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### **RESEARCH ARTICLE**

# The U-shaped pattern of size-dependent mortality and its correlated factors in a subtropical monsoon evergreen forest

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### Abstract

- Tree mortality is an important ecological process influencing multiple functions of forest ecosystems. Previous studies have shown two basic size-mortality patterns, including a competition-driven declining and a disturbance-driven increasing mortality rate with tree size. Subtropical forests, which have a high species diversity and subject to frequent monsoon disturbances, are widely distributed in eastern Asia. However, the tree size-mortality pattern in the mature subtropical forests remains unclear.
- 2. Here we analysed patterns of size-dependent mortality from tree species to forest community using a 5-year inventory data from 117 species and 163,612 individuals in a 20-ha forest dynamic plot in a mature subtropical monsoon evergreen forest in eastern China. To explain the spatial variability in mortality patterns, two major biotic drivers (competition and tree size) and multiple local-scale environmental factors were further analysed.
- 3. Our results showed that tree size was the best predictor of tree mortality at the scales of both species and community. A species-level analysis identified four size-mortality patterns that are shaped by species-specific attributes such as maximum size and life form. For 27 out of 92 species that comprised 59% of tree individuals, the relationship between size and mortality exhibited a U-shaped pattern of a first decline followed by an increase. An overall community-scale size-dependent mortality also showed a U-shaped pattern.
- 4. Tree mortality was also influenced by the competition and environmental conditions, but the relative importance varied widely across tree sizes and species. The competition showed significant correlations with the mortality of small trees while the effect of environmental conditions on mortality was strongest for large trees. A principal component analysis showed that a combination of biotic and abiotic factors explained 42.3% of the spatial variation in mortality at large sizes.
- 5. Synthesis. Our results reveal four identifiable size-dependent mortality patterns that differ across diverse species, jointly leading to a U-shaped size-mortality pattern at the community level. This finding calls for the need to establish the details of every potential size-mortality pattern with consideration of the different effects of biotic and abiotic factors on tree mortality of specific size.

### KEYWORDS

dead trees, forest dynamic plot, mortality driver, subtropical monsoon forest, tree mortality

### 1 | INTRODUCTION

Tree mortality, the death of forest trees not caused by deforestation, is a pivotal ecological process linking vegetation dynamics and soil biogeochemistry. Changes in the rates of tree mortality can dramatically alter species composition, structure and ecosystem functions. For example, a regional analysis based on long-term forest inventory data has demonstrated that the mortality rate is crucial in controlling the biomass of tropical forest trees (Johnson et al., 2016). In forests that are unaffected by die-offs, an increase in the background mortality rate of 0.5% per year would kill trees with an additional 380-Tg carbon loss (Van Mantgem et al., 2009). The occurrence of large-scale forest die-off, such as the death and damage to 97 million trees in the United States after the catastrophic hurricane (Zeng et al., 2009), had dramatic impacts on forest dynamics and the potential for mortality to reset succession (Uriarte et al., 2019; Zeng et al., 2009). Given the increasing rates of mortality and episodic die-off occurrence under global changes (McDowell et al., 2020), it is urgent to understand the drivers of tree mortality at the local and landscape scales.

Tree size is an important biotic factor in affecting tree mortality (Muller-Landau et al., 2006). It has been observed that tree mortality depends on the tree size and the size-mortality relationship presents several patterns. Mortality rates are usually high for small trees due to size-asymmetric competition for resources. However, some studies found that, as trees grow larger, mortality rates increase for a variety of reasons, including loss of physiological functions (Bennett et al., 2015; Rowland et al., 2015), senescences (Mencuccini et al., 2005) and high vulnerability to exogenous disturbances (Esquivel-Muelbert et al., 2014; Tanner et al., 2014). Therefore, when a tree exhibits both of these sizedependent responses, a U-shaped mortality pattern may occur (Goff & West, 1975; Harcombe, 1987). This shape of the sizemortality relationship has been observed for many forests (Coomes et al., 2012; Hurst et al., 2011; Rüger et al., 2011; Runkle, 2000) and applied in model simulations (Bugmann, 2001). However, compared to the traditional U-shaped pattern, some taxonomic groups show more complex relationships between tree sizes and mortality rates. In the eastern and central United States, a clear increase in density-dependent competitive mortality occurs at intermediate sizes among most taxa, and that size-dependent mortality is W-shaped (Dietze & Moorcroft, 2011). Besides, some studies have detected monotonic size-mortality relationships. Species with mechanically vulnerable large individuals are indicated by a disturbance-driven increase in mortality over tree size (Coomes et al., 2003), whereas species that are primarily controlled by competition processes conform better to a reverse J-shaped mortality function (Hülsmann et al., 2018). Due to such diverse patterns of size-dependent mortality, a universal size-mortality relationship is still illusive especially in the simulations of ecosystem carbon

cycling in global biogeochemical cycles. Thus, it is important to study the size-mortality relationships and explore their interactions with correlated factors in different forests.

The difference in the size-mortality pattern is expected to be driven by species traits. Changes in species composition greatly influence functional traits (e.g. tree architecture, wood density and leaf span), and consequently regulate tree mortality (lida, Poorter, et al., 2014; Wright et al., 2010). For instance, mortality rates tend to be higher for species with the small upper diameter and wide crowns as a consequence of structure failure by dynamic loading over the whole size classes (lida, Kohyama, et al., 2014). Fast-growing species are more acquisitive to light, and present the potential of greater competitive mortality rates (Canham et al., 2006; Kunstler et al., 2011). Meanwhile, their light woods render these species more likely to die from pathogen infections and structural failure of the stem or roots caused by windstorms at small size classes (Aleixo et al., 2019; lida, Kohyama, et al., 2014). Therefore, analysing the size-mortality trends of different functional groups can provide information about the demographic strategies among species. Here we expect that taller species show a greater mortality increase in response to neighbourhood crowding before they reach the canopy. Smaller species with the wide crown in the sub-canopy present higher vulnerability to hurricane disturbance as their wide crown render them more sensitive to dynamic loading due to wind or falling debris in the understory (Clark & Clark, 1991; lida, Poorter, et al., 2014), and their stems or roots are more likely to being broken or uprooted (Esquivel-Muelbert et al., 2020). Such differential susceptibility to various agents could explain diverse size-mortality patterns in species-rich forests.

Another major biotic factor causing tree mortality is competition. There is evidence that the strength of competition may vary with tree sizes. For example, competitive mortality is strongest at small sizes and became progressively less negative as trees grow older and larger (Zhu et al., 2015, 2018). Small trees are expected to experience size-asymmetric competition for light due to intense shading by taller canopy neighbours, leading to higher rates of mortality (Luo & Chen, 2011; Uriarte et al., 2004). Thus, the response of the focal tree to competition not only relates to the density of the neighbours but also depends on its size (Rozendaal et al., 2020; Zhu et al., 2018). We hypothesize that, in species-rich forests, competition appears to have a stronger influence on the mortality of smaller trees and causes higher rates of mortality in these size classes.

Apart from biotic interactions, tree mortality is also directly influenced by abiotic environmental conditions. At the regional scale, environmental differences such as temperature and aridity are regarded as the primary drivers of tree mortality. Studies generally consider either climate variables or moisture indices to explain the spatial variations of tree mortality (Anderegg et al., 2013; Williams et al., 2013; Worrall et al., 2013). At a finer spatial scale, tree mortality is affected by local environmental conditions, such as topography (Bellingham & Tanner, 2000; Ferry et al., 2010), microclimate (Dietze & Moorcroft, 2011; Huang & Anderegg, 2012) and soil fertility (Phillips et al., 2004; Russo et al., 2005). For example, tree mortality in Amazonia is the highest on fertile soils and steep slopes (Phillips et al., 2004; de Toledo et al., 2011). Moreover, topography can influence tree mortality by driving local-scale variation in soil chemistry, hydrology and microclimate (Adams et al., 2014; Andersen et al., 2014). Topography can mediate drought effects on tree mortality by redistributing soil moisture (Hawthorne & Miniat, 2018). However, previous studies only investigated a small number of environmental conditions and the drivers of the local environment are generally not analysed in detail. Thus, comprehensive assessments on the dependence of tree mortality on multiple biological and environmental factors are still limited in forest ecosystems at the local scales.

The East Asian subtropical monsoon forests (20-40°N), as an important terrestrial carbon sink, account for about 8% of the net ecosystem productivity of forests around the globe (Yu et al., 2014). However, the poor representations of vegetation turnover time, which is often used as a metric of mortality in vegetation models (Thurner et al., 2017), have added large inter-model variations to the gross primary productivity in this region (Cui et al., 2019). Thus, understanding the dependence of tree mortality upon abiotic and biotic factors is necessary to evaluate accurately the carbon turnover of the East Asian Monsoon region and its response to future climate conditions. The coastal region often suffers frequent typhoon that is typical of the monsoon climate, and this mature forest is also in face of intense competition as light is one of the most limiting resources for subtropical evergreen forests. Therefore, tree mortality patterns in the subtropical monsoon forests may be collectively shaped by both environmental and biological factors. Here, based on 5-year forest inventory data of a 20-ha forest dynamic plot in a subtropical forest, we evaluated the size-mortality patterns from species to the community level and identified those sizes classes most susceptible to a changing environment. This 20ha forest dynamic plot, appearing in a steep topography, consists of a mixture of evergreen and deciduous tree species (Figure S1) and has high tree diversity (Table S1). Tree mortality and abiotic factors (e.g. soil microclimate, soil chemistry and topography) have been measured with a high spatial resolution (Qiao et al., 2020; Wang et al., 2019). Thus, we asked the following questions: (a) what pattern dominates the relationship between tree size and mortality rate from species to the community level in this subtropical monsoon forest, (b) how biotic and environmental factors differently contribute to the spatial variation of tree mortality rate and (c) how these correlated factors vary with tree size across space?

### 2 | MATERIALS AND METHODS

### 2.1 | Study site

The study site is a subtropical monsoon evergreen broad-leaves forest, located in the Tiantong Forest Park (121.78°E, 29.80°N) in

Zhejiang Province, China. Before the late 1970s, most forests suffered from felling and logging and then naturally regenerated into secondary forests. Although all vegetation is secondary regrowth, many mature forests in this area are approximate to the climax communities of monsoon evergreen broad-leaved forest, in part because areas of forest, close to the Buddhist temples, is distributed in the core area of the park and has been well protected for more than 50 years (Wang et al., 2007). The natural vegetation of this subtropical forest is characterized by a mixture of evergreen and deciduous species and the dominated tree species includes Schima superba, Castanopsis fargesii, Choerospondias axiliaris and Machilus thunbergii (Yang et al., 2011). In all, 60 deciduous species comprised 8.6% of stems, whereas 57 evergreen species comprised 91.4% of stems (Figure S1). They live in different topographic and edaphic habitats. Compared to evergreen trees, deciduous trees are distributed in environments with greater availability of soil nutrients and light (Figure S2). This region has a subtropical monsoon climate with warm, moist summers and dry, cold winters. The mean annual temperature is 17°C. The mean annual precipitation is 1,600 mm, with more than 80% during April-September (National Meteorological Information Center, China Meteorological Administration; http://data.cma.cn). The type of soil is acid yellow-red soil with sandy and silty texture (Yang et al., 2016).

#### 2.2 | Forest inventory data

In 2010, all trees with a diameter at breast height (DBH)  $\ge 1$  cm were tagged and tree information including species identity, spatial coordinates, DBH, life form and survival status (alive or dead) was compiled in both 2010 and 2015. Totally, 163,612 trees belonging to 45 families, 77 genera and 117 species were recorded from 2010 to 2015 (Table S1). A tree is diagnosed as dead if defoliation reaches 100% or completely vanished (Lu et al., 2019). All trees were grouped into three categories by DBH as 1–15, 15–30 and >30 cm.

### 2.3 | Competition index

To evaluate the effect of local competition on tree mortality, we calculated the total basal area of all conspecific and heterospecific neighbours within a 20-m radius of each focal tree, respectively. We used the 20-m radius because competitive influences were most important at the spatial scale of 20 m neighbour radius, and intraspecific interactions are often disappeared beyond this distance (Murphy et al., 2017; Wang et al., 2010). For trees <20 m from the edge of the plot, we calculated the neighbour basal area to the distance of the plot boundary.

### 2.4 | Topography, microclimate and fertility

In 2010, the 20-ha forest dynamic plot was divided into 500 subplots (20 m  $\times$  20 m). Three topographic variables were recorded in each

subplot, including elevation, convexity and slope. Convexity was defined as the elevation of the focal subplot minus the average elevation of the eight adjacent subplots (Valencia et al., 2004). Slope was calculated as the averaged angular deviation from horizontal of the four triangular planes formed by connecting three corners of a subplot (Harms et al., 2001). Aspect was transformed into a north-south range, using the formula cosine  $(180^{\circ} - A) + 1.1$ , where A denotes the aspect in degrees from the north (Wang et al., 2007). Soil measurements and samplings were conducted in 187 subplots regularly arranged in the 20-ha plot (Figure S3). Soil temperature was monitored by settled temperature sensors at a depth of 10 cm. The average data per half-hour were stored in thermo-data loggers (iButton, DS1922, Wdsen electronic technology Co.). Soil moisture was measured every 3 weeks using manual TZS soil moisture equipment (TZS).

Three soil samples were collected from three random locations within each subplot at each of three depth intervals (0–20, 20–40 and 40–60 cm) during the summer (May and June) in 2016. After the removal of visible stones, litter residues and root fragments, fresh soils were air-dried for 30 days and sieved to 2 mm for chemical determination. Total nitrogen (N) was analysed using the modified Kjeldahl acid-digestion method (Page et al., 1982). Total phosphorus (P) was determined using the molybdenum blue colorimetry method (Murphy & Riley, 1962). Soil pH of each soil sample was measured by Metterler Toledo pH meter (1:2,  $H_2O$ ). Because we aimed to obtain the spatial variations of soil properties rather than assess the variability within the depth, the average values of the variable across the three depths were used in this study.

### 2.5 | Statistical analysis

We estimated size-dependent mortality at the species and community levels. The death probability  $p_i$  follows a binomial distribution of being either dead (1 = dead) or alive (0 = alive) over the census interval. The probability of death  $p_i$  for tree *i* is predicted from its annual mortality rate  $M_i$  and scaled to the time interval  $\Delta t$  as  $p_i = 1 - e^{-M_i \Delta t}$ . The annual mortality rate  $M_i$  was modelled as a function of the stem diameter of tree *i*,  $D_i$  (lida, Poorter, et al., 2014; Kohyama et al., 2015; Rüger et al., 2011):

$$M_{i} = e^{m_{1j} + m_{2j} \ln(D_{i}) + m_{3j} D_{i}},$$
(1)

where  $m_{1j}$ ,  $m_{2j}$  and  $m_{3j}$  are the species-specific parameters. The parameter  $m_{1,j}$  determines the mortality rate of species *j* at DBH = 1 cm, and  $m_{2,j}$  and  $m_{3,j}$  shows the effect of *D* and ln(*D*) on mortality rate. We conducted a Bayesian analysis (see Appendix S1 for details of model fitting) and fit the model in R using JAGS, a program for statistical modelling. All individuals of species with fewer than 10 trees were aggregated into a multi-species population and marked as 'other'. Differentiation of  $M_i$  concerning *D* is

$$\frac{dM_i}{dD_i} = \left(\frac{m_{2j}}{D_i} + m_{3j}\right) M_i,\tag{2}$$

Because  $M_i$  is non-negative, the monotonicity of the relationship between size and mortality is controlled by the sign of the estimated parameters  $m_2$  and  $m_3$  and the available DBH range for species *j*. The ratio of  $-\frac{m_{2i}}{m_{3j}}$  determines the threshold DBH at which mortality is either minimum or maximum. Here we defined  $\lambda_j = -\frac{m_{2i}}{m_{3j}}$ . If the  $\lambda_j$  of species *j* is not in the interior of the available DBH range,  $M_i$  is said to be monotonic, either increasing or decreasing over stem diameter. Otherwise, we can expect a threshold-dependent mortality pattern. Full descriptions of the classification of the size-mortality patterns and the model fitting are given in Appendix S1. To reduce the effect of survivorship bias, and to make community-level analysis consistent to species-level one (Kohyama et al., 2018), we estimated the size-class average of mortality to be the arithmetic mean of individual tree mortalities with 0.5 cm stem-size bins.

To assess how the effects of abiotic and biotic factors on tree mortality varied across size classes, four topographic variables (elevation, convexity, slope and aspect), five soil environmental variables (soil temperature and moisture, soil N, P and pH) and two biotic variables (stem size and competition index) were analysed as correlated factors in tree mortality for each size group. All variables were matched to trees in the 187 subplots in our analysis. We evaluated the correlated factors of tree mortality using general linear regression modelling and principal component analysis (PCA). Standardized coefficients of a multiple bivariate logistic regression model were used to indicate the importance of the variables. All analyses were performed in R version 4.0.3 (R Development Core Team, 2020).

### 3 | RESULTS

# 3.1 | Spatial distributions of environmental factors and dead trees

The elevations of the 20-ha forest dynamic plot ranged from 304.3 to 602.9 m, associated with the convexity ranged from -2.4 to 3.0 m and the slopes from 18.8° to 46.4° (Figure S4). The plot is on a southfacing mountain slope (Figure 1b). Mean soil moisture and temperature across the 187 subplots were  $22.9 \pm 2.3\%$  and  $16.5 \pm 1.2°$ C. For the spatial pattern, soil moisture was the highest in the west (30.1%) and the lowest in the east (16.7%). On the contrary, subplots on the low elevation in the east have the highest soil temperature at 22.2°C (Figure S4). The spatial variations of the numbers of dead individuals were between 3 and 95 among all 500 subplots (Figure 1).

# 3.2 | Size dependence of tree mortality at the species and community levels

Overall, 14,678 individual trees died over the 5 years. The dependence of the annual mortality rate on DBH showed diverse patterns among 92 species (Figure 2a). As illustrated by Appendix S1 and Figure S5, the dependence of mortality on tree size is jointly

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**FIGURE 2** The size-mortality patterns for 92 species. (a) Size dependence of annual mortality rate among 92 species. Predictions are restricted to the observed DBH range of each species to avoid extrapolation. (b) The relative proportion of species and individuals for each size-mortality pattern. (c) The relationship between DBH range and  $\lambda$  among 92 species. Specifically,  $\lambda = -\frac{m_2}{m_3}$ , which  $m_2$  and  $m_3$  are the estimated parameters from the size-mortality function. Species of which the DBH range intersects with the 1:1 line (dotted line) show a nonlinear size-mortality relationship, and the intersection point represents the threshold DBH that shifts the size dependence of mortality

determined by the signal of parameters  $m_2$  and  $m_3$  as well as  $\lambda$ . Among the 92 species, there were 27 U-shaped species and 3 unimodal species (Figure 2b). The annual mortality progressively declined with tree size for 58 species and increased for 4 species (Figure 2b). The number of individuals with the U-shaped pattern of size-dependent mortality is the largest among the four patterns (Figure 2b). The different mortality-size patterns can also be indicated by the relationship between  $\lambda$  and DBH range (Figure 2c; Figure S5; Appendix S1). The stem diameter at which the annual mortality rate reaches the maximum or minimum can be defined as the threshold for the size dependence of mortality. The threshold size of the U-shaped patterns was positively related to species-specific maximum height (Figure S6).

At the community level, the dependency of mortality rate on stem size shifted from negative to positive, forming a U-shaped mortality pattern (Figure 3a). The record of dead individuals included 13,883 small trees, 643 medium trees and 152 large trees. From 2010 to 2015, the annual tree mortality rates were 0.025, 0.021 and 0.019 for small, medium and large trees, respectively (Figure 3b).

# 3.3 | Correlated factors on the spatial variation of tree mortality at the community level

To explore the possible drivers of spatial variation in tree mortality rate, we examined the spatial correlations of tree mortality with multiple biotic and environmental variables. As shown in Figure 4, tree size was the most important predictor for tree mortality among the measured variables at small and medium sizes. The effect of conspecific and heterospecific competition shifted with size classes and showed a decreasing trend of competitive strength with increasing size. The mortality rate of the small tree was positively affected by the conspecific competition and negatively affected by the heterospecific competition (Figure 4a). Conversely, the competition had no significant effect on the mortality rate at medium and large sizes (Figure 4b,c).

In addition to tree size and competition, we also found that environmental change had a significant but relatively weaker effect for small and medium sizes (Figure 4). For small trees, the mortality was significantly increased with elevation, P and soil moisture, and decreased with slope and N for small trees (Figure 4a), whereas the



**FIGURE 4** Estimated coefficients of tree mortality for each variable for small (a), medium (b) and (c) large trees. Variables with coefficients more than zero (vertical dashed line) increase tree mortality and less than zero decrease mortality. Error bars represent the 95% confidence intervals in the estimated coefficients. Factors were classified by biotic factors (pink), topography (purple), soil chemistry properties (blue) and microclimate (green). See Table S2 for the explanation of abbreviations



**FIGURE 5** Principal component analysis (PCA) for (a) small, (b) medium and (c) large trees. Factors were classified by biotic factors (pink), topography (purple), soil chemistry properties (blue) and microclimate (green). See Table S2 for the explanation of abbreviations

only slope had slight positive effects on the mortality at the medium size (Figure 4b). In comparison to small and medium trees, large trees were more sensitive to environmental changes. Specifically, the mortality of large trees was positively correlated with convexity, slope, P and soil temperature, but negatively correlated with pH and soil moisture (Figure 4c).

# 3.4 | Principal components for explaining the spatial variation of tree mortality

A principal component analysis (PCA) was applied to explore the combinations of controlling factors in explaining the spatial variation of tree mortality. The first two principal components explained 33.2% and 23.9% of the spatial variation of mortality for small trees (Figure 5a; Table S3), and 30.8% and 15.6% for medium trees (Figure 5b; Table S3). The PCA on large trees showed that PC1 and PC2 accounted for 24.7% and 18.6% of the total variation, respectively, with soil chemistry (i.e. N, P, pH) scoring high on the first dimension (Figure 5c; Table S3). The second dimension had strong loadings for DBH, competition index (i.e. conspecific competition and heterospecific competition) and elevation, moderately loadings for soil temperature, and slope (Figure 5c; Table S3). However, the dependence of the mortality rate on the biological and environmental dimensions was insignificant for small and medium trees (Table S4).

### 4 | DISCUSSION

# 4.1 | Species-specific patterns of size-dependent mortality

Our study suggests that tree species are classified into four sizemortality groups, including a U-shaped pattern, unimodal pattern, monotonic increase and an exponential decline (Figure 2; Table 1). The variety in patterns of tree mortality among species reflects such factors as differences in life spans, susceptibility to various agents and compositional distribution in the landscape (Franklin et al., 1987). The unimodal mortality pattern is rare in previous studies, but three species that share 10% of total individuals in the studied plot show unimodal patterns. The peak in intermediate mortality could result from self-thinning, whereby these species might suffer intense conspecific competition and consequently drive higher density-dependent mortality at intermediate sizes (Dietze & Moorcroft, 2011). The absence of the intermediate-sized increases for other species is likely due to the large lower limits in the forest census that cause the peaks of these species to be below the size threshold. Overall, we found 30 out of 92 species demonstrate threshold-dependent changes, with the U-shaped and unimodal pattern for 27 and 3 species, respectively (Figure 2b). It implies that the threshold-dependent pattern might be an important characteristic of tree mortality in this subtropical evergreen forest. This is the first study of the threshold-dependent mortality pattern across species and provides objective and quantitative descriptions. Notably, the threshold size varies among species with a range of 1.1-51.8 cm and 1.1-25.0 cm for the U-shaped and unimodal mortality pattern, respectively (Figure 2c). The smaller threshold size for unimodal patterns than the U-shaped pattern could attribute to the stronger conspecific negative density dependence at smaller sizes (Zhu et al., 2015, 2018). Besides, the threshold size significantly increased with their maximum DBH (Figure S6), indicating an earlier and stronger response in small-statured species. Thus, one next pivotal step is to explore the changes of such thresholds for size-mortality relationships across the subtropical forests in monsoon Asia.

As we hypothesized, the variation of size-dependent mortality in our analysis is biologically linked to the diverse species composition,

**TABLE 1** Summary of the four hypothesized size-mortality patterns. The detailed information about the size-mortality function can be found in Appendix A.  $[D_{\min}, D_{\max}]$  denotes the size range for each species;  $m_2$  and  $m_3$  are the parameters of the size-mortality model and  $\lambda = -(m_2/m_3)$ 

Size-related mortality pattern		Description of the shapes of the size-morality pattern
a. Monotonic increase: mortality rate increases with tree size	Mortality	The size-mortality function is monotonic increasing in the following three conditions. First, if both of the parameters $m_2$ and $m_3$ are positive, the function is always increasing regardless of $\lambda$ . When $m_2$ and $m_3$ have opposite signs, the mortality rate is increasing on $[D_{\min}, D_{\max}]$ if $m_2$ is negative and $\lambda$ is less than the minimum stem size or if $m_2$ is positive and $\lambda$ is larger than the maximum stem size
a. Exponential decline: mortality rate declines gradually with tree size	Mortality DBH	The size-mortality function is progressive declining in the following three conditions. First, if both of the parameters $m_2$ and $m_3$ are negative, the function is always decreasing regardless of $\lambda$ . When $m_2$ and $m_3$ have opposite signs, the mortality rate is declining on $[D_{\min}, D_{\max}]$ if $m_2$ greater than zero and $\lambda$ less than the minimum stem size or if $m_2$ less than zero and $\lambda$ larger than the maximum stem size
a. U-shaped pattern: higher rates of mortality at small and large sizes	Mortality	If $D_{\min} < \lambda < D_{\max}$ , $m_2 < 0$ ; the mortality rate is declining on $[D_{\min}, \lambda]$ and then increasing on $[\lambda, D_{\max}]$ . Note that $D_{\min}$ is a positive value in the natural system so that $m_2$ and $m_3$ have opposite signs when $D_{\min} < \lambda < D_{\max}$
a. Unimodal pattern: mortality rate increases first to a peak at the medium size, and then declines	Mortality	If $D_{\min} < \lambda < D_{\max}, m_2 > 0$ ; the mortality rate is increasing on $[D_{\min}, \lambda]$ and then decreasing on $[\lambda, D_{\max}]$

which is represented by different expressions of plant traits. The functional trait and associated life-history strategies can influence tree susceptibility to different mortality agents. Specifically, all four species that showed an increase in size-dependent mortality are softwood such that trees with lower wood density suffer greater mortality at a larger size (Poorter et al., 2010). Among 92 species, 67% of the unimodal pattern and 82% of the declined pattern was dominated by the canopy trees that can reach higher height, whereas species with the U-shaped mortality pattern showed no significant difference in their life form. Small-stature species with high shade tolerance are expected to have a good ability to survive in the subcanopy, that is, being small and resistant to low-light conditions (Valladares & Niinemets, 2008). As they growing bigger and older, species that have a small upper diameter and wide crown system are exposed to higher stress and structural instability, leading to an increase in mortality. In contrast, less shade-tolerant canopy species are more likely to have increased mortality at low or medium DBH as restricted access to light and show an exponential decrease or unimodal pattern of size-dependent mortality. Overall, the relationship between tree size and mortality in the subtropics could be highly dependent on the local context of taxon functional composition and demographic dynamics. An extensive taxon-level trait dataset might improve the demonstration of size threshold and identify the intrinsic tree factors driving changes in size thresholds, especially for forests with rich species.

### 4.2 | The community-level pattern of sizedependent mortality

Our first hypothesis of a U-shaped pattern of size-dependent mortality is supported by most tree individuals (Figure 2b) and thus can be applied to the whole community (Figure 3). The size dependence of mortality rate shifts from decrease to increase as stem size became larger (Figure 3a). This finding of a U-shaped pattern is consistent with greater mortality rates for small trees in boreal and temperate forests (Hurst et al., 2011; Lines et al., 2010; Synek et al., 2020). Many other studies also reported the asymmetric U-shaped mortality pattern with much higher mortality rates for large trees in several mesic old-growth forests (Lorimer et al., 2001) and tropical forests (Arellano et al., 2019).

Ecologically, the U-shaped pattern of size effect on tree mortality rates could be collectively explained by the competition- and disturbance-driven assumptions. The competition-driven hypothesis suggests that small trees have fairly high mortality rates as a consequence of asymmetric competition with large trees, resulting in a monotonically descending size-mortality pattern (Brown et al., 2004; Enquist & Niklas, 2001; Weiner, 1990). In contrast, the disturbance-driven hypothesis assumes that although large trees receive more light, they become increasingly vulnerable to environmental fluctuation and exogenous disturbance such as winds, insect attack and other stresses (Lindenmayer & Laurance, 2016; Wells et al., 2001; Woods, 2004). Together, these two processes are referred to as a U-shaped mortality pattern. In this study, the mortality rates are slightly higher for small than medium trees, indicating a competition-driven mortality pattern (Figure 3a). This pattern is likely driven by light competition because shading is expected to be an important driving force to vegetation growth and survival in species-rich but light-limited subtropical forests (Huang et al., 2018; Nemani et al., 2003). After then, the mortality rates increase with size for large trees (Figure 3a). It appears that processes such as wind disturbances may be the dominant causes of mortality for the observed increases in large-tree mortality in this coastal region (Uriarte et al., 2019; Zeng et al., 2009). It has been reported that, in the monsoon Asia, typhoons increase the mortality rates of large trees by destroying tree crowns and promoting tree tipping over (Yang et al., 2006; Yang et al., 2011; Zhang et al., 2013).

# 4.3 | The impacts of biotic and abiotic factors on mortality depend on tree size

We found that tree mortality is impacted by both competition and environmental conditions, and the strength of these correlated factors changes with size classes (Figures 4 and 5). Neighbourhood effects on tree mortality are only detected at small sizes (Figure 4). This is consistent with the idea that competitive exclusion is most commonly observed for small trees (Das et al., 2016; Uriarte et al., 2004). Observations from 151 tropical forest plots have suggested that competition does not influence the mortality rate of trees larger than 10 cm DBH in both Amazonia and tropical Africa (Rozendaal et al., 2020). As trees increase in size, the effect of the competition is decreasing and other mortality drivers such as variation in environmental factors (e.g. soil moisture) gain importance (Holzwarth et al., 2013; Rowland et al., 2015). Besides, consistent with a previous study (Franklin et al., 1987), intraspecific competition is the primary driver of tree mortality in the closed forest canopy (Figure 4a). The positive effect of the intraspecific competition on small-tree mortality is likely due to higher susceptibility to natural enemies or greater intraspecific competitive exclusion for the shared resources, such as below-ground soil resources and above-ground light, and available space both below- and above-ground (Canham et al., 2004; Chesson, 2000; Luo & Chen, 2011).

In contrast to the competition, we found evidence that local environmental conditions disproportionately affect the mortality of larger trees in this subtropical monsoon evergreen forest. Specifically, the spatial variation of tree mortality explained by environmental factors is low for small trees (Figures 4 and 5) and insignificant for mid-sized trees (Figures 4 and 5). However, the mortality of large trees shows strong dependences on topography and edaphic attributes (Figure 4; Figure 5). This finding is supported by vegetation analyses in tropical forests of Amazonia, where the relationships of mortality rates with soil and topography are constrained to specific tree size classes at both local and regional scales (Ferry et al., 2010; Quesada et al., 2009; de Toledo et al., 2011). The strong **FIGURE 6** Histograms showing estimates of biotic (a-c) and environmental (d-l) variables on tree mortality across 34 species with more than 120 individual trees. The results are from generalized linear models, in which the effects of specific variables are allowed to vary among species. The dashed lines are at zero so that bars to the right of the line indicate species whose mortality is positively affected by variables and vice versa



topographic effects on large-tree mortality can be contributed to the complex environmental conditions in this mountain area, which also plays an important role in shaping community composition and maintaining the diversity of this subtropical forest (Figure S7). For mid-sized trees, the size-mortality relationship varies greatly among species (Figure 2a), associated with week correlations between mortality rates and environmental factors (Figure 4). These results suggest that no clear correlation between spatial heterogeneity and tree mortality in mid-sized trees could result from the mixture of different species with varied traits. As discussed above, the differential response of tree mortality across size classes to correlated factors corresponds to a U-shaped mortality pattern. The greater dependence of large-tree mortality on environmental factors may help explain the increase in mortality rates in large sizes relative to other types of forests. Previous community-wide studies accessing mortality drivers have typically focused only on a single size class. Our study suggests that examining specific mortality drivers for different sizes of trees can improve our understanding of forest demographic dynamics and assist forest managers and policymakers in identifying the most vulnerable tree size classes in forests.

As a secondary forest, the studied forest plot follows a successional trajectory characterized by a transition from evergreen conifer species of *Pinus massoniana*, to the evergreen broad-leaved *Schima superba*, and ultimately towards climax *Castanopsis carlesii* (Song & Wang, 1995). The causes of tree mortality appear to become more complex throughout the successional stage (Franklin et al., 1987). As succession proceeds, competitive sorting takes place and species get reduced in habitat breadth (Christensen & Peet, 1984). So local species richness declines and species get excluded to a subset of sites. One mechanism for this competitive thinning by exclusion is the high mortality of small individuals of certain species on certain sites. In the study area, species varies substantially in response to environmental conditions and biotic factors (Figure 6). Thus, the various patterns of size-dependent mortality among species could be linked to the likely compositional changes in this secondary succession forest. Our results suggest that natural history and the successional community dynamics are essential for understanding and predicting the dynamics of forest structures and functions in the eastern Asian monsoon region.

## 5 | CONCLUSIONS

In conclusion, we identify a U-shaped mortality pattern in a subtropical monsoon mature forest in eastern Asia. The effect of stem size flips from negative to positive as a tree grows larger. The species-level analyses reveal four different size-mortality patterns, resulting in a high diversity of size-dependent mortality rates across species. The variation in size-dependent mortality across tree species suggests an important role of species composition in shaping the size-mortality pattern of the tree community. Thus, it should be noted that the findings in this study are from a single large forest plot and the community-level relationship between tree size and mortality could vary across the eastern Asian monsoon region due to its large heterogeneity of forest structure. Interestingly, competition shows a significant effect on mortality for small trees while the effect of environmental variables was strongest in the large trees. This finding indicates that the relationships between tree mortality and local environmental factors are dependent on tree size. Overall, this study underscores that a better understanding of tree mortality from the species to the community level will benefit local forest management and regional ecological forecasting.

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#### AUTHORS' CONTRIBUTIONS

J.Y. and R.L. conceived the ideas and designed the methodology; Y.H., X.W., Q.Y. and G.S. collected the data; Y.J. and R.L. analysed the data and led the writing of the manuscript draft. All other authors edited and revised the paper.

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#### DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi. org/10.5061/dryad.69p8cz90v (Lu et al., 2021).

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### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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