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Article

Functional traits mediate seedling survival response to climate in a temperate forest

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ABSTRACT

Functional traits are increasingly used to forecast the response of plant performance to abiotic and biotic conditions. However, it remains unclear how functional traits will mediate the complex responses of plants to interactive drivers in a rapidly changing world. Here, we collected 17-year monitoring data on seedlings of 28 locally coexisting species and 8 functional traits in a temperate forest, and built multi-level regression models to evaluate (1) whether seedling survival varied among species along the acquisitive-conservative strategy gradient, and which functional trait affected seedling survival; and (2) how survival of species with different functional strategies responded to negative density dependence (NDD) and climate variation. We found that species with an acquisitive strategy had higher seedling survival. Specifically, seedling survival was positively correlated with specific root length (SRL), specific leaf area (SLA), and leaf area (LA), but inversely correlated with leaf dry mass content (LDMC). Functional strategies along the acquisitive-conservative gradient showed no significant effects on survival response to conspecific and phylogenetic negative density dependence. Negative effects of heterospecific negative density dependence on seedling survival were weaker for species with higher LDMC, but stronger for seedlings with larger SRL. In addition, species with more conservative strategies had higher resistance to drought stress and freezing damage. For example, species with lower SRL and SLA, and higher LDMC had higher survival under severer seasonal drought. Also, heavier seeds and thicker roots enhanced freezing resistance, whereas higher SRL and LA intensified the negative effects of cold weather. Our study provides strong evidence that functional traits could widely mediate the effects of local biotic interactions and climatic variation on plant performance dynamics, and help to infer community assemblages and species coexistence in the context of a changing world.

1. Introduction

Understanding community assembly is one of the most enduring questions in ecology, which has important implications for the conservation and management of ecosystems [1,2]. Trait-based approach has been increasingly considered as an effective way to predict plant performance [3,4] through the use of functional traits, such as morphological and physiological traits, to infer the mechanisms in determining community composition and structure [3,5,6]. However, the magnitude of trait-performance relationships may strongly depend upon functional strategy of species as well as biotic (e.g., neighborhood crowding) and abiotic conditions (e.g., precipitation and temperature), especially in the context of a drying and warming climate [3,7,8].

Functional traits can represent important strategies of resource acquisition of species, which have been put forward to be crucial for plant performance [5,9]. However, previous studies tend to test the effects of one or several single traits [10,11], but ignore how plant performance changes with the acquisitive-conservative gradient with integrated functional traits. Generally, plants with resource-acquisitive traits (e.g., high specific leaf area (SLA), leaf area (LA), leaf nitrogen content (LNC), and specific root length (SRL)) can promote rapid resource capture and nutrient absorption under high resource availability and favorable condi-

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tions and thus exhibiting high photosynthesis rates [9,12]. Conversely, plants with resource-conservative traits (e.g., high leaf dry matter content (LDMC), root diameter (RD), wood density (WD), and seed mass (SM)) have more efficient conservation and utilization with nutrients and water [13,14]. Therefore, it is important to evaluate how demographic performance varies with the acquisitive-conservative strategy gradient, which would further improve the predictable strength of functional traits to plant demographic rates, and contribute to strategies categorization by which plants respond to environmental conditions.

Functional traits can also affect the relationship between demographic performance and negative density dependence (NDD, plant performance will be hindered when located at high local neighborhood crowding) that subsequently shapes community dynamics and structure [15–17]. Previous works have showed that high SLA further exacerbates the negative effects of neighborhood crowding on growth; meanwhile, heavier seeds can facilitate plant performance under a crowded condition [18,19]. However, other studies have also reported that functional traits (e.g., SLA, SM) of plant in tropical forests have weak or no influence on vital rates in response to neighborhood crowding [17,20]. It is notable that the crowding index in such studies is often calculated without separating conspecific and heterospecific neighbors, which makes it difficult to distinguish how functional traits mediate the effects of conspecific negative density dependence (CNDD, typically interpreted as intraspecific competition) and heterospecific negative density dependence (HNDD, typically interpreted as interspecific competition) on plant performance. CNDD has been shown to be stronger than HNDD worldwide [21,22]. Moreover, heterospecific neighbors which are more closely phylogenetically related to the focal individual have stronger negative effects (phylogenetic negative density dependence, PNDD) on seedling survival [23,24]. Therefore, further studies are needed to test the trait-mediated effects of CNDD, HNDD, and PNDD on demographic rates.

Furthermore, functional traits can mediate the response of the plant to climate change, which is critical for understanding the structure and dynamic of plant communities in fluctuant environments and for forecasting their resilience to future changes in climate [25,26]. Some studies have demonstrated that species with high WD tend to be more resistant to drought and freeze-induced embolism [27,28]. Moreover, plants with acquisitive-resource strategies (e.g., high SLA and LNC) may be more sensitive to water stress indicators, like vapor pressure deficit (VPD) and rainfall [19,25]. Recently, we have showed that climate has a predominant effect on seedling survival in a temperate forest [29] and have found that maximum cumulative water deficit (MCWD) is increasing in this region (Fig. 1). However, there is still a lack of understanding of how species traits mediate the effects of climate on plant vital rates in temperate forests, especially under drought conditions with increased VPD and MCWD [8,30]. In addition, freezing cold is a general limiting factor for plant performance in temperate forests [31], and trait variations among species could further accelerate or relieve the injuries to root, stem, or bud tissue caused by freezing cold [32]. Confirming the functional traits that are most closely related to the effects of climate stress on plant performance is a critical step toward predicting community dynamics and succession under climate change [19].

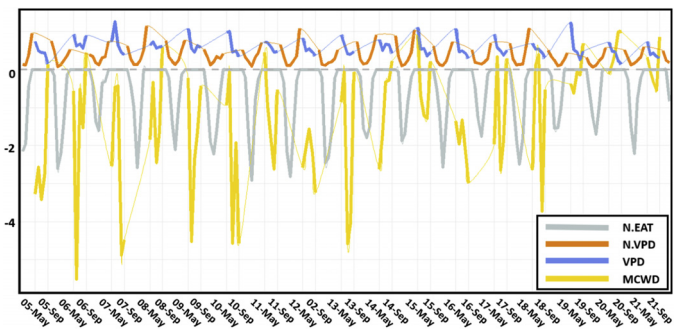

Fig. 1. Four monthly dry and freezing indexes from 2005 to 2021. N.VPD, vapor pressure deficit in non-growing season; N.EAT, negative-effective accumulative temperature in non-growing season; VPD, vapor pressure deficit in growing season; MCWD, maximum cumulative water deficit in growing season.

As the pivotal stage along community development and succession, seedling is considered to be particularly vulnerable to environmental stress given the rapid internal biophysiological changes and low stored resources [33]. Seedling survival dynamic plays a central role in forecasting key ecological processes, including population dynamics, species diversity, community structure, and ecosystem function [34]. Furthermore, seedling dynamics vary dramatically among years [35]. However, most studies have always relied on short-term data, which makes it difficult to reveal the true role of functional traits on seedling survival. Herein, we used a long-term seedling monitoring dataset over 17 years and trait information for 28 tree species in a 25-ha temperate forest plot in Northeast China to develop trait-based models of seedling survival. We ask the following questions:

Q1: Is seedling survival correlated with the acquisitive-conservative strategy gradient, and how do functional traits affect seedling survival?

Because resource-conservative species tend to have greater resistance than resource-acquisitive species [9,36], we predict that species with more conservative strategies (e.g., higher LDMC, RD, SM, and WD) would have higher average survival rates compared to species with more acquisitive strategies (e.g., higher SLA, SRL, LNC, and LA).

Q2: How do species along an acquisitive-conservative gradient respond to NDD and climate?

Functional strategies could alter species' ability to resist specific enemies and competition [36], and so we expect that more conservative species have greater resistance to CNDD, followed by PNDD, and HNDD, but species with an acquisitive strategy might have the opposite trend [37]. We also speculate that species with conservative strategies (e.g., high LDMC and SM) have relatively higher survival, but resource-acquisitive species (e.g., high SLA and SRL) survive poorly under drought (high VPD and MCWD), due to slower respiratory rates and less tough tissue caused by stem breakage in conservative species [13,38].

2. Materials and methods

2.1. 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 (Fig. S1). This region has a temperate continental climate with warm summers and long cold winters with a mean annual rainfall of 620 mm and a mean annual temperature of 3.8 °C. The CBS plot was established in 2004 by the Chinese Academy of Science (CAS) in collaboration with the Forest Global Earth Observatory (ForestGEO, http://www.forestgeo.si.edu) [39].

In 2004, 150 seed traps (0.5 m^2) were established to monitor seed rain and litterfall and three 1 m^2 seedling plots were placed 2 m away from three sides (west, north, east) of each seed trap (Fig. S1). Every year since 2005, seedlings (i.e., woody plants < 1 cm DBH, diameter at breast height) have been tagged and identified to species from June 25 to July 15 at each seedling plot. The height of each seedling was measured from the ground to the apical bud. In this study, we used annual seedling census data collected from 2005 to 2021, which include a total of 58,686 seedlings and 28 species.

2.2. Neighborhood crowding and climate

Crowding in conspecific neighborhood (*T*.con) and heterospecific neighborhood (*T*.het) was calculated based on basal area divided by

the distance between conspecific and heterospecific neighbor and the focal seedling (Eq. 1) [40], using trees and shrubs with DBH ≥ 1 cm in the 2004, 2009, 2014, and 2019 plot censuses data. We determined the best combination (for diameter [a] and distance [b], the exponent [a, b] ranges from 0 to 2 in increments of 0.25 with distances of 10, 20, and 30 m) by AIC scores at the community level (Fig. S6) [41]. Finally, 30 m scale was used to quantify the effects of neighbors on seedling survival in this target forest because the strength of CNDD gradually enhanced as the radius increased (Fig. S7), which indicated that these neighbors at broader scales (e.g., 30 cm) also have effects on seedling survival. Moreover, previous studies have generally indicated that direct neighborhood interactions generally occur within a radius distance of 30 m [42,43].

$$C = \sum_{i}^{N} \mathrm{BA}_i^{a=1} / \mathrm{DISTANCE}_i^{b=2} \tag{1}$$

where i is an individual tree; C 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 within the distance.

To calculate phylogenetic relatedness of neighbors (T.phy), a total of 63 species were added to this phylogeny using the *plantlist* [44] and *V.PhyloMaker* [45] packages. We calculated the mean observed phylogenetic distance (MOPD) between the focal individual and all heterospecifics [24]. Further, as the phylogenetic mean distance may be influenced by species richness, we used a null model to calculate expected phylogenetic distances by randomly generating 999 local neighborhoods (selected from the pool of all species in the phylogeny for neighbors ≥ 1 cm) at a given species richness and to calculate the mean and standard deviation of expected phylogenetic distances (MEPD and SDEPD) among species in each focal individual neighborhood. T.phy was calculated as follows (Eq. 2):

$$T.phy = \frac{-1 \times (\mathrm{MODP} - \mathrm{MEPD})}{\mathrm{SDEPD}} \tag{2}$$

Larger positive values of T.phy indicate that species are more closely related to the focal species [23,24].

Climate factors were collected at the meteorological station around 4 km from the CBS plot (Fig. S2). Totally, four factors were included in our analysis through selecting predictor variables in linear model only when the variance inflation factor (VIF) was less than five [46]. Vapor pressure deficit (VPD) and monthly maximum cumulative water deficit during the growing season (MCWD) were selected to represent the magnitude of drought stress to survival [47]. The VPD during non-growing seasons (N.VPD) was calculated because of strong seasonal variations in strength of VPD in Northeast China. Freezing cold was represented by negative-effective accumulative temperature (N.EAT, $< -10°C$) [48].

2.3. Species traits

We used eight functional traits describing major variation in plant functional strategies across four tissue types: leaves, stem, roots, and seeds [5,49]. Species leaf traits (specific leaf area, SLA; leaf area, LA; leaf nitrogen content, LNC; and leaf dry mass content, LDMC), root traits (specific root length, SRL; and root diameter, RD), wood density (WD), and seed mass (SM) were measured for these species in the CBS plot (Table S1) [50,51]. We synthesized these traits in a principal component analysis (PCA) to characterize variation in multivariate phenotypes across species [52]. Furthermore, we included a broken stick model to determine which PCA axis should be used in this study [53]. We found that the eigenvalue was larger than the length of broken stick only within the first PCA axis (PCA1 explained 38.96% of the total trait variation) (Fig. S8), and the PCA1 showed a clear functional strategy gradient from the resource-conservative strategy to resource-acquisitive strategy (Table S2). Therefore, only the PCA1 was retained within this study to meet our objective that how functional strategies (resource-acquisitive and resource-conservative) influence and mediated the climate impacts on seedling survival. Finally, correlation analysis was used to test the significance of contribution of each trait to the first PCA (PCA1) dimension (Table S3).

2.4. Statistical analyses

We built Bayesian hierarchical generalized linear mixed models with binomial errors to measure the effects of species traits, biotic interactions, and climate on annual survival (Eq. 3):

$$y_{i,s,q} \sim \mathrm{Bernoulli}\theta_{i,s,q} \tag{3}$$

(1) Biotic interactions models:

$$\begin{aligned}\mathrm{logit}\theta_{i,s,q} = {} & B_\beta_{0,s} + B_\beta_{1,s} T.con_{i,s,q} + B_\beta_{2,s} T.het_{i,s,q} \\ & + B_\beta_{3,s} T.phy_{i,s,q} + B_\emptyset_q\end{aligned} \tag{4}$$

(2) Climate models:

$$\begin{aligned}\mathrm{logit}\theta_{i,s,q} = {} & C_\beta_{0,s} + C_\beta_{1,s} N.\mathrm{EAT} + C_\beta_{2,s} N.\mathrm{VPD} \\ & + C_\beta_{3,s} \mathrm{MCWD} + C_\beta_{4,s} \mathrm{VPD} + C_\emptyset_q\end{aligned} \tag{5}$$

where, for given seedling i of species s in quadrat q, $B_\beta_{c,s}$ (c is the number of neighboring or climate factors) represents the effects of neighborhood crowing on seedling survival and the $C_\beta_{c,s}$ represents the climate dependence of survival. $B_\beta_{0,s}$ and $C_\beta_{0,s}$ are the average survival across species, and $B_\emptyset_q$ and $C_\emptyset_q$ indicate the random effect of quadrat.

To evaluate how species traits can mediate responses of survival to surrounding neighbors and climate, we built nine species-level submodels (eight traits + PCA1) as functions of species functional traits and strategy for climate and biotic interactions, respectively [11]. We modeled species-specific average survival ($B_\beta_{0,s}$, and $C_\beta_{0,s}$), sensitivity to density of neighbors ($B_\beta_{1,s}$, $B_\beta_{2,s}$, and $B_\beta_{3,s}$), and climate ($C_\beta_{1,s}$, $C_\beta_{2,s}$, $C_\beta_{3,s}$, $C_\beta_{4,s}$) in a higher-level model as (Eq. 4):

$$B_\beta_{c,s} = B_\beta_{c,0} + B_\beta_{c,1} * Trait \tag{6}$$

$$C_\beta_{c,s} = C_\beta_{c,0} + C_\beta_{c,1} * Trait \tag{7}$$

where $\beta_{c,0}$ and $\beta_{c,1}$ represent intercepts and slopes, respectively, and the first term of the regression $\beta_{0,s}$ is a species-specific intercept that represents species average survival. $\beta_{0,1}$ represents the relationship between survival and the trait value ($Trait$) of the focal species. Also, $\beta_{c,1}$ represents the relationship between the effect of each variable of the first level and the trait value of focal species. For instance, $B_\beta_{1,1}$ represents the mediated effects of species trait on conspecific densities.

All functional traits and neighborhood crowding were log-transformed to prevent the tail of their skewed distribution from dominating the model fit. In addition, we standardized all explanatory variables by subtracting their mean and dividing by their standard deviation to facilitate model convergence [54].

We fit models with Stan using the *rstan* package in *R* version 4.1.3 (*R* Development Core Team: http://r-project.org) [55]. We used weakly

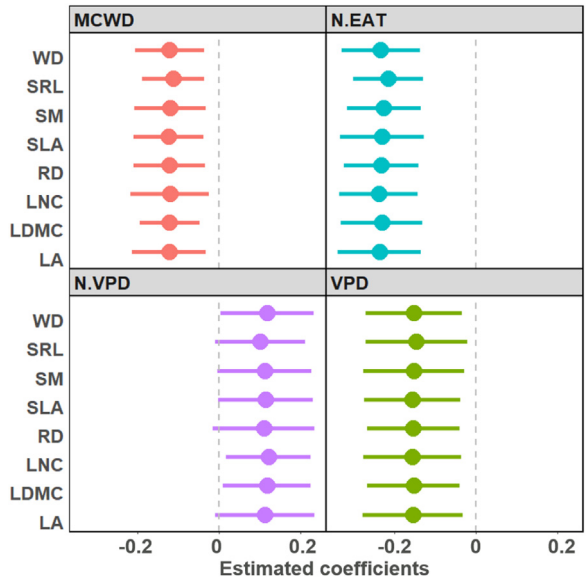

Fig. 2. Standardized regression coefficients modeling the effects of climate factors on seedling survival. WD, wood density; SRL, specific root length; SM, seed mass; SLA, specific leaf area; RD, root diameter; LNC, leaf nitrogen content; LDMC, leaf dry mass content; LA, leaf area; PCA1, acquisitive-conservative gradient; VPD, vapor pressure deficit in growing season; MCWD, maximum cumulative water deficit in growing season; N.VPD, vapor pressure deficit in non-growing season; N.EAT, negative-effective accumulative temperature in non-growing season. Circles show posterior medians of β-coefficients, and lines indicate 95% credible intervals (intersected with zero line means not significant).

informative priors as suggested by the Stan user guide [56]. We ran four parallel chains, and we considered models to have converged when the Gelman and Rubin diagnostics with a threshold of 1.05 [57], and β-parameters were considered statistically significant when 95% credible intervals did not coincide with zero.

3. Results

By testing pairwise correlations of functional traits (SLA (−0.44, $p < 0.05$), SRL (−0.38, $p < 0.05$), LNC (−0.24, $p < 0.05$), LA (−0.23, $p < 0.05$), WD (−0.12, $p > 0.05$), LDMC (0.40, $p < 0.05$), RD (0.42, $p < 0.05$), SM (0.44, $p < 0.05$)) and PCA1 (Table S3), we showed a clear gradient of functional strategies, ranging from the resource-conservative strategy with larger LDMC, RD, and SM but smaller SLA, SRL, LNC, and LA to the resource-acquisitive strategy associated with smaller LDMC, RD, and SM but larger SLA, SRL, LNC, and LA (Table S2).

Seedling survival was negatively correlated with the acquisitive-conservative gradient (Fig. S3). Particularly, seedling survival decreased with increased LA, SRL, and SLA, while larger LDMC inhibited survival in biotic models and climate models (Fig. S3). The phylogenetic relatedness of heterospecific neighbors had a significantly negative impact on survival (Fig. S4), and its strength tended to be stronger than the negative effect of heterospecifics, but weaker than the negative effects of conspecifics (Fig. S4). As predicted, drought stress and freezing cold (i.e., higher MCWD, VPD, and N.EAT) were significantly negatively correlated with survival (Fig. 2, MCWD, VPD, N.EAT), while improved N.VPD showed promoted effects on seedling survival (Fig. 2, N.VPD).

The effects of acquisitive-conservative gradient on seedling survival response to CNDD, PNDD, and HNDD were not significant (Fig. S5). However, the effects of HNDD on survival were intensified for species with higher SRL, but were offset for species with higher leaf dry mass (Fig. 3, Trait on *T.*het). In addition, resource-conservative species had increased seedling survival under freezing cold and drought stress, while

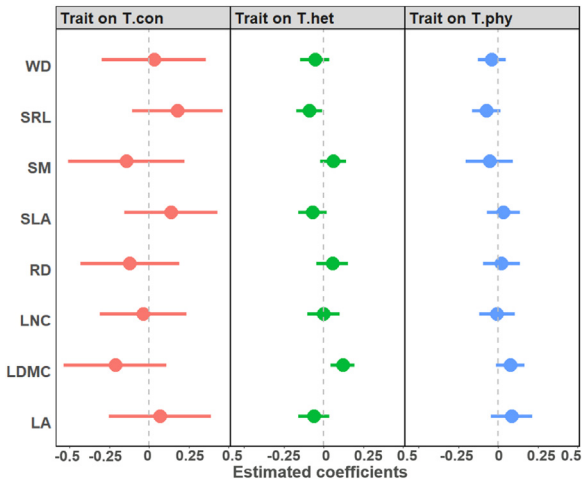

Fig. 3. Trait-mediated effects of neighbors on seedling survival. T.con/T.het/T.phy, conspecific/heterospecific adult density/phylogenetic relatedness of neighbors; Circles show posterior medians of β-coefficients, and lines indicate 95% credible intervals intersected with zero line means not significant). See Fig. 2 for trait abbreviations.

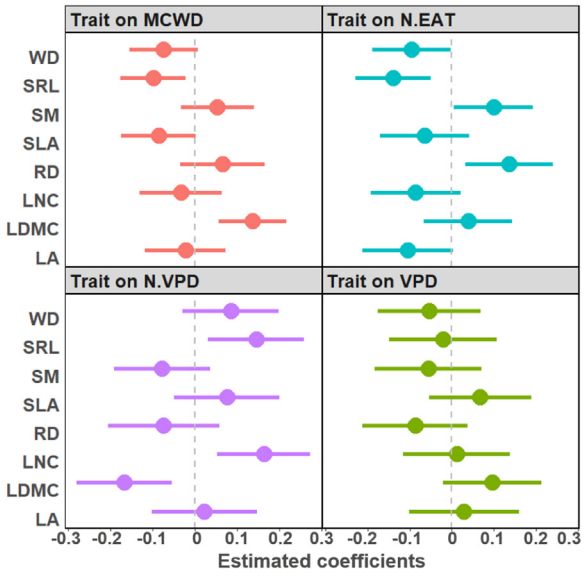

Fig. 4. Trait-mediated effects of climate impacts on seedling survival. Circles show posterior medians of β-coefficients, and lines indicate 95% credible intervals (intersected with zero line means not significant). See Fig. 2 for climate and trait abbreviations.

resource-acquisitive species had improved survival when VPD increased during non-growing season (Fig. S5). Specifically, species with larger LA, SRL, and WD had lower survival under a freezing condition, and thicker roots and heavier seeds would enhance seedling survival as N.EAT increased (Fig. 4, Trait on N.EAT). Similarly, species with larger LDMC, smaller SRL, and smaller SLA had better survival under a higher MCWD condition (Fig. 4, Trait on MCWD). Moreover, higher LNC and SRL further promoted the positive relationship between N.VPD and seedling survival, which was weakened for species with higher LDMC (Fig. 4, Trait on N.VPD).

4. Discussion

In this study, we used a 17-year dataset to test the direct effects of functional strategies on seedling survival, and the indirect effects of

functional strategies on survival response to NDD and climate. We found that seedling survival was negatively associated with the acquisitive-conservative strategy gradient, and was positively associated with SLA and SRL, but was negatively related to LDMC. Furthermore, functional traits could capture demographic-rate variation in responses to environmental conditions. In particular, survival of seedlings with relatively conservative traits (e.g., higher LDMC, RD, and SM) is robust to the negative effects of interspecific competition (HNDD), drought stress (higher VPD and MCWD), and freezing cold (higher N.AET), whereas survival of seedlings with more acquisitive traits (e.g., larger SLA and SRL) is more strongly reduced by harsh conditions.

4.1. Species traits effects on survival

We found that an acquisitive-conservative gradient with integrated functional traits were more strongly related to seedling survival than single one, and seedling survival was significantly negatively correlated with the acquisitive-conservative trait gradient. Specifically, our results showed that seedling survival was positively related to larger SRL and SLA, but negatively associated with higher LDMC. Numerous studies had shown that species with acquisitive strategies tend to have relatively fast growth but higher mortality compared to species with more conservative strategies [9,58,59]. However, we found that seedling survival was negatively correlated with the acquisitive-conservative trait gradient, which was consistent with a recent study in a temperate forest in Northeast China in which leaf area showed a significantly positive effect on seedling survival [60]. It should be noted that the trait-demography relationship might vary with ontogenetic stage (e.g., seedling, adult). Actually, more acquisitive traits (e.g., larger SLA) could determine seedling light interception efficiency, and lead to higher photosynthetic rate under limited light conditions, which may be beneficial for seedling survival [61]. On the contrary, species with more conservative traits tend to survive better at adult stage because they conserve and utilize nutrients and water efficiently and exhibit greater resistance to harsh environments like drought stress or freezing damage [14], but they may have lower survival at seedling stage because of the low resource-acquisition rates. For instance, *Pinus koraiensis* is a dominant and typical resource-conservative species in the temperate mixed forest, which have a particularly high mortality rate at seedling stage. Previous research has shown that *P. koraiensis* seedlings have almost no fine roots for nutrient absorption except one taproot, while have an enhanced performance with increasing age [62]. Future works should pay more attention to the functional trait variations at different ontogenetic stages, which is significative to further uncover the relationships between demographic rates (e.g., regeneration, growth, survival) and functional strategies.

In addition, not all functional traits were significantly associated with seedling survival, which may be due to the fact that our analysis used the species-level traits rather than the individual-level traits [3,63], which has been proved to have stronger predictions than species-level traits in this plot. Therefore, it is worth elucidating the relationships between seedling ontogenesis and individual-level traits of plants in future work [63]. Moreover, edaphic feature is another important factor in driving seedling demographics [64], and previous studies have shown that soil chemical properties [65,66], and soil moisture [41] are closely associated with seedling survival and growth. However, our recent study in the same plot showed that the weak effects on seedling survival from soil moisture and nutrients [29], therefore, we did not include the edaphic feature in this study. However, it should be pointed out that other soil factors, such as soil texture and metal ions (e.g., Fe^{2+}, Mn^{2+}) may also play key roles in plant dynamics [67,68], and it requires more comprehensive consideration of edaphic feature to improve the predictive ability in future work. Moreover, the impacts of species trait on seedling survival might be better captured by considering the effects of biotic (e.g., neighbor plants) and abiotic (e.g., climate variabilities) conditions [11].

4.2. Trait-mediated effects of neighborhood crowding on survival

We found that conspecific neighbors had the strongest negative effects (CNDD) on seedling survival, followed by heterospecifics were phylogenetically related to focal individuals (PNDD), and heterospecific neighbors (HNDD). Previous experimental work at this site has suggested that host-specific soil-borne pathogens and insects are partially responsible for decreased seedling survival in the presence of conspecific neighbors [69]. Furthermore, seedling survival was negatively influenced by the phylogenetic relatedness of heterospecific neighbors, which may be due to two non-mutually exclusive mechanisms. Firstly, closely related neighbors would suffer from stronger intraspecific competition from similar resource requirements and occupying similar niches [70]. Secondly, closely related neighbors would share more pathogens and insect herbivores due to the phylogenetic signaling of natural enemy host range [71].

In line with our expectations, species along the acquisitive-conservative gradient respond differently to different forms of neighbors. Functional traits mediated effects of HNDD but not of CNDD and PNDD, suggesting that species-level functional traits play a role in altering interspecific competition but not intraspecific competition. Specifically, the effects of HNDD on seedling survival was smaller for species with higher values of LDMC. Previous studies have suggested that LDMC is related to leaf lifespan, and that it is involved in a fundamental trade-off between rapid production of biomass as well as efficient conservation and utilization of nutrients [72–75], which may potentially strengthen the advantage of competition against heterospecifics. Moreover, we found that species with larger SRL exhibited more negative effects of HNDD on seedling survival. There have been studies already suggested that plants with high SRL might gain an advantage in water and nutrient acquisition over those of low SRL [76,77], however, roots with high SRL also exhibited small average diameter (assuming that density of the root tissue is constant) [78]. There have been evidences proved that SRL tends to be negatively correlated with root C: N ratios and root lifespan [12,79], probably leading to poorer performance under a more crowded condition with heterospecifics. In this study, we found that functional traits could only mediate the effects of heterospecifics on seedling survival probably because the traits are at the species level. Future work needs to include individual level functional traits [3,63], which might further reveal the correlations between functional traits and intraspecific competition from conspecific and phylogenetic neighbors.

4.3. Trait-mediated effects of climate on survival

Based on the long-term monitoring data, we found a rising trend for MCWD macroscopically (Fig. 1), which indicated the frequency and magnitude of water stress increased over time, and suggested that seedlings in this plot experienced increasingly severe water stress during the growing season. The significantly negative correlation between seedling survival and MCWD may be caused by the combination of physiological, mechanical, and hydraulic failure from drought [30,80]. Also, we found a negative correlation between VPD and survival, which further suggested that seedlings may be subjected to severe drought stress during growing season. Recent studies have demonstrated that high VPD during growing season could trigger water loss from the leaves, which further decreased the photosynthesis and resulted in a reduced growth and survival [81,82]. It is noted that VPD in the growing season was approximately twice as high as in non-growing season, and we found a positive correlation between N.VPD and

seedling survival, which supported the viewpoint that a increase in VPD at certain times of the year can increase plant growth performance [81]. Furthermore, freezing cold is another factor that strongly affects plant vital rates in northeast China. We found accumulated temperature below −10 °C would inhibit seedling survival, probably because of the damage to root, stem, or bud tissue caused by frost and extreme-cold events [83].

Our results showed that species with conservative strategy had a strong resistance to water stress when rainfall was less than evapotranspiration (higher MCWD). More specifically, under high MCWD conditions, species with higher values of LDMC had higher survival. In contrast, species with higher SLA and SRL had lower survival, which could be attributed to two reasons. First, higher leaf mass tends to confer drought tolerance and herbivore resistance covary with other axes of functional variation on species because of the thick leaf [84]. Meanwhile, higher SLA and SRL are often associated with shorter leaf and root span as well as thinner leaf and root diameter, which could lead to a lower drought tolerance and herbivore resistance [76]. One recent study also indicates that plants can cope with soil water limitation by continuing to function with limited water availability (i.e., tolerance through, for example, high LDMC associated with more rigid cell walls, allowing maintenance of leaf turgor at lower water potential), but limiting vital rates to periods of greater water availability (i.e., escape through e.g., large SLA and SRL that are more strongly related to early senescence than to any other drought trait) [84]. Secondly, compared to SLA, high LDMC means species have a structure with greater proportion of dry matter in relation to saturated weight [75], which symbolizes a slower production of biomass, a longer leaf lifespan, and a more efficient conservation of leaf water when drought events occur [72].

Resource-conservative strategies conferred species a stronger resistance to freezing cold during the non-growing season. Our results showed the negative effects of cold stress were buffered for species with heavy seeds and thick roots, but aggravated for species with high SRL. Larger seeds have been shown to bigger mean plant size (e.g., canopy area, mean height, and stem diameter), longer plant life span, and tougher construction, which confer species greater abilities to establish in harsh environments, and have stronger resistance to extreme environments, like freezing-cold conditions during non-growing season in temperate regions [85,86]. In addition, fine plant root injuries tend to occur primarily at cold temperature extremes, and roots are less cold-tolerant than other tissue, whereas cold damage to roots can directly influence tree seedling survival and growth [87]. In this study, we found that species with thick roots (higher RD) had a high resistance against freezing cold than thin roots (higher SRL), which can be explained by the fact that thinner roots are more likely to be damaged on root tissue by soil freezing and expansion from temperature extremes [87]. Moreover, the positive relationship between VPD during non-growing season and seedling survival was strengthened for species with acquisitive strategies (e.g., large SRL and LNC) but weakened for resource-conservative species (e.g., high LDMC). Our results further supported the established view that conservative species are more common in harsh conditions, while acquisitive species often dominate in favorable environments [9,88].

5. Conclusion

Seedling survival was negatively correlated with the acquisitive-conservative gradient in a temperate forest. Furthermore, functional traits could mediate the response of the seedling dynamics to biotic interactions and climate, and conservative strategy would confer species a stronger ability withstanding competition, drought stress, and freezing cold. Our study provides strong evidence that functional traits play an important role in species' responses to interannual climatic fluctuations that subsequently shape community dynamics and maintain biodiversity in diverse ecosystems, especially in the context of a changing world.

Data availability statement

All data that support the findings of this study can be found in the article and / or Supporting Information.

Declaration of competing interest

The authors declare that they have no conflicts of interest in this work.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.fmre.2023.12.002.

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