001), which could further intensify the CNDD mortality for seedling.

Effects of conspecific densities on seedling survival could be weakened by increased EAT because energy availability will favor the photosynthetic rate and growth rate for plants (Pausas & Austin, 2001), which could improve the seedling resistance to pathogens and insects. Conversely, cold weather (the minimum temperature during non-growing season) significantly weakened the CNDD effects. The activity and population size of insects and pathogens to specific species possibly suffered a conspicuous limitation under colder environments (Smull et al., 2019; Swinfield et al., 2012). In addition, the CNDD effects would be buffered by heavy snowpack because sites covered by snow are opportune refuges for seedling against herbivore discovery that may be a severe threat for survival during winter. Furthermore, sufficiently cold winter temperatures and deep snowpack may make the muddy days less frequent, which will help the seedling survive April and May as the ecosystem transitions between the growing and dormant seasons (Cline, 1997; Pescador et al., 2018). Overall, efforts to successfully evaluate and predict ecosystem dynamics may be futile without a clearer understanding of the influence of climate change on the strength and direction of various biotic interactions such as density-dependent mortality (Romero et al., 2018).

Impacts of biotic and abiotic variables differ with species traits

Our results showed that the relative importance of biotic interactions and interannual climate variability to seedling survival differed among trait groups (Tree and Shrub; Shade-tolerant and shade-intolerant; Gravity-dispersed and Wind-dispersed), indicating that the responses of seedling to biotic and abiotic factors are correlated with plant species' traits (Kobe & Vriesendorp, 2011). For example, compared with tree seedlings, shrub seedlings did not suffer significant CNDD effects. In fact, there were relatively few conspecific shrub adults (≥1 cm in DBH) around shrub seedlings; therefore, shrub seedlings would not sustain the severe conspecific stress found for tree seedlings. Additionally, shrub seedlings were stronger and more robust (≥30 cm in height), compared with tree seedlings for which there was no minimum cut-off (Bai et al., 2012).

Previous studies have indicated that shade-intolerant species tend to have shorter lived, and less well defended leaves, which may be more susceptible to insect and pathogen damage (Coley & Barone, 1996). However, our finding seems to reject this hypothesis that shade-tolerant species are better at resisting specific enemy pressures compared with shade-intolerant species. This result is consistent with new research in the same forest (Jia et al., 2020), probably because shade-tolerant species are often attacked by invasive, necrotrophic fungal pathogens and incidence is high in shaded habitats that are conducive to disease (Augspurger, 1984). In contrast, shade-intolerant species are infected by less invasive biotrophic pathogens (Garcia-Guzman & Heil, 2014), and necrotrophic pathogens may kill large numbers of susceptible plants (Jarosz & Davelos, 1995).

Spatial distribution of gravity-dispersed species may be more aggregated and be affected by CNDD due to high seedling density close to the conspecific neighboring adults (Howe & Miriti, 2004). Comparatively, the wind-dispersed species have a relatively higher probability to escape from enemies that live near the parents (Howe & Miriti, 2004; Bai et al., 2012). We observed stronger CNDD with gravity-dispersed species than wind-dispersed seedlings. The relative impact of conspecific densities explained the most variation among all the other variables for gravity-dispersed species. This explained the result that biotic interactions accounted for the higher proportion that affected seedling survival in gravity-dispersed species compared with other trait groups. We found that gravity-dispersed species experienced a stronger CNDD than wind-dispersed species, probably because wind-dispersed seedlings had lower adult conspecifics nearby compared with gravity-dispersed seedlings (Appendix S1: Figure S7). However, the per-capita CNDD may well be as strong for wind-dispersed species if the wind- and gravity-dispersed seedlings had the same amounts of conspecifics nearby; future works should further test the CNDD process from biological reality for these two species-trait groups.

Overall, our study provides the first quantification of the relative contribution of interannual climate variability, biotic interactions, and habitat conditions in a temperate forest. We showed the closest relationship between climate and seedling survival, followed by biotic interactions and then habitat conditions. Species traits that interact with biotic and abiotic factors could lead to differential seedling survival. The relative importance of each factor varied significantly with different species-trait groups, which provided further evidence for the framework for generating hypotheses about the mechanisms underlying tree species' responses to climate change (Fauset et al., 2012). Future work should further combine climate fluctuation with temporally changing insects, pathogens, and herbivores in forest regeneration, and investigate the feedback with soil biota across life histories to gain a more mechanistic understanding of regeneration dynamics. Testing the magnitude of climate-based contributions to species coexistence by combining with biotic interactions is a critical next step for understanding how diverse communities are structured.

ACKNOWLEDGMENTS

This work was financially supported by the National Natural Science Foundation of China (Grant 31961133027), the Strategic Priority Research Program of the Chinese Academy of Sciences (Grant XDB31030000), the National Natural Science Foundation of China (Grant 31770666 and 32001121), the Key Research Program of Frontier Sciences, Chinese Academy of Sciences (Grant ZDBS-LY-DQC019) and the K.C. Wong Education Foundation. Kai Zhu was supported by the US National Science Foundation (DEB 1926438, 2045309). We are grateful to Meihui Zhu, Shuyue Wang, and Shuang Liang for their valuable comments and suggestions in data analysis and improving this manuscript. We also thank the field workers who collected data in the plots.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Code (Xu, 2021) is available in Zenodo at https://doi.org/10.5281/zenodo.5713726.

ORCID

Zhichao Xu https://orcid.org/0000-0002-3620-5441
Kai Zhu https://orcid.org/0000-0003-1587-3317

REFERENCES

Ali, A., S. Lin, J. He, F. Kong, J. Yu, and H. Jiang. 2019. "Climatic Water Availability Is the Main Limiting Factor of Biotic Attributes across Large-Scale Elevational Gradients in Tropical Forests." *Science of the Total Environment* 647: 1211–21.

Augspurger, C. K. 1984. "Seedling Survival of Tropical Tree Species: Interactions of Dispersal Distance, Light-Gaps, and Pathogens." *Ecology* 65: 1705–12.

Augspurger, C. K. 2013. "Reconstructing Patterns of Temperature, Phenology, and Frost Damage over 124 Years: Spring Damage Risk Is Increasing." *Ecology* 94: 41–50.

Bai, X., S. A. Queenborough, X. Wang, J. Zhang, B. Li, Z. Yuan, D. Xing, F. Lin, J. Ye, and Z. Hao. 2012. "Effects of Local Biotic Neighbors and Habitat Heterogeneity on Tree and Shrub Seedling Survival in an Old-Growth Temperate Forest." *Oecologia* 170: 755–65.

Ballare, C. L., C. A. Mazza, A. T. Austin, and R. Pierik. 2012. "Canopy Light and Plant Health." *Plant Physiology* 160: 145–55.

Bates, D., M. Maechler, B. M. Bolker, and S. C. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.

Born, J., R. Bagchi, D. Burslem, R. Nilus, C. Tellenbach, A. R. Pluess, and J. Ghazoul. 2015. "Differential Responses of Dipterocarp Seedlings to Soil Moisture and Microtopography." *Biotropica* 47: 49–58.

Chesson, P. 2000. "Mechanisms of Maintenance of Species Diversity." *Annual Review of Ecology and Systematics* 31: 343–66.

Chisholm, R. A., and T. Fung. 2018. "Comment on "Plant Diversity Increases with the Strength of Negative Density Dependence at the Global Scale"." *Science* 360: eaar4685.

Clark, D. B., and D. A. Clark. 1989. "The Role of Physical Damage in the Seedling Mortality Regime of a Neotropical Rain Forest." *Oikos* 55: 225–30.

Cline, D. W. 1997. "Snow Surface Energy Exchanges and Snowmelt at a Continental, Midlatitude Alpine Site." *Water Resources Research* 33: 689–701.

Coley, P. D., and J. A. Barone. 1996. “Herbivory and Plant Defenses in Tropical Forests.” *Annual Review of Ecology and Systematics* 27: 305–35.

Comita, L. S. 2017. “How Latitude Affects Biotic Interactions.” *Science* 356: 1328–9.

Comita, L. S., and S. P. Hubbell. 2009. “Local Neighborhood and species’ Shade Tolerance Influence Survival in a Diverse Seedling Bank.” *Ecology* 90: 328–34.

Comita, L. S., and S. M. Stump. 2020. “Natural Enemies and the Maintenance of Tropical Tree Diversity: Recent Insights and Implications for the Future of Biodiversity in a Changing World.” *Annals of the Missouri Botanical Garden* 105: 377–92.

Connell, J. H. 1971. “On the Role of Natural Enemies in Preventing Competitive Exclusion in some Marine Animals and in Rain Forest Trees.” In *Dynamics of Populations*, edited by P.J. den Boer and G.R. Gradwell, 298–312. Wageningen: Centre for Agricultural Publishing and Documentation.

Davies, S. J., Iveren Abiem, Kamariah Abu Salim, Salomón Aguilar, David Allen, Alfonso Alonso, Kristina Anderson-Teixeira, et al. 2021. “ForestGEO: Understanding Forest Diversity and Dynamics through a Global Observatory Network.” *Biological Conservation* 253: 108907.

Detto, M., M. D. Visser, S. J. Wright, and S. W. Pacala. 2019. “Bias in the Detection of Negative Density Dependence in Plant Communities.” *Ecology Letters* 22: 1923–39.

Fauset, S., T. R. Baker, S. L. Lewis, T. R. Feldpausch, K. Affum-Baffoe, E. G. Foli, K. C. Hamer, and M. D. Swaine. 2012. “Drought-Induced Shifts in the Floristic and Functional Composition of Tropical Forests in Ghana.” *Ecology Letters* 15: 1120–9.

Fisher, R., N. McDowell, D. Purves, P. Moorcroft, S. Sitch, P. Cox, C. Huntingford, P. Meir, and F. I. Woodward. 2010. “Assessing Uncertainties in a Second-Generation Dynamic Vegetation Model Caused by Ecological Scale Limitations.” *New Phytologist* 187: 666–81.

Garcia-Guzman, G., and M. Heil. 2014. “Life Histories of Hosts and Pathogens Predict Patterns in Tropical Fungal Plant Diseases.” *New Phytologist* 201: 1106–20.

Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. “Pervasive Density-Dependent Recruitment Enhances Seedling Diversity in a Tropical Forest.” *Nature* 404: 493–5.

Howe, H. F., and M. N. Miriti. 2004. “When Seed Dispersal Matters.” *Bioscience* 54: 651–60.

Huelsmann, L., and F. Hartig. 2018. “Comment on "Plant Diversity Increases with the Strength of Negative Density Dependence at the Global Scale".” *Science* 360: eaar3824.

Janzen, D. H. 1970. “Herbivores and the Number of Tree Species in Tropical Forests.” *American Naturalist* 104: 501–28.

Jarosz, A. M., and A. L. Davelos. 1995. “Effects of Disease in Wild Plant-Populations and the Evolution of Pathogen Aggressiveness.” *New Phytologist* 129: 371–87.

Jia, S., X. Wang, Z. Yuan, F. Lin, J. Ye, G. Lin, Z. Hao, and R. Bagchi. 2020. “Tree Species Traits Affect which Natural Enemies Drive the Janzen-Connell Effect in a Temperate Forest.” *Nature Communications* 11: 286.

Johnson, D. J., W. T. Beaulieu, J. D. Bever, and K. Clay. 2012. “Conspecific Negative Density Dependence and Forest Diversity.” *Science* 336: 904–7.

Johnson, D. J., N. A. Bourg, R. Howe, W. J. McShea, A. Wolf, and K. Clay. 2014. “Conspecific Negative Density-Dependent Mortality and the Structure of Temperate Forests.” *Ecology* 95: 2493–503.

Johnson, D. J., R. Condit, S. P. Hubbell, and L. S. Comita. 2017. “Abiotic Niche Partitioning and Negative Density Dependence Drive Tree Seedling Survival in a Tropical Forest.” *Proceedings of the Royal Society B-Biological Sciences* 284: 20172210.

Kobe, R. K., and C. F. Vriesendorp. 2011. “Conspecific Density Dependence in Seedlings Varies with Species Shade Tolerance in a Wet Tropical Forest.” *Ecology Letters* 14: 503–10.

Kuang, X., K. Zhu, Z. Yuan, F. Lin, J. Ye, X. Wang, Y. Wang, and Z. Hao. 2017. “Conspecific Density Dependence and Community Structure: Insights from 11 Years of Monitoring in an Old-Growth Temperate Forest in Northeast China.” *Ecology and Evolution* 7: 5191–200.

LaManna, J. A., S. A. Mangan, A. Alonso, N. A. Bourg, W. Y. Brockelman, S. Bunyavejchewin, L.-W. Chang, et al. 2017. “Plant Diversity Increases with the Strength of Negative Density Dependence at the Global Scale.” *Science* 356: 1389–92.

LaManna, J. A., M. L. Walton, B. L. Turner, and J. A. Myers. 2016. “Negative Density Dependence Is Stronger in Resource-Rich Environments and Diversifies Communities When Stronger for Common but Not Rare Species.” *Ecology Letters* 19: 657–67.

Le Bagousse-Pinguet, Y., N. Gross, F. T. Maestre, V. Maire, F. de Bello, C. R. Fonseca, J. Kattge, E. Valencia, J. Leps, and P. Liancourt. 2017. “Testing the Environmental Filtering Concept in Global Drylands.” *Journal of Ecology* 105: 1058–69.

Mao, Z., A. Corrales, K. Zhu, Z. Yuan, F. Lin, J. Ye, Z. Hao, and X. Wang. 2019. “Tree Mycorrhizal Associations Mediate Soil Fertility Effects on Forest Community Structure in a Temperate Forest.” *New Phytologist* 223: 475–86.

McCarthy-Neumann, S., and R. K. Kobe. 2008. “Tolerance of Soil Pathogens Co-Varies with Shade Tolerance across Species of Tropical Tree Seedlings.” *Ecology* 89: 1883–92.

McLeod, A. R., A. Rey, K. K. Newsham, G. C. Lewis, and P. Wolferstan. 2001. “Effects of Elevated Ultraviolet Radiation and Endophytic Fungi on Plant Growth and Insect Feeding in Lolium Perenne, Festuca Rubra, F-Arundinacea and F-Pratensis.” *Journal of Photochemistry and Photobiology B-Biology* 62: 97–107.

Newsham, K. K., K. Oxborough, R. White, P. D. Greenslade, and A. R. McLeod. 2000. “UV-B Radiation Constrains the Photosynthesis of Quercus Robur through Impacts on the Abundance of Microsphaera Alphitoides.” *Forest Pathology* 30: 265–75.

Pancotto, V. A., O. E. Sala, M. Cabello, N. I. Lopez, T. M. Robson, C. L. Ballare, M. M. Caldwell, and A. L. Scopel. 2003. “Solar UV-B Decreases Decomposition in Herbaceous Plant Litter in Tierra del Fuego, Argentina: Potential Role of an Altered Decomposer Community.” *Global Change Biology* 9: 1465–74.

Parker, J. 1963. “Cold Resistance in Woody Plants.” *Botanical Review* 29: 123–201.

Pasinelli, G. 2000. “Sexual Dimorphism and Foraging Niche Partitioning in the Middle Spotted Woodpecker Dendrocopos Medius.” *Ibis* 142: 635–44.

Pausas, J. G., and M. P. Austin. 2001. “Patterns of Plant Species Richness in Relation to Different Environments: An Appraisal.” *Journal of Vegetation Science* 12: 153–66.

Pescador, D. S., A. M. Sanchez, A. L. Luzuriaga, A. Sierra-Almeida, and A. Escudero. 2018. “Winter Is Coming: Plant Freezing Resistance as a Key Functional Trait for the Assembly of Annual Mediterranean Communities.” *Annals of Botany* 121: 335–44.

Peters, H. A. 2003. “Neighbour-Regulated Mortality: The Influence of Positive and Negative Density Dependence on Tree Populations in Species-Rich Tropical Forests.” *Ecology Letters* 6: 757–65.

Rohde, A., and R. P. Bhalerao. 2007. “Plant Dormancy in the Perennial Context.” *Trends in Plant Science* 12: 217–23.

Romero, G. Q., T. Goncalves-Souza, P. Kratina, N. A. C. Marino, W. K. Petry, T. Sobral-Souza, and T. Roslin. 2018. “Global Predation Pressure Redistribution under Future Climate Change.” *Nature Climate Change* 8: 1087–91.

Silvertown, J. 2004. “Plant Coexistence and the Niche.” *Trends in Ecology & Evolution* 19: 605–11.

Smull, D. M., N. Pendleton, A. R. Kleinhesselink, and P. B. Adler. 2019. “Climate Change, Snow Mold and the Bromus Tectorum Invasion: Mixed Evidence for Release from Cold Weather Pathogens.” *AoB Plants* 11: plz043.

Song, X., D. J. Johnson, M. Cao, M. N. Umana, X. Deng, X. Yang, W. Zhang, and J. Yang. 2018. “The Strength of Density-Dependent Mortality Is Contingent on Climate and Seedling Size.” *Journal of Vegetation Science* 29: 662–70.

Stewart, I. T. 2009. “Changes in Snowpack and Snowmelt Runoff for Key Mountain Regions.” *Hydrological Processes* 23: 78–94.

Swinfield, T., O. T. Lewis, R. Bagchi, and R. P. Freckleton. 2012. “Consequences of Changing Rainfall for Fungal Pathogen-Induced Mortality in Tropical Tree Seedlings.” *Ecology and Evolution* 2: 1408–13.

Takeuchi, Y., H. Kubo, H. Kasahara, and T. Sakaki. 1996. “Adaptive Alterations in the Activities of Scavengers of Active Oxygen in Cucumber Cotyledons Irradiated with UV-B.” *Journal of Plant Physiology* 147: 589–92.

Uriarte, M., J. R. Lasky, V. K. Boukili, and R. L. Chazdon. 2016. “A Trait-Mediated, Neighbourhood Approach to Quantify Climate Impacts on Successional Dynamics of Tropical Rainforests.” *Functional Ecology* 30: 157–67.

Uriarte, M., R. Muscarella, and J. K. Zimmerman. 2018. “Environmental Heterogeneity and Biotic Interactions Mediate Climate Impacts on Tropical Forest Regeneration.” *Global Change Biology* 24: E692–704.

Wang, X., L. S. Comita, Z. Hao, S. J. Davies, J. Ye, F. Lin, and Z. Yuan. 2012. “Local-Scale Drivers of Tree Survival in a Temperate Forest.” *PLoS One* 7: e29469.

Wang, Y., X. Shen, and M. Jiang. 2021. “Spatial-Temporal Variation Characteristics of Different Grades of Precipitation in Changbai Mountain from 1961 to 2018.” *Climatic and Environmental Research* 26: 227–38.

Wright, S. J. 2002. “Plant Diversity in Tropical Forests: A Review of Mechanisms of Species Coexistence.” *Oecologia* 130: 1–14.

Xu, Z. 2021. “Zhichao-Xu/SEEDLING_A: (Xu.2021.002).” *Zenodo*. https://doi.org/10.5281/zenodo.5713726

Yao, J., B. Bachelot, L. Meng, J. Qin, X. Zhao, and C. Zhang. 2020. “Abiotic Niche Partitioning and Negative Density Dependence across Multiple Life Stages in a Temperate Forest in Northeastern China.” *Journal of Ecology* 108: 1299–310.

Zhou, X., C. Zhao, Y. Cui, M. Liu, X. Ao, N. Li, and J. Li. 2020. “Analyzing the Characteristics of Temporal and Spatial Evolution of Snowfall in Northeast China from 1961 to 2017.” *Journal of Glaciology and Geocryology* 42: 766–79.

Zhu, K., C. W. Woodall, J. V. D. Monteiro, and J. S. Clark. 2015. “Prevalence and Strength of Density-Dependent Tree Recruitment.” *Ecology* 96: 2319–27.

Zuidema, P. A., P. J. Baker, P. Groenendijk, P. Schippers, P. van der Sleen, M. Vlam, and F. Sterck. 2013. “Tropical Forests and Global Change: Filling Knowledge Gaps.” *Trends in Plant Science* 18: 413–9.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Xu, Zhichao, Daniel J. Johnson, Kai Zhu, Fei Lin, Ji Ye, Zuoqiang Yuan, Zikun Mao, Shuai Fang, Zhanqing Hao, and Xugao Wang. 2022. “Interannual Climate Variability Has Predominant Effects on Seedling Survival in a Temperate Forest.” *Ecology* e3643. https://doi.org/10.1002/ecy.3643