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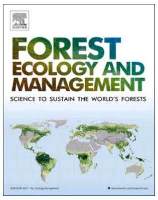

The dynamics of conspecific tree and seedling neighbors on seedling survival in a subtropical forest

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ABSTRACT

Negative intraspecific interactions could provide opportunities for heterospecific regeneration, thereby maintaining species coexistence in forest communities. Increasing conspecific tree and seedling neighbor densities often have negative correlations with seedling survival. If and how the strength of interactions change with seedling age remains a knowledge gap. In this study, we followed 2184 newly germinated seedlings belonging to 26 species for five years in a subtropical evergreen broad-leaved forest in eastern China. We tested the density distribution pattern of different aged live seedlings and used generalized linear mixed models to assess the dynamic influence of conspecific tree and seedling neighbors on seedlings survival across years. Our results showed that the density distribution of newly germinated seedlings was more clustered than the other aged live seedlings. Over five years, the clustered density distribution of live seedlings gradually weakened. Particularly, the density distribution of five years old seedlings was statistically random. Meanwhile, the degree of positive correlation between the density of live seedlings and the density of conspecific tree neighbors decreased with seedling age. Correspondingly, the conspecific seedling neighbors had a significant negative correlation with newly germinated seedlings survival in the first year and had a greater effect than conspecific tree neighbor density. As seedlings age, the conspecific tree neighbors had a greater negative relative effect on seedlings survival than the conspecific seedling neighbors. Our findings demonstrate that intraspecific negative interactions are an important mechanism on seedling survival and the magnitude of those interactions change with seedling age. In younger seedlings, intraspecific negative interactions were mainly from conspecific seedling neighbors and weakened as the seedlings aged. In later seedling ages, the interactions from conspecific tree neighbors dominated. Ultimately, these effects reduce species clumping dynamically and provide space for establishment of heterospecifics which would maintain diversity in the forest.

1. Introduction

Understanding the mechanisms of species coexistence in communities is an enduring ecological challenge. In recent decades, ecologists have increasingly found density-dependent predation and intraspecific resource competition would result in negative intraspecific interactions (Chesson, 2000). This process increased relative to interspecific interactions causing heterospecific species stabilizing regeneration (Tilman, 1982, Chesson, 2000, Adler et al., 2018). In addition, Janzen (1970) and Connell (1971) have found conspecific trees, as the host of specific pathogens and herbivores, could attract or transmit these natural enemies on their offspring. Janzen-Connell effects (hereafter called J-C effect) also result in negative intraspecific interaction, thus maintaining species diversity in the community.

Conspecific tree and seedling neighbors were regarded as the vital factors of intraspecific negative interactions on seedling survival (Webb and Peart, 1999, Comita et al., 2010, Chen et al., 2010, Johnson et al., 2012). Many field and laboratory studies of the J-C effect have proved

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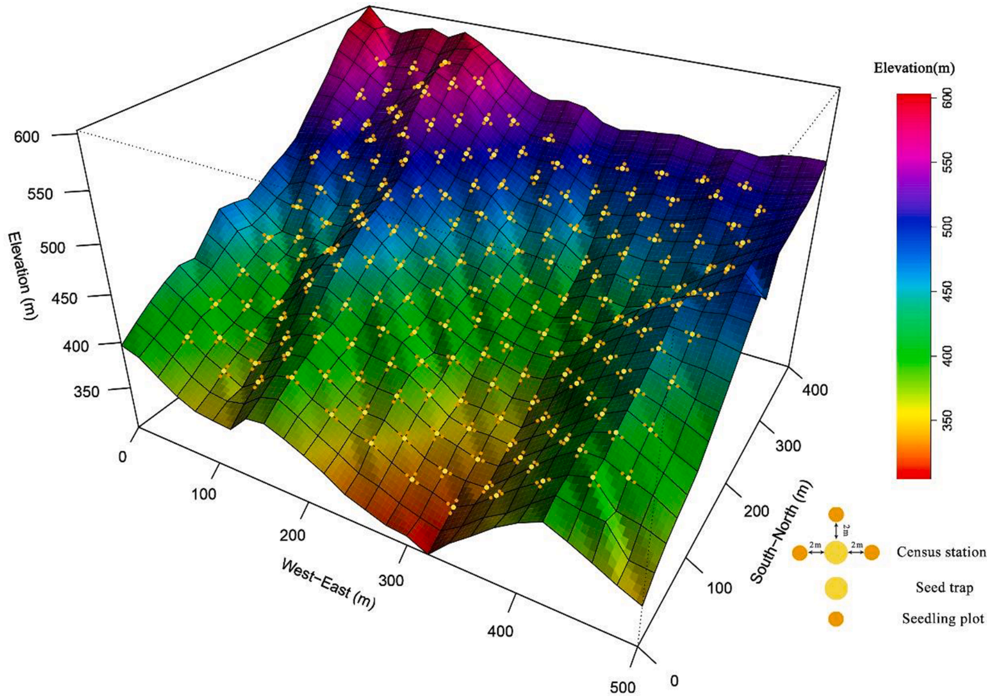

Fig. 1. Distribution of seedling plots in the Tiantong plot.

specific pathogens and herbivores is clumped in large trees, thus inhibiting conspecific seedlings survival around them (Norghauer et al., 2006, Liu et al., 2012, Bagchi et al., 2014, Liu et al., 2015, Chen et al., 2019). This seedling mortality would decrease with the distance to the conspecific trees (Terborgh, 2012, Comita et al., 2014, Murphy et al., 2017). While, conspecific seedling neighbors clumping could also increase seedling mortality due to rapid spread of natural enemies (Carson et al., 2008, Bagchi et al., 2014). In addition, seedlings aggregating to the conspecific trees (Janzen, 1970) would also cause intraspecific asymmetric (tree-seedling) (Tomé et al., 1994) and symmetric (seedling-seedling) competition (Grubb, 1977) for similar resource requirements (Hogan, 1986, Weiner and Thomas, 1986, Tomé et al., 1994, Lentz, 1999, Lewis and Tanner, 2000).

Density of conspecific seedlings determine the intensity of intraspecific negative interactions on seedling survival (Chesson, 2000). The conspecific high-density seedlings would be detected by density-responsive predator easily (Connell, 1971) or suffer the symmetric competition (Weiner and Thomas, 1986, Ammer et al., 2010). Therefore, the intensity of intraspecific negative interactions would be increased in high density area. Correspondingly, low density of conspecific seedlings would avoid density-responsive predator and symmetric competition (Connell, 1971, Harms et al., 2004), thus decreasing intensity of intraspecific negative interactions. Whereas the effect of conspecific trees would come out through distance-responsive predation (Janzen, 1970).

As seedlings die, the density distribution of live seedling would be changed. Typical seed dispersal produce a mass of offspring around the parent tree (Forcier, 1975). The density distribution of newly germinated seedlings would aggregate to the conspecific trees (Hubbell, 2001). However, due to negative density dependent mortality, the high density of seedlings would suffer with large reductions (Janzen, 1970). As time goes on, the aggregate distribution would be weakened. In the later stage of seedlings, the effects of physical environment will determine the density distribution of seedlings (Grubb, 1977).

The density distribution of seedlings can vary with age, however, few studies focus on the temporal distribution characteristic of seedling densities. Meanwhile, this characteristic will cause changes of intraspecific interactions. Ignoring it would increase bias in detection of intraspecific interactions. Here, we examine the dynamics of seedling survival in a subtropical forest over the course of five years in relation to conspecific tree and seedling neighbors. Specifically, we calculate the coefficient of variation of seedling densities and built generalized linear mixed models of seedling survival to address the following questions: (1) How did the density distribution of seedlings change with age? (2) Does the conspecific tree and seedling neighbors have correlations with seedling survival varying with time? (3) If so, do these dynamics respond to temporal variation of seedling density distribution pattern?

2. Materials and methods

2.1. Study site and data collection

The study was conducted in a 20 ha (500 m × 400 m) dynamics plot in a subtropical broad-leaved evergreen forest in Tiantong Forest Park in eastern China (hereafter called Tiantong plot) (Yang et al., 2011). This region has a subtropical monsoon climate and receives 1374 mm mean annual rainfall. The hot-humid-summer is from June to August; cold-dry-winter is from December to February. Mean annual temperature is 16.2 ℃, the maximum mean monthly temperature is 28.1℃ and minimum is 4.2℃ (Song and Wang, 1995). All trees (DBH $\geq$ 1 cm) in Tiantong plot were tagged, mapped, measured and identified to species in 2010. The dominant families are Theaceae, Lauraceae and Fagaceae (Yang et al., 2011).

To monitor seedling dynamics in Tiantong plot, we established 187 seedling census stations in two diagonal corners of each 20 m × 20 m area within the Tiantong plot. To avoid conspecfic tree neighbors out of plot, we selected the stations at least 40 m far away from the border (Fig. 1). Each census station includes one seed trap in the center and three 1 m × 1 m seedling plots. These seedling plots were located at 2 m from the center of seed trap in three random directions (Fig. 1). From October 2011 to April 2012, we tagged all the free-standing woody seedlings (DBH $\leq$ 1 cm) in 561 seedling plots. In October 2012, the newly germinated standing woody seedlings in seedling plots were tagged, mapped, measured to initial height and identified to species. We investigated 2,184 newly germinated seedlings belonging to 26 species, 19 genera, 11 families. Then, we monitored these seedlings from

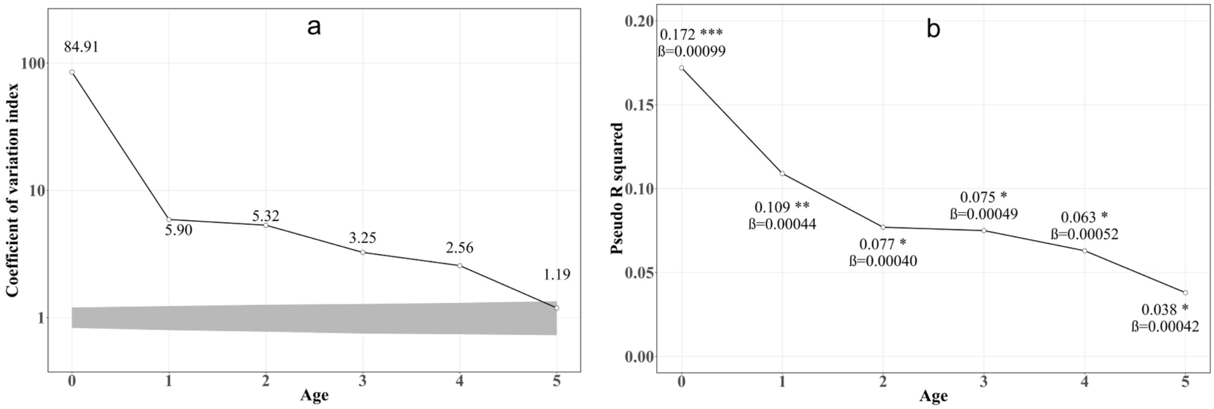

Fig. 2. Coefficient of variation index of conspecific live seedling density (a) and marginal pseudo R squared between the conspecific tree neighbors index and live seedlings density (b) in different ages. Age of "0″ represent the newly germinated seedlings. Gray area represents the 95% confidence interval. Above of confidence interval represent the clumped density distribution; Below of confidence interval represent the disperse density distribution; Between of confidence interval represent the random density distribution. "***" represent *P* value < 0.001, "**" represent *P* value < 0.01, "*" represent *P* value < 0.05.β represent coefficient of conspecific tree neighbors index.

October 2012 to October 2017. In October of each year during the study period, we surveyed the height and survival condition of these seedlings.

2.2. Data analyses

To test how density patterns of live seedlings differ with age, we calculate the coefficient of variation of conspecific seedling densities. The value of the coefficient of variation will increase with cluster densities (Blackman, 1942). To combine coefficients of variation for all species and consider their importance, we multiply by the station occurrences of each species to create a weight. This index can be specified as:

$$C_l = \mathrm{Var}\ (x_l)/\mathrm{E}\ (x_l) \tag{1}$$

$$w_l = n_l \Big/ \sum_{l=1}^{m} n_l \tag{2}$$

$$\mathrm{C} = \sum_{l=1}^{m} c_l w_l \tag{3}$$

where C_l is the coefficient of variation of species l(except the species whose live seedlings are in only one station). x_l is the live seedling numbers of species $l$in each station (equation (1)).w_l is the weight of each species l. $n_l$is the number of stations containing live seedlings of species l. m is the number of species (equation (2)). C is the coefficient of variation index (equation (3)).

In order to estimate density distribution pattern of live seedlings (clumped, disperse or random), we simulate the live seedling densities in Poisson distribution for 1999 times and calculate their coefficient of variation index (C_{random}). Then, through C_{actual} comparing withC_{random}, we could judge the actual density pattern of live seedlings. The detailed calculation process are as follows. Firstly, we calculate the seedling numbers x_l of each species l in different station (set of seedling densities). Then, we use mean of x_l ($\lambda_\mathrm{l} = \sum \mathrm{x_l}/\mathrm{n_l}$) and station numbers n_l build set of seedling densities in Poisson distribution for species l. After simulating of the whole species, we could calculate the C for this simulated data. We repeated the aboved steps for 1999 times. We could have C_{random}. Finally, we calculated the 95% confidence interval of C_{random} (lower limit is 50th minimum value; upper limit is 50th maximum value) to test the density distribution pattern of live seedlings. C_{actual} above of confidence interval of C_{random} indicates the density distribution of live seedlings is clumped; C_{actual} below indicates dispersion; C_{actual} between indicates random.

To examine the correlation between the density of live seedlings and conspecific tree neighbors along with the survival time, we built generalized liner mixed-effects models (GLMMs) with Poisson errors for different ages of live seedlings. The model with the random effects can be specified as:

$$Y_{ikl} \sim \mathrm{Poisson}\ (\lambda_{kl}) \tag{4}$$

$$Log(\lambda_{kl}) = [\alpha + \beta \times x]_{\mathrm{fixed.part}} + [\mu_l + \mu_k]_{\mathrm{random.part}} \tag{5}$$

where Y_{ikl} is number of live seedlings of species l in seedling plot i belonging to seedling station k, λ_{kl} is the parameter of Poisson distribution. λ_{kl} is equal to expected value and variance of Y_{ikl} (equation (4)). Position (μ_k) and species (μ_l) are the two subparts of the random effects. In the fixed part of the equation (5), α and β represent an intercept and a vector of coefficients of explanatory variables x respectively. x is the index of conspecific tree neighbors which were defined as the total of the basal area of conspecific trees (DBH ≥ 1 cm) within best fit range (based on comparison of models using different neighborhood radii; see the details in Table S1) and divided by the distance from the focal tree to the center of focal seedling plot (Comita and Hubbell, 2009, Lin et al., 2012, Lin et al., 2014, Liu et al., 2016). We calculate the marginal pseudo-R-squared of fixed effect (Johnson, 2014) to estimate how much the distribution of conspecific tree neighbors can explain the density of live seedlings.

To examine the dynamic effect of conspecific tree and seedling neighbors on seedling survival in Tiantong plot and consider other potential biotic and abiotic factors, we built GLMMs with binomial errors in each year of study period. The model with the random effects can be specified as:

$$Y_{ijkl} \sim \mathrm{binomial}\ \left(1, \pi_{ijkl}\right) \tag{6}$$

$$\mathrm{logit}\left(\pi_{ijkl}\right) = [\alpha + \beta \times x]_{\mathrm{fixed.part}} + \left[\mu_l + \mu_{j|k} + \mu_k\right]_{\mathrm{random.part}} \tag{7}$$

where Y_{ijkl} is 1 if focal seedling i of species l in the seedling plot$j$of station $k$alive in one year and 0 otherwise, $\pi_{ijkl}$is the survival probability of focal seedling (equation (6)). Position ($\mu_{j|k} + \mu_k$) and species (μ_l) are the two subparts of random part. Especially, the position has two levels, first level was seedling plot j belonging the station k($\mu_{j|k}$) and seconds is station k (μ_k).α and β is same as equation (5).

In this study, in addition to the intraspecific factors of conspecific tree and seedling neighbors, we also used heterospecific tree and seedling neighbors, and seedling height. The conspecific and heterospecific tree neighborhood index were similar with above mentioned (index of

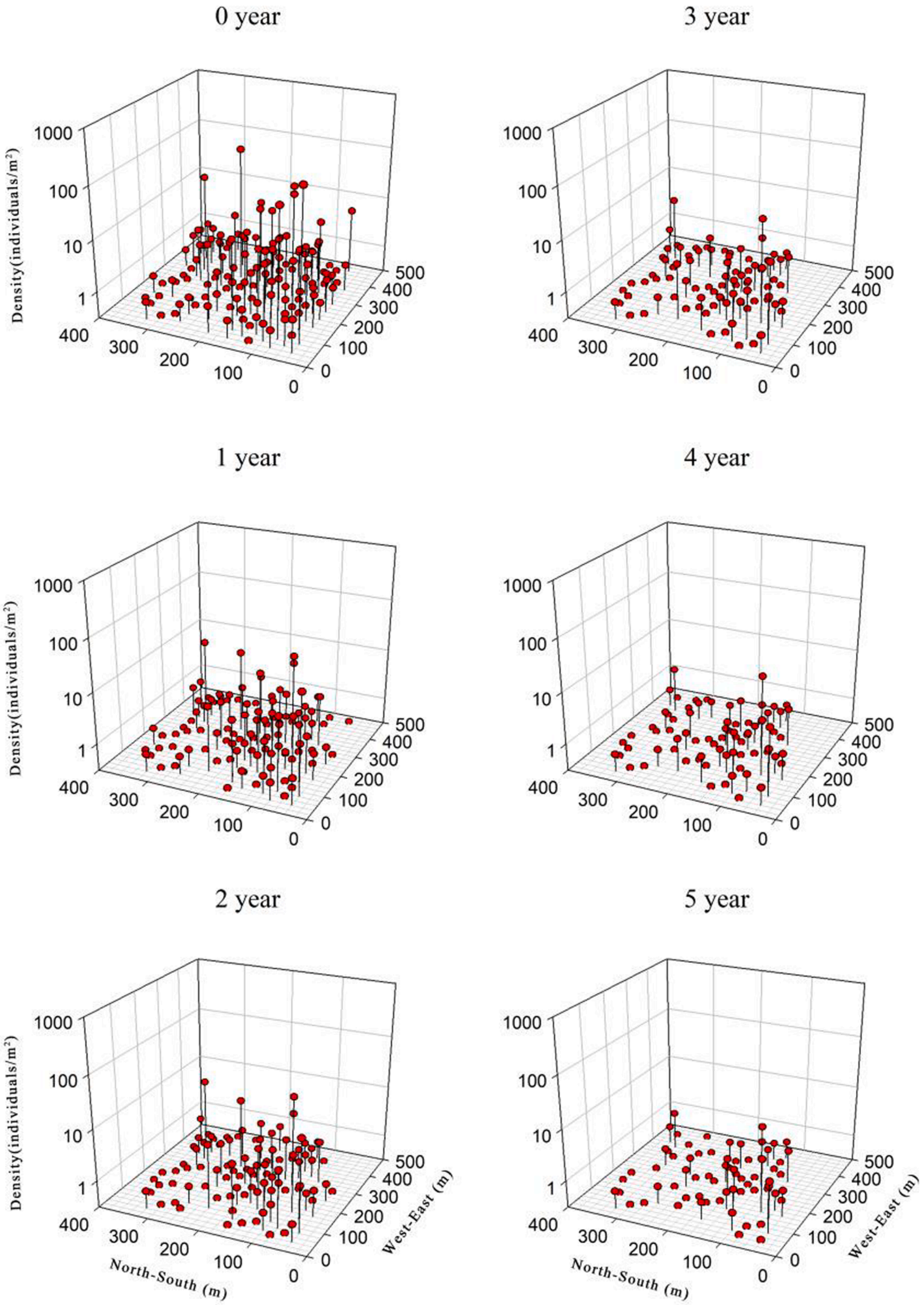

Fig. 3. Density distribution of live seedlings in different ages. Age of "0″ represent the newly germinated seedlings. Z aixs represent the density of total live seedlings in a station.

conspecific tree neighbors). The best fit neighborhood is based on comparison of models in Table S2 and the distance is from the focal tree to the center of seedling plot including the focal seedling. The conspecific and heterospecific seedling neighborhood index were density of conspecific or heterospecific seedlings which were located in the same seedling plot and germinate in the same time. Seedlings germinating in the same time are likely to be influenced by symmetric seedling competition (Berkowitz et al., 1995, Davis et al., 1998, Paine et al., 2008, Peay, 2018, Wang et al., 2018, Wu et al., 2018). Meanwhile, Taylor and Aarssen (1989) found the seedling competition was from the mast seedlings in the same year. Therefore, seedling height is defined as the previous year's height.

The abiotic factors include topography (elevation, aspect and slope), light (canopy openness) and soil condition (pH value, total nitrogen concentration and total phosphorus concentration). The elevation was measured by total station on center of each seedling station. The aspect and slope of each seedling plot were measured by compass and tripod with three axes of rotation (Benro A650FHD3, China, Guangdong) (details of measuring and calculating methods in Xing, 2015). In addition, aspect values were linearized into a north–south range with the formula cosine (x) + 1.1, where x is the aspect in degrees from north (Wang et al., 2007). The canopy openness of each seedling plot was estimated by the photograph 10 cm above ground level and calculated by a canopy image analysis software (WinSCANOPY; Regent

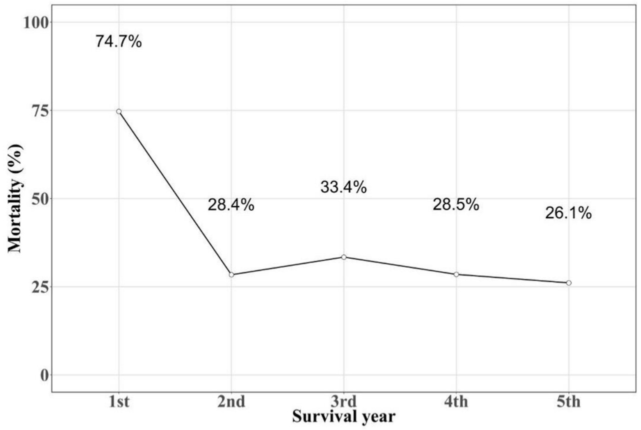

Fig. 4. The mortality of seedlings across years.

Instruments INC, Canada) in RGB mode. Soil samples were collected in the center of seedling station (details of collecting methods in Fang et al., 2017). Soil pH value (pH) were analyzed with a Beckman glass electrode. Soil total nitrogen concentration (TN) was measured by an elemental analyzer (Vario Micro Cube; Elementar, Langenselbold, DE). Soil total phosphorus concentration was measured by a continuous flow analyzer (SAN^{++}; Skalar, Breda, NL).

We use *AICc* weight and model-average estimator of potential explanatory variable to estimate the relative importance of potential factors on seedling survival respectively (Burnham and Anderson, 2002). Firstly, we select the *m* explanatory variables to combine the fixed variables from the *n* potential explanatory variables without repeat, resulting in $2^n(\sum_{i=0}^{n} C_n^i = 2^n)$ GLMMs. Secondly, we calculated the *AICc* weight of each GLMMs (equations S1 and S2) and estimated the *AICc* weight of potential explanatory variable (equations S3 and S4). Finally, we selected the optimal models ($\Delta AICc \leqslant 2$ Table S3) to calculate the model-average estimator ($\widehat{\beta}$) and standard error ($\widehat{s.e.}$) (equations S5, S6, S7 and S8). The methods for calculating *AICc* weight showed the relative importance of the explanatory variables. In addition, the model-averaged variables estimate the correlations of key biotic and abiotic factors on seedling survival by synthesizing the optimal models and reducing the multi-collinearity (Liu et al., 2016).

All explanatory variables were normalized by the mean of the variable and dividing by the standard deviation. All analyses were conducted in R 3.3.2 (R Development Core Team 2018). The GLMMs were fit by the “glmer” function of “lme4 1.1–13” package (Bates et al., 2013) and marginal pseudo-R-squared were fit by the “r.squaredGLMM” function of “MuMIn 1.40.0” packages (Nakagawa and Schielzeth, 2013, Johnson, 2014).

3. Results

3.1. The density distribution of live seedlings in different ages

The density distribution of newly germinated seedlings was most clustered of any age class (Fig. 2a). The strength of this clustered density distribution weakened with time (Fig. 2a). Furthermore, the five-year-old seedlings’ density distribution did not depart from null expectations of randomness (Fig. 2a). In addition, newly germinated seedlings was most correlated with conspecific tree neighbors’ aggregation (Fig. 2b). Then, this correlation also weakened with time (Fig. 2b). The maximum density of newly germinated seedlings in one station was 241 individuals/m2 (Fig. 3). Over five years, 82.3% of seedling stations include 1 or 2 five-year-old seedlings (Fig. 3).

3.2. Temporal dynamics of conspecific tree and seedling neighbors on seedling survival

The newly germinated seedlings suffered the highest mortality (74.7%) in the first year. In the next year, mortality decrease to 28.4% (Fig. 4). Conspecific seedling neighbor density had a significant negative correlation on newly germinated seedlings survival (Fig. 5). During the next four years, the conspecific seedling neighbors did not have significant correlation with seedling survival (Fig. 5). Conspecific tree neighbors did not have significant correlations with seedling survival during the first three years (Fig. 5). However, in the fourth and fifth survival year, significant negative correlations were observed for seedling survival with a larger relative effect size than conspecific seedling neighbors (Fig. 5). Seedling height had consistent significant positive correlations with seedling survival and had the largest relative effect size among the biotic factors in the first four years. The heterospecific tree neighbors had significant positive correlations with seedling survival in second and third survival year. (Fig. 5). Canopy openness had significant positive correlations with seedling survival in the first two years.

4. Discussion

The negative relations of conspecific densities on seedling survival varied with time. In our study, we found clumped density distribution of newly germinated seedlings tended to random most intensively in the first survival year and only because of conspecific seedling neighbors. As the seedlings age increasing and density distribution tending toward random, the negative relations with conspecific tree neighbors emerge as significant factors for seedling survival suggesting a switch from symmetric to asymmetric intraspecific negative interactions during early ontogeny.

Due to dispersal limitation, newly germinated seedlings were clustered nearby the conspecific trees (Willson and Traveset, 2000). Previous studies point towards natural enemies existing in high concentrations around conspecific densities. Both the conspecific seedling and tree neighbors should have significant negative effects on newly germinated seedling survival for establishment (Augspurger, 1984, Augspurger and Kelly, 1984, Packer and Clay, 2000, Comita and Hubbell, 2009, Liu et al., 2012, Jurinitz et al., 2013, Johnson et al., 2014, Johnson et al., 2017). However, in our study, we only found the conspecific seedling neighbors have significant relation to newly germinated seedlings establishment and conspecific tree neighbors’ relation was the least influential biotic factor in this stage. These results indicate intraspecific negative interactions in seedling establishment was mainly related with conspecific seedlings neighbors in this study region. The conspecific tree neighbors determined seedlings distribution in early stage, but not necessarily the dynamics. The reason for this phenomenon could be newly germinated seedlings is not established yet, thus easily suffering from density-responsive predation in the area of conspecific seedling neighbors clumping (Connell, 1971, Hyatt et al., 2003). In addition, high density of conspecific seedling neighbors would cause the overlap of above- and underground resource demands (Hogan, 1986, Lentz, 1999). Thus, newly germinated seedlings would be difficult to established in the area with high density of conspecific seedling neighbors.

The distance-dependent mortality from conspecific tree neighbors became more influential on seedling dynamics in later ages (Murphy et al., 2017). After seedling established, their densities declined rapidly. Lower density would cause the symmetric intraspecific negative interactions to weaken (Paine et al., 2008). Whereas, distance-responsive predation from conspecific tree neighbors has little impact on low seedling densities (Janzen, 1970). Thus, the soil-borne species-specific pathogens would infect on established seedlings around conspecific trees (Carson et al., 2008, Liu et al., 2015). Furthermore, the older individuals would be easier to suffer from soil-borne species-specific pathogens on their root systems (Packer and Clay, 2000). Therefore, we

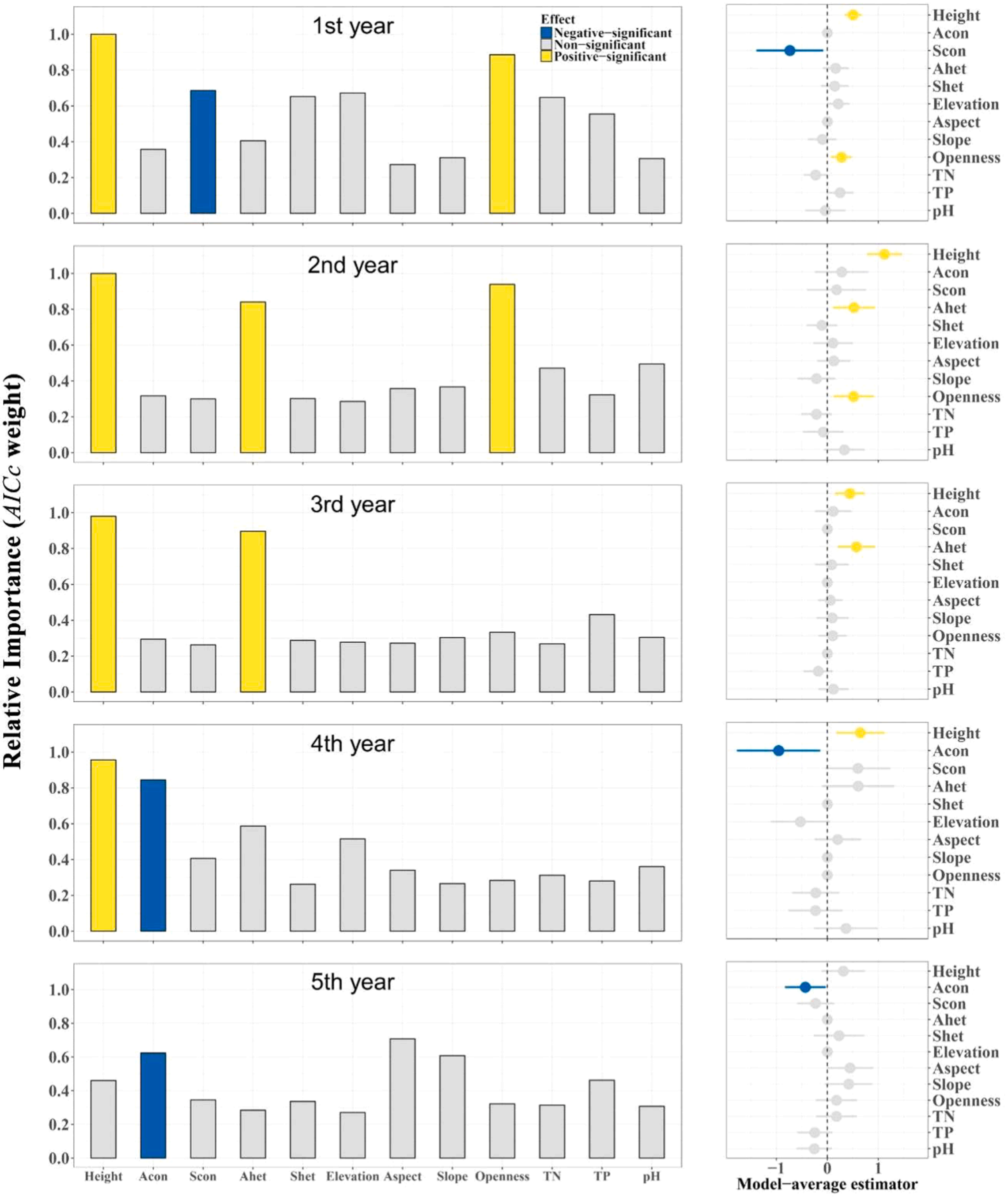

Fig. 5. The relative influence of potential factors on seedling survival across years. The variables examined are the log-transformed seedling height (HT), conspecific tree neighborhood index (Acon) and seedling density (Scon), heterospeicific tree neighborhood index (Ahet) and seedling density (Shet), elevation, aspect, slope and canopy openness (Openness) in seedling plot, total nitrogen (TN), total phosphorus (TP) and pH value of soil. Error bars represent 1.96 $\widehat{\widehat{\text{s.e.}}}_{\cdot j}$ around the model-average estimator ($\widehat{\widehat{\beta}}_j$). Blue and yellow point indicate parameter estimates significantly different from zero at the alpha = 0.05 level. Some gray point with no error bars indicates this parameter estimate does not include in the optimal models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

could found the effect of conspecific tree neighbors on seedling survival in later ages.

Seedling ages play a crucial role on seedlings density distribution and dynamics. In general, newly germinated seedlings suffered the highest mortality in the first survival year for establishment (Gilbert et al., 2001, Murphy et al., 2017, Kuang et al., 2017). Only a fraction of seedlings could be established through this demographic bottleneck for population (Gurevitch et al., 2006). Due to symmetric intraspecific negative interactions, the mortality risk would increase with the density of seedlings (Chesson, 2000). Therefore, the aggregated density distribution tends to random rapidly and conspecific seedling neighbors turn a dominant effect. As seedling established, seedlings mortality is stable. Seedlings turns to develop by absorbing above- and below ground resource (Grubb, 1977). In this stage, negative plant-soil feedback around conspecific tree would inhibit established seedling growth. Over longer periods of time, seedlings with slow growth rate would be likely to die (Mangan et al., 2010). Thus, in the later stage of seedlings, the distance-dependent seedling mortality from conspecific tree neighbors could be detected.

Although the negative intraspecific interactions are potential mechanism affecting seedling density distribution and dynamics, the environmental factors influencing survival should not be neglected, especially light condition (Augspurger, 1984, Augspurger and Kelly, 1984, Dai et al., 2002, Lin et al., 2014, Inman-Narahari et al., 2016). We found light availability had a significant positive effect on seedling survival in the early stages, indicating newly germinated seedlings benefit from well-lit conditions. Because, the high light conditions could reduce pathogen activity (Augspurger and Kelly, 1984). However, light effects weakened as seedling ages. Because, light promote established seedlings growth more efficiently than survival (Liu et al., 2017). This would be the reason that Johnson et al. (2017) could not found significant effect of light on old seedlings survival. In addition, due to the steep topography of Tiantong plot (Yang et al., 2011), the density distribution of seedlings are influenced by topography factors, especially slopes. The slope have a significant negative effect on density distribution of seedlings in all ages (Fig. S1). The reason is that most seedlings are hardly to regenerate in steep slope with bare soil in evergreen forest (Kitajima and Fenner, 2000). In addition, the heterospecific tree neighbors crowding could result in fewer encounters between a host and its species-specific pests and pathogens (Wills, 1996, Peters, 2003). Thus, the focal seedlings survival would increase with the heterospecific tree neighbors crowding. In species-level, the clumped density distribution of newly germinated seedlings was mainly belonged to *Machilus leptophylla* (Fig. S2). Furthermore, its conspecific seedling neighbors also have significant negative correlation with seedling establishment (Fig. S3). Therefore, we estimate the negative correlation of conspecific seedling neighbors on establishment would contribute to this prolifically germinating species. If there is no dominant species with mast newly germinated seedlings, we would hardly detect this negative correlations.

Conspecific seedling and tree neighbors were major intraspecific negative interaction factors influencing seedling survival and the relative effect varied with seedling age. Most previous studies for conspecific negative density dependence focus on the seedling stage as a whole. Our findings suggest that there are reversals in the influence of each factor as seedlings age and not accounting for this variation could lead to incomplete understand of the effects across the seedling stage and how different factors wax and wane in importance to tree community dynamics and diversity.

5. Authors’ contributions

HL, DJJ and XW conceived and designed the ideas. HL, QY, MX, ZM, XF and YS collected the data. HL and QY analyzed the data and contributed analysis tools. HL, DJJ and XW drafted and revised the article. All authors agree to be accountable for the aspects of the work.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data Accessibility

Our data will be archived at https://github.com/kkkliuheming/seedling-data.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.118924.

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