

# Life Stage of Neighbors Determines Neighborhood Effect on Tree Mortality in a Subtropical Forest

Yi He

East China Normal University

Heming Liu (✉ [hmliu@des.ecnu.edu.cn](mailto:hmliu@des.ecnu.edu.cn))

East China Normal University <https://orcid.org/0000-0002-6873-4735>

Qingsong Yang

East China Normal University

Ye Cao

East China Normal University

Mengfang Liang

East China Normal University

Shuangshuang Zhou

East China Normal University

Xihua Wang

East China Normal University

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## Research Article

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# Abstract

Neighborhood effects are a crucial ecological process that allow species to coexist in a forest. Conspecific and heterospecific neighbors, as major classified groups, affect tree mortality through various mechanisms associating with neighbor life stages. However, how neighbor life stages influence neighborhood effects and by what mechanisms remains a knowledge gap. Here we censused the mortality of 82,202 trees representing 30 species in a 20-ha subtropical forest and classified their neighbors into the following life stages: earlier, same and later. Then, we ran generalized linear mixed models to estimate the effect of neighbors at different life stages on tree mortality. Our results showed that conspecific later stage neighbors have effects on increasing tree mortality overall, whereas conspecific earlier stage neighbors have effects on decreasing. Furthermore, these opposing effects could offset each other so that the overall effect of conspecific neighbors on juvenile mortality seems small. In contrast, heterospecific neighbors have effects on decreasing tree mortality overall. These effects are consistent with those of later stage heterospecific neighbors. Our findings demonstrate that neighbors importantly impact tree mortality, and their specific effects are closely related to neighbor life stages. Any single effect from one neighbor life stage could disturb or dominate the total effects of the neighbors. Therefore, the neighbors must be divided into different life stages to best explain the neighborhood effect on forest dynamics.

# Introduction

The neighbor effect has long been invoked to explain species coexistence and biodiversity maintenance in communities (Peters, 2003; Zhu et al., 2015; Fichtner et al., 2018). Heterogeneous distributions of trees arise mainly due to the interactions between neighbors and focal trees (Silander and Pacala, 1985; Kim and Underwood, 2015). Resource enrichment and habitat amelioration can enhance positive interactions (Callaway and Walker, 1997; Brooker et al., 2008; Maestre et al., 2009; le Roux et al., 2013), while the spread of natural enemies and resource competition can cause negative ones (de Souza and Valio, 2001; Hyatt et al., 2003; Getzin et al., 2006; Gunton and Kunin, 2007). These interactions regulate tree mortality patterns that maintain species coexistence (Zhang et al., 2009; Paine et al., 2012).

The conspecific neighbor effect is an important index of intraspecific interaction (Comita et al., 2014). Negative intraspecific interactions occur in aggregated conspecific individuals through resource competition and/or encountering natural enemies (Janzen, 1970; Connell, 1971; Zhu et al., 2015; Liu et al., 2016; Liu et al., 2021). The strength of negative intraspecific interactions increases with the density of conspecific neighbors. Trees tend to have a higher probability of mortality when conspecific neighbors are denser, closer, or more abundant (Castagneri et al., 2010; Comita et al., 2010; Johnson et al., 2012; Wang et al., 2012). This situation thereby provides space for heterospecific recruitment and ensures the coexistence of different species (Yao et al., 2020). However, positive intraspecific interactions may also happen among conspecifics due to similar habitat preference and/or beneficial microorganisms (such as nitrogen-fixing bacteria) (Wu et al., 2016). Therefore, positive and negative interactions may exist simultaneously and significantly as part of the conspecific neighbor effect.

The heterospecific neighbor effect is a synthesis of interspecific interactions. Previous studies have found that negative interspecific interactions likely result from strong heterospecific competition for resources (Tilman, 1987; Hubbell et al., 2001; Getzin et al., 2006). In addition, positive interspecific interactions are attributed to the herd protection hypothesis, which posits that heterospecific neighbors can effectively hinder the spread and reduce the risk of detection and of invasion of specific natural enemies such as pests or pathogens, thus reducing individual mortality (Wills and Green, 1995; Peters, 2003; Zhu et al., 2015; Yao et al., 2020). Further, if heterospecific neighbors have similar habitat preferences as individuals, we can detect positive interspecific interactions within those habitats (Lebrija-Trejos et al., 2014; Wu et al., 2016; Yao et al., 2020). Finally, some studies have found that the strength of negative and positive interspecific interactions likely correlates with the density of heterospecific neighbors (Peters, 2003; Wu et al., 2017).

Neighbors at different life stages can differently affect tree mortality via various mechanisms. If the life stage of conspecific neighbors is earlier than the adult individual, the conspecific offspring will most likely face dispersal limitation (Vincent et al., 2011). This hardly affects the mortality of the parent tree (Weiner, 1990). In contrast, conspecific neighbors at the same and later life stages compete with the focal individual for resources and can further the spread of species-specific natural enemies, which could result in tree mortality (Weiner, 1990). Conspecific crowding could also be a result of shared habitat preference, and in that case, tree mortality would decrease due to increased habitat suitability (Lebrija-Trejos et al., 2014; Wu et al., 2016; Yao et al., 2020). Correspondingly, the crowding of later-stage heterospecific neighbors leads to shading and fewer encounters between a host and its species-specific pests and pathogens. These heterospecific effects often reduce tree mortality.

Previous studies have proven that conspecific and heterospecific neighbors affect tree mortality. However, the relative effects of neighbors at different life stages have yet to be described. To fill this research gap, we examined the effect of neighbors of different life stages on tree mortality in a subtropical forest through generalized linear mixed models. Specifically, we addressed the following questions: (1) Do conspecific and heterospecific neighbors affect tree mortality? (2) If so, are there differences among the effects of neighbors at various life stages, both of the neighbors and of the focal trees? Then if so, how do these differences interact?

## Material And Methods

### Study site and data collection

This study was conducted in a 20-ha (500 m × 400 m) forest dynamics plot in a subtropical forest in the Tiantong National Forest Park (29 ° 48 ' N, 121 ° 47 ' E), (hereafter called the Tiantong plot), Zhejiang province, eastern China. In this region, the tree canopy is dominated by the Fagaceae and Theaceae families. This region has a typical monsoon climate with a hot, humid summer and a dry, cold winter. The minimum and maximum monthly mean temperatures are 4.2 °C in January and 28.1 °C in July, respectively. The annual mean temperature is 16.2 °C. Average annual precipitation is 1374.7 mm, and it

mainly occurs from May to August. The soil texture is mainly sandy to silty clay loam, and its pH value ranges from 4.4 to 5.1 (Song and Wang, 1995). The topography of the Tiantong plot is rough, with elevation ranging from 304.26 m to 602.89 m and slope ranging from 14 ° to 50 ° (Yang *et al.*, 2011) (Fig. 1). All free-standing trees (DBH  $\geq$  1 cm) in the Tiantong plot were tagged, mapped, measured and identified to species in 2010 and re-censused in 2015.

All species were classified into one of three life forms: shrub, subtree and tree. Each life form was divided into three life stages: sapling, juvenile and adult according to their DBH (Table S1). Then, we selected 30 tree species for analysis, each of which had at least 50 individuals in each life stage (Table S2). The total abundance of these species accounted for 86.88% of all individuals in the Tiantong plot.

## Data analyses

We calculated the mortality of sapling, juvenile and adult individuals in all 20 m  $\times$  20 m grids, and used the Wilcoxon signed-rank test to examine the differences in tree mortality across the life stages.

To examine the effects of neighbors in various life stages on tree mortality, we classified neighbors into three ontogenetic stages: earlier life stage than the focal tree, same life stage as the focal tree and later life stage than the focal tree (see details in Table 1). Then, we quantified the neighbor effect using the neighborhood index. This index can be defined as:

$$NI_i = \sum_j^n (Ba_j / Distance_j) \quad (1)$$

Here  $NI_i$  is the neighborhood index of focal tree  $i$ .  $n$  is the total number of neighbors.

$Ba_j$  is the basal area of neighbor  $j$ .  $Distance_j$  is the distance from neighbor  $j$

within the optimal radius (based on comparison of models using different neighborhood

radii; see details in Table S3) (Zhu *et al.*, 2015; Johnson *et al.*, 2017) to focal tree  $i$ .

The optimal radius of the neighbor effect differs among the ontogenetic and the life stages.

Environmental filtering is an important mechanism contributing to tree mortality (Wang *et al.*, 2012; Shen *et al.*, 2014; Wu *et al.*, 2017; Yao *et al.*, 2020). Therefore, we need to consider effects of environmental variables in our study as well. These variables were divided into topographic and soil variables. Topographic variables include elevation, slope, convexity and aspect. These variables were estimated within 5 m  $\times$  5 m quadrats. Altimetric points of the corners of 20 m  $\times$  20 m grids were measured in the Tiantong plot. Then, they were interpolated to the corners of the 5 m  $\times$  5 m quadrats

using kriging. Elevation of each quadrat was defined as the mean value of its four corners (Harms *et al.*, 2001; Valencia *et al.*, 2004). Convexity was calculated as the quadrat's elevation minus the mean elevation of the eight surrounding quadrats (Yamakura *et al.*, 1995). Joining three corners of the quadrat can form a triangular plane, and each quadrat can be divided into four triangular planes. Slope and aspect were determined as the deviation of the average angle of the four planes from the horizontal plane and the north direction, respectively (Lai *et al.*, 2009). To ensure continuity of aspect data, it was transformed by  $\cos(\alpha)+1.1$  (Wang *et al.*, 2007). Total nitrogen (TN), total phosphorus (TP), pH value and soil moisture content were defined as soil variables. Soil samples were collected by the protocol defined by John *et al.* (2007). The details of collecting methods are described in Fang *et al.* (2017). TN and TP were measured using an elemental analyzer (vario MICRO cube, Elementar, Germany) and flow-injection auto-analyser (SAN++, Skalar, Netherlands), respectively. Soil pH was determined using a Mettler Toledo pH meter (1:2, H<sub>2</sub>O). Soil moisture content was measured using the ring knife sampling method (volume of water in soil divided by volume of soil). These soil variables were also interpolated to the corners of the 5 m × 5 m quadrats using kriging.

Initial tree size can also affect tree mortality significantly, apart from neighborhood and environmental variables (Wang *et al.*, 2012; Piao *et al.*, 2013; Wu *et al.*, 2017). Therefore, we also included log-transformed size (DBH in 2010 census) as a potential variable. In addition, to weaken the variation of baseline mortality among species and position, we defined species and grid number (each individual (DBH ≥ 1 cm) was assigned to a 20 m × 20 m grid) as random variables (Zhu *et al.*, 2015).

Generalized linear mixed-effects models (GLMMs) with binomial errors were used to examine the effects of potential variables on tree mortality. The generalized linear mixed-effect models can be specified as:

$$Y_{ijk} \sim \text{binomial}(1, p_{ijk}) \quad (2)$$

$$\text{Ln}(p_{ijk}/(1-p_{ijk})) = [a + \beta * X]_{\text{fixed part}} + [\mu_j + \mu_k]_{\text{random part}}$$

Here  $Y_{ijk}$  is 1 if individual  $i$  of species  $j$  in grid  $k$  was dead in the 2015 recensu, and 0 if otherwise, with  $p_{ijk}$  as the predicted probability of being dead. Position ( $\mu_k$ ) and species ( $\mu_j$ ) are two random variables.  $a$  and  $\beta$  refer to an intercept and a

vector of coefficients of explanatory variable  $X$ , respectively.

$AIC$  weight and model-average estimator of each potential explanatory variable were used to estimate its relative importance and effect, respectively. Methods of calculation were as follows: we first selected the  $m$  (from 0 to  $n$ ) explanatory variables from the  $n$  potential explanatory variables without repeated sampling and got  $2^n$  ( $\sum_{i=0}^n C_n^i = 2^n$ ) different combinations. Then each combination was set as the fixed part of a GLMM, resulting in  $2^n$  different GLMMs. Secondly, we calculated the  $AIC$  weight of each GLMM (equations S1 and S2) and estimated the  $AIC$  weight of each potential explanatory variable (equations S3 and S4). Finally, we selected the optimal model group ( $\Delta AIC \leq 2$ ) and calculated the model-average estimator and standard error (equations S5, S6, S7 and S8) of each potential explanatory variable in these models (Burnham and Anderson, 2002). This process for model selection reduces the influence of multiple-collinearity among potential explanatory variables and accounts for all influencing factors comprehensively (Liu *et al.*, 2021).

To avoid edge effects, we excluded all trees that were within 25 m (the optimal radius for saplings and juveniles) of the edge of the plot from all analyses, as focal trees. All environmental factors were conditioned to avoid edge effects. Each continuous explanatory variable was standardized (subtracting the mean value of the variable and dividing by one standard deviation) before all analyses. All analyses were performed in R 3.5.1 statistical software (R Development Core Team 2018), using the “lme4 1.1-19” package (Bates *et al.*, 2013). All statistical analyses were considered significant at  $P < 0.05$ .

## Results

### Tree mortality in different life stages

Tree mortality in the Tiantong plot was 12.88% overall. Saplings, the most abundant, also suffered the highest mortality (14.63%), followed by juveniles and adults (Fig. 2a). In addition, the median value of mortality in all grids also decreased significantly in the order of sapling > juvenile > adult (Fig. 2b).

### Conspecific and heterospecific neighbor effects on tree mortality

Conspecific neighbors had a significant positive effect on sapling mortality (Fig. 3a). In the juvenile and adult stages, conspecific neighbors did not have significant effects (Fig. 3b & c). Correspondingly, heterospecific neighbors had significant negative effects on tree mortality in all stages (Fig. 3). However, in the sapling stage, the conspecific neighbor effect was more important than that of heterospecific neighbors (Fig. 3a). In addition, initial DBH and convexity had significant negative effects on tree mortality in all stages (Fig. 3) and aspect had a significant positive effect on juvenile mortality (Fig. 3b).

### **Ontogenetic neighbor effects of conspecifics and heterospecifics on tree mortality**

In saplings, conspecific later stage neighbors had a significant positive effect on tree mortality, whereas same stage neighbors did not (Fig. 4). Heterospecific same stage neighbors had a significant positive effect on tree mortality, whereas later stage neighbors had an opposite effect (Fig. 4). For juveniles, conspecific earlier stage neighbors had a significant negative effect on tree mortality, whereas later stage neighbors had an opposite effect (Fig. 5a & c). Heterospecific earlier and later neighbors had significant negative effects (Fig. 5a & c). For adults, conspecific earlier stage and heterospecific same stage neighbors had significant negative effects on tree mortality (Fig. 6). In addition, TN and TP had significant positive effects on sapling mortality by offsetting the effect of later stage neighbors (Fig. 4a). Elevation had significant positive effects on juvenile and adult mortality by minimizing conspecific later and same stage neighbor effects, respectively (Figs. 5 & 6).

## **Discussion**

Conspecific and heterospecific neighbors significantly affected ontogenetic tree mortality (Zhu et al., 2015). However, neighbors in different life stages than the focal tree showed inconsistent effects. In our study, we found that conspecific earlier and later stage neighbors had opposite effects on juvenile mortality. Heterospecific same and later stage neighbors also had opposing effects on sapling mortality. The later stage neighbors were the only group whose singular effect was mostly consistent with the effect of all neighbors combined. In short, failing to consider some life stages of neighbors might result in concluding that related environmental factors are more consequential than neighbor effects.

Mortality attributed to conspecific negative density dependence is significantly widespread in the sapling stage, but this effect weakens as the tree grows (Zhu et al., 2015; Yao et al., 2020). Meanwhile, heterospecific neighbors reduce tree mortality throughout all life stages. Previous studies have shown that mortality due to conspecific negative density dependence is caused by specialized natural enemies and/or intraspecific competition for resources (Janzen, 1970; Connell, 1971; Zhu et al., 2015). Saplings, as the earliest life stage, suffer to a greater degree from natural enemy damage and from intraspecific competition than do older trees (Weiner, 1990). Therefore, saplings are more strongly impacted by conspecific neighbors. This result is consistent with findings of previous studies showing that density-dependent survival at the seedling and sapling stages plays a significant role in fostering tree species coexistence and maintaining diversity in forests (Bai et al., 2012; Johnson et al., 2014; Lin et al., 2014; Yan et al., 2015; Yao et al., 2020). Unlike conspecific neighbors, denser heterospecific neighbors can

effectively hinder the spread of specific natural enemies and reduce objective tree mortality (Wills and Green, 1995; Peters, 2003). This herd protection has also been found in other studies on conspecific negative density dependence (CNDD) (Comita and Engelbrecht, 2009; Zhu et al., 2015; Yao et al., 2020). Furthermore, heterospecific neighbors have a negative correlation with adult tree mortality. This result indicates that heterospecific trees survive better around adult trees, which consequently promotes species coexistence.

Clumping of conspecific later stage and heterospecific same stage neighbors contributes the most to sapling mortality. Saplings are the youngest trees in this study. They are more susceptible to natural enemies and are less competitive. Saplings could be subject to invasion upon the crowding of conspecific later stage neighbors because the neighbors could spread specific natural enemies, while also having asymmetric advantages in the competition for resources (Weiner, 1990; Clark and Clark, 1992; Uriarte et al., 2004; Yao et al., 2020). Consequently, conspecific later stage neighbors are the major contributor of all conspecific neighborhood effects to sapling mortality. In addition, conspecific later stage neighbors comprise the largest component of conspecific neighbors (Fig.S1). Thus, conspecific neighbors cause sapling mortality altogether (Fig. 3a), but this effect can be attributed mainly to conspecific later stage neighbors. This may also be why most studies on CNDD have found that the clumping of conspecific neighbors causes sapling mortality (Bai et al., 2012; Lin et al., 2014; Yan et al., 2015; Yao et al., 2020), even though these studies did not distinguish among conspecific neighbors' life stage. In contrast, clumping of heterospecific later stage neighbors could reduce sapling mortality by hindering the spread of specific natural enemies (Peters, 2003). However, heterospecific sapling neighbors demonstrate the opposite effect, increasing focal sapling mortality. For one, herd protection is weakened in same stage heterospecific neighbors (Ramage et al., 2017), and they also have symmetric advantages in the competition for light resources, which can result in greater sapling mortality (Comita and Engelbrecht, 2009; Rüger et al., 2009; Bai et al., 2012; Piao et al., 2013).

Conspecific earlier and later stage neighbors show opposing effects on juvenile mortality, and this conflict destabilizes the overall conspecific neighbor effect. Conspecific earlier stage neighbors for juveniles are saplings. They are usually smaller and weaker than juveniles. Therefore, they hardly influence juvenile mortality (Weiner, 1990). However, that conspecific sapling neighbors are clumped demonstrates that this habitat is suitable for regeneration (Grubb, 1977; Silvertown, 2004; Pérez-Ramos et al., 2012). The mortality of juveniles decreases correspondingly, and consequently, conspecific saplings significantly and negatively affect juvenile mortality. In contrast, adults are at a later stage than juveniles. As mentioned above, they could also spread specific natural enemies and they have asymmetric competitive advantages compared to juveniles. However, juveniles are more adept at resisting natural enemies and asymmetric competition than are saplings (Boege and Marquis, 2005; DeMalach et al., 2016; Yao et al., 2020). Therefore, the positive effect of conspecific adult neighbors on juvenile mortality is weaker than it is on saplings. Furthermore, due to the weaker positive effect of conspecific adult neighbors and the counteraction of conspecific sapling neighbors, the overall conspecific neighbor effect on juvenile mortality is offset by these opposing effects. In our study, we could not even detect an overall conspecific

neighbor effect on juvenile mortality (Fig. 3b). Again, overlooking the life stages of neighbors when measuring their effect on focal tree mortality can result in a biased, incomplete conclusion.

Clumping of earlier stage conspecific neighbors suggests that an adult tree is healthy with a low chance of mortality. In our study, we found that when more conspecific earlier stage neighbors were clumped around the focal adult tree, its mortality was lower. Adult trees are generally surrounded by offspring due to dispersal limitation (Vincent et al., 2011). The healthier the focal adult tree, the stronger its offspring will be and the more likely that they will survive into the next life stage (Moles et al., 2004; Sanín et al., 2013). In general, the healthy adult tree is unlikely to die. Thus, the more the conspecific earlier stage neighbors assemble in clumps, the healthier the adult tree will be. In a previous study, Hou et al. (2004) also found that earlier stage neighbors exhibited clumped distributions to a greater degree around living adult trees than dead ones. Lastly, although we considered the effects of environmental filtering on tree mortality by including some environmental factors in the analysis, other environmental factors that could have contributed to clumping of earlier stage conspecific neighbors and adult tree survival, such as canopy light, were excluded (Dechnik-Vázquez *et al.*, 2016; Liu et al., 2017).

Environmental filtering is a vital process contributing to tree mortality across complex topographies (Wang et al., 2012; Yao et al., 2020). The topography of the Tiantong plot is rough (Yang et al., 2011; Fang et al., 2017). There are two parallel valleys with north-south direction in the Tiantong plot (Fig. 1). These two valleys make it so that convexity is an important environmental variable in the Tiantong plot (Fang et al., 2017). In our study, trees tended to have a higher probability of mortality in low convexity habitats across all life stages. This may be because trees in lower convexity habitats might be disturbed more easily and get less light. Remember that light conditions are always reduced from a south to a north slope. Thus, juveniles occurring toward a north slope suffer higher mortality than juveniles near a south slope. In addition, initial tree size is always a strong predictor for tree survival (Wang et al., 2012; Ma *et al.*, 2013; Wu et al., 2017). We also detected this effect across all life stages.

Environmental variables might have indirectly affected tree mortality through their correlations with the distributions of large neighbors. In this study, we classified the neighbors into different ontogenetic life stages. We found that removing some later stage neighbors from the analysis allowed the effects of some environment variables to become significant. These environment variables were found to correlate with the variables of these later stage neighbors (Fig.S2). Thus, this correlation reflects that the distribution of large individuals is influenced by environmental variables (Wang et al., 2012; Yao et al., 2020), so environmental variables likely affected tree mortality indirectly through neighborhood effects.

Our study proved that both conspecific and heterospecific neighbors play a major role in tree mortality (Peters, 2003; Zhu et al., 2015). However, these influences differ based on the life stage of the neighbors. Conspecific earlier stage neighbors generally have effects on decreasing focal tree mortality because their clumping either reflects that the focal tree is healthy or that the micro-habitat is suitable for focal tree survival. In contrast, conspecific later stage neighbors have effects on increasing focal tree mortality through CNDD. Furthermore, these opposing effects could minimize the overall conspecific neighbor

effect. Due to herd protection, the assembling of heterospecific later stage neighbors could reduce focal tree mortality. In addition, large tree neighbors always dominate the neighborhood effects. At the same time, some environmental variables are closely correlated with the distribution of large trees. This correlation could result in the neighborhood effect on tree mortality partially including an indirect environmental effect. Overall, these results suggest that there are multiple mechanisms at play among neighbors at different life stages in ontogenetic tree mortality, and thereby they highlight the necessity for dividing neighbors into different life stages when assessing the overall neighborhood effect contributing to species coexistence.

## Declarations

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### Data Accessibility

Our data will be archived at <https://github.com/kkkluiheming/tree-mortality>

### Authors' Contributions

HL, YH and XW conceived and designed the study. QY, YC, HL, YH, SZ and ML collected the data. YH and HL provided analysis tools and analyzed the data. HL, YH and XW drafted and revised the article. All authors agree to be accountable for all aspects of the work.

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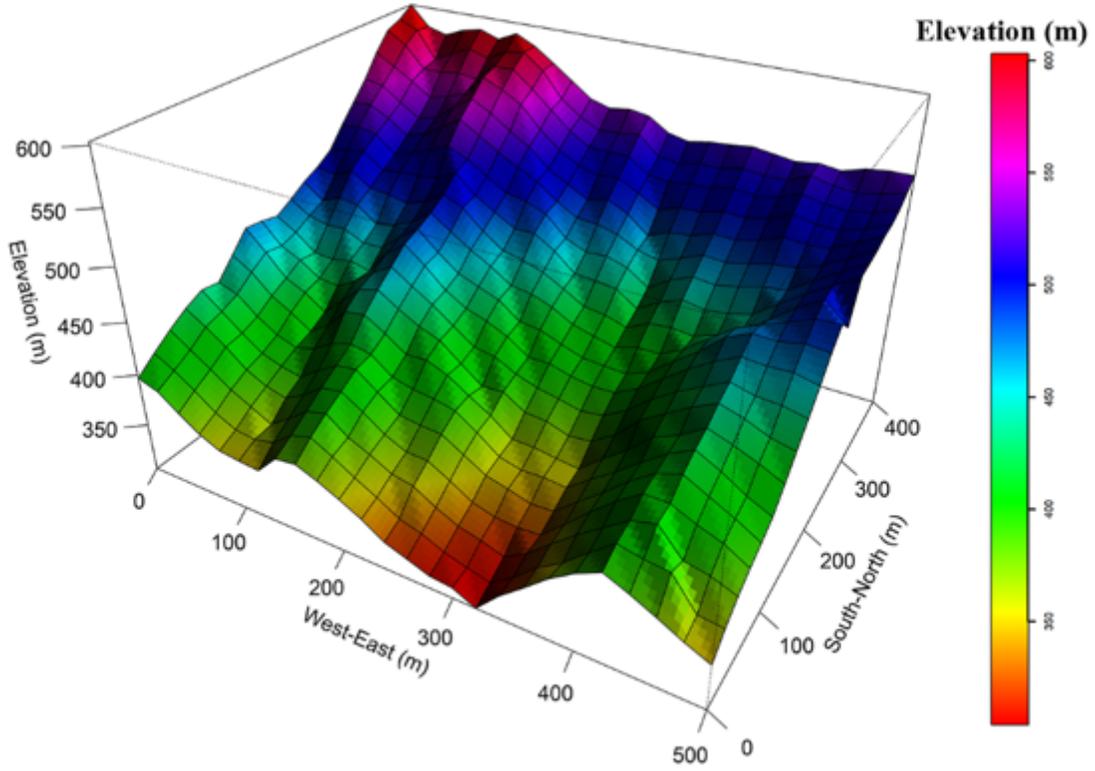
## Tables

**Table 1.** Division of different life stages of neighbors across ontogenetic stages of focal trees. All focal trees and neighbors were classified as saplings, juveniles or adults.

Ontogenetic stages	Life stage of neighbors		
	Earlier stage	Same stage	Later stage
Sapling stage		Sapling	Juvenile & Adult
Juvenile stage	Sapling	Juvenile	Adult
Adult stage	Sapling&Juvenile	Adult	

## Figures

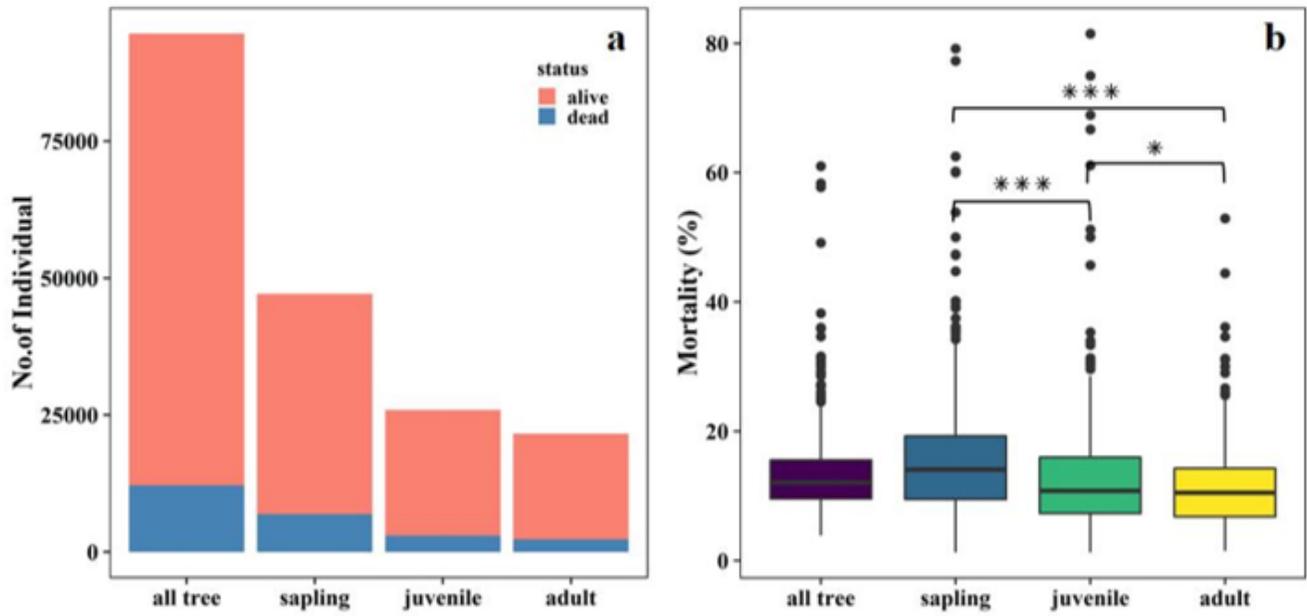
**Figure 1**



**Figure 1**

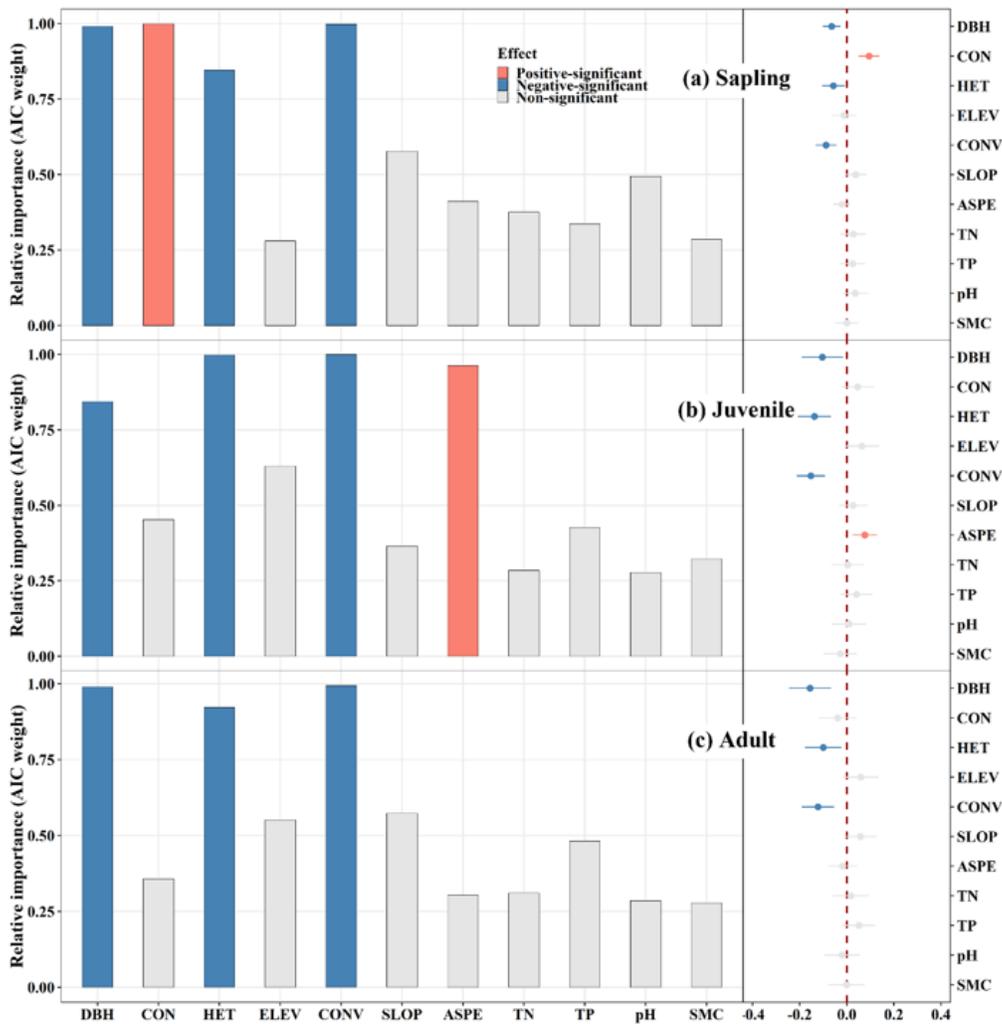
The topography of the 20-ha Tiantong forest dynamics plot.

**Figure 2**



**Figure 2**

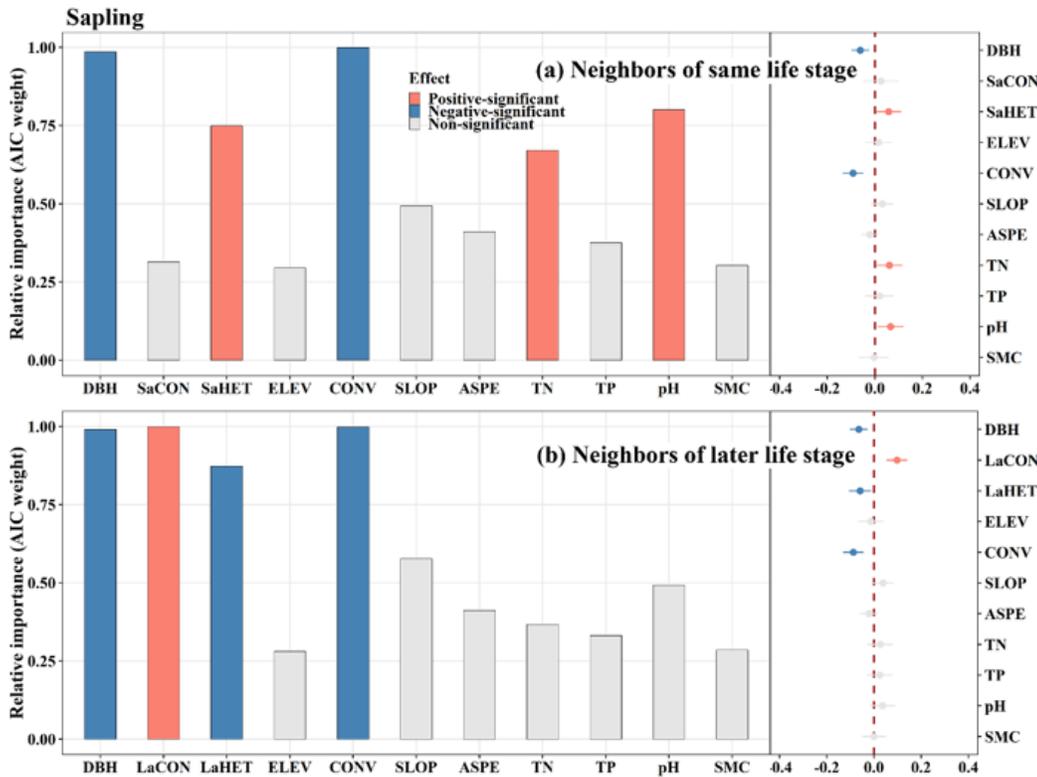
Tree abundance (a) and mortality (b) at different life stages. The significant effect of Wilcoxon signed-rank test is indicated by \* ( $P < 0.05$ ), \*\* ( $P < 0.01$ ) and \*\*\* ( $P < 0.001$ ).



**Figure 3.** The relative influence of potential variables on tree mortality. The variables examined are the log-transformed initial DBH of tree (DBH), conspecific neighborhood index (CON), heterospecific neighborhood index (HET), elevation (ELEV), slope (SLOP), aspect (ASPE), convexity (CONV), total nitrogen (TN), total phosphorus (TP), pH value (pH) and moisture content (SMC) of soil. Error bars represent  $1.96 \frac{\hat{\sigma}_j}{\hat{\beta}_j}$  around the model-average estimator ( $\hat{\beta}_j$ ). Blue and red points indicate that parameter estimates differ significantly from zero at the  $\alpha=0.05$  level.

### Figure 3

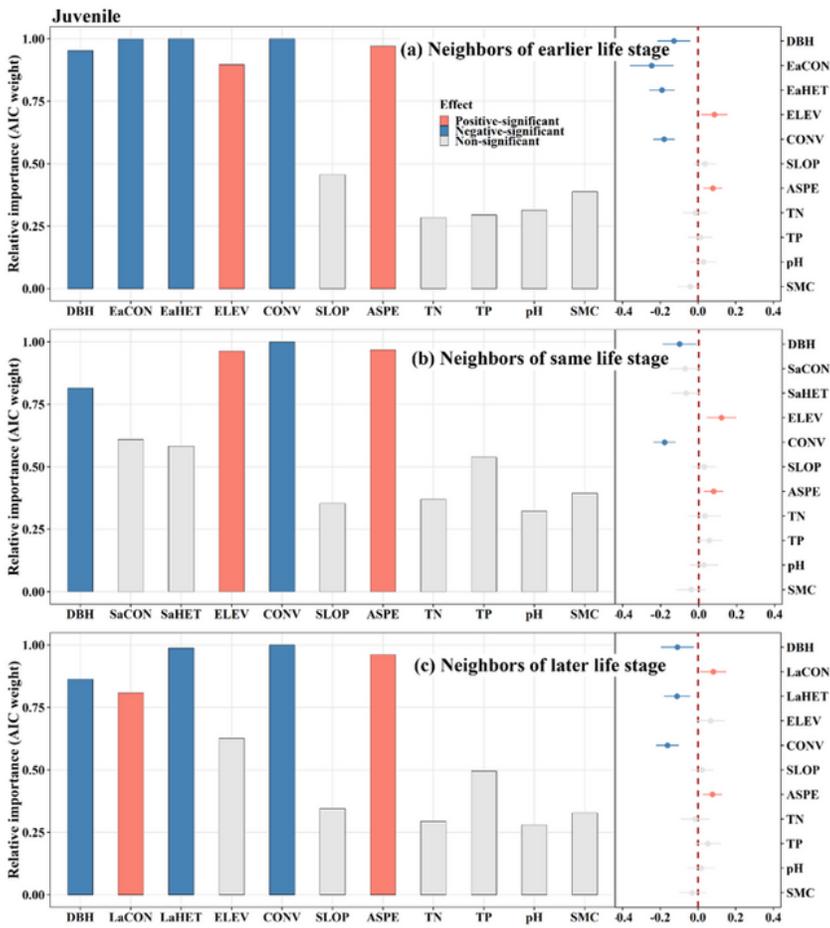
See image above for figure legend.



**Figure 4.** The relative influence of potential variables on sapling mortality. The variables examined are the log-transformed initial DBH of tree (DBH), conspecific neighborhood index at the same life stage (SaCON), conspecific neighborhood index at the later life stage (LaCON), heterospecific neighborhood index at the same life stage (SaHET), heterospecific neighborhood index at the later life stage indicates (LaHET), elevation (ELEV), slope (SLOP), aspect (ASPE), convexity (CONV), total nitrogen (TN), total phosphorus (TP), pH value (pH) and moisture content (SMC) of soil. Error bars represent  $1.96 \frac{\hat{A}}{S.e._j}$  around the model-average estimator ( $\hat{\beta}_j$ ). Blue and red points indicate that parameter estimates differ significantly from zero at the alpha=0.05 level.

## Figure 4

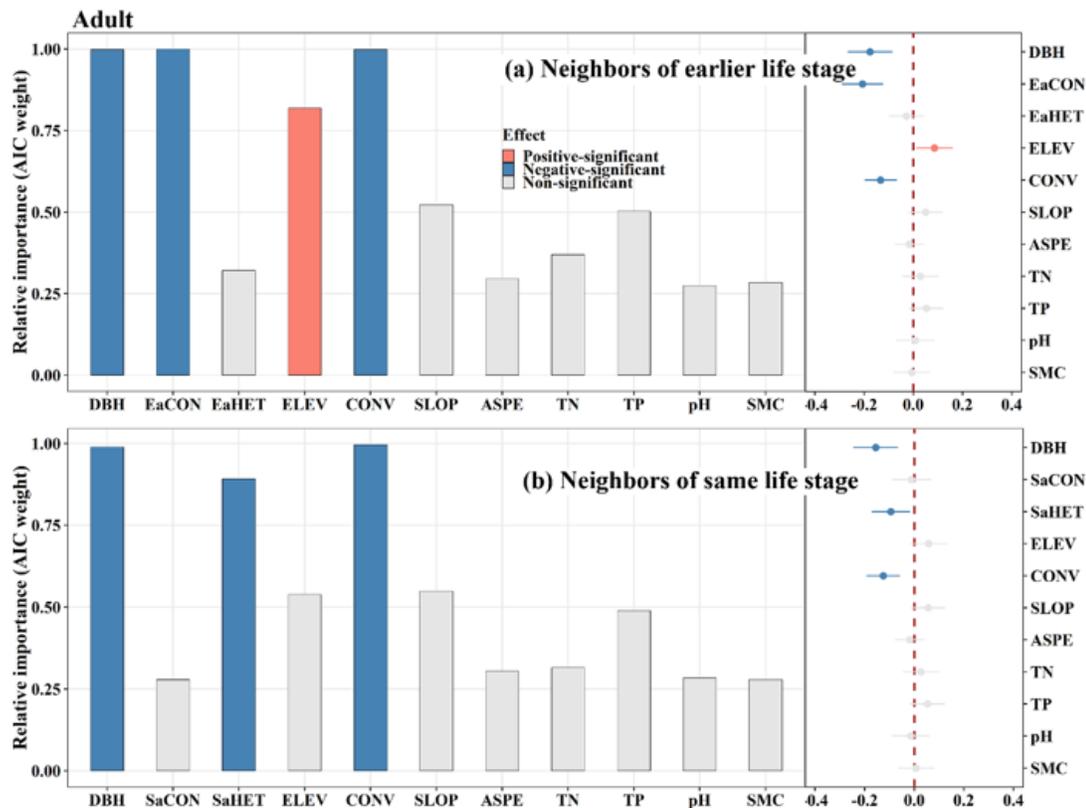
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**Figure 5.** The relative influence of potential variables on juvenile mortality. The variables examined are the log-transformed initial DBH of tree (DBH), conspecific neighborhood index at the earlier life stage (EaCON), conspecific neighborhood index at the same life stage (SaCON), conspecific neighborhood index at the later life stage (LaCON), heterospecific neighborhood index at the earlier life stage (EaHET), heterospecific neighborhood index at the same life stage (SaHET), heterospecific neighborhood index at the later life stage (LaCON), elevation (ELEV), slope (SLOP), aspect (ASPE), convexity (CONV), total nitrogen (TN), total phosphorus (TP), pH value (pH) and moisture content (SMC) of soil. Error bars represent  $1.96 \frac{\hat{\beta}_j}{S.E._j}$  around the model-average estimator ( $\hat{\beta}_j$ ). Blue and red points indicate that parameter estimates differ significantly from zero at the  $\alpha=0.05$  level.

## Figure 5

See image above for figure legend.



**Figure 6.** The relative influence of potential variables on adult mortality. The variables examined are the log-transformed initial DBH of tree (DBH), conspecific neighborhood index at the earlier life stage (EaCON), conspecific neighborhood index at the same life stage (SaCON), heterospecific neighborhood index at the earlier life stage (EaHET), heterospecific neighborhood index at the same life stage (SaHET), environmental variables including elevation (ELEV), slope (SLOP), aspect (ASPE), convexity (CONV), total nitrogen (TN), total phosphorus (TP), pH value (pH) and moisture content (SMC) of soil. Error bars represent  $1.96 \frac{\hat{\sigma}_j}{\hat{\beta}_j}$  around the model-average estimator ( $\hat{\beta}_j$ ). Blue and red points indicate that parameter estimates differ significantly from zero at the  $\alpha=0.05$  level.

Figure 6

See image above for figure legend.

## Supplementary Files

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