

Effects of light and topography on regeneration and coexistence of evergreen and deciduous tree species in a Chinese subtropical forest

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Abstract

1. Evergreen broad-leaved forests are widely distributed in eastern Asia with evergreen broad-leaved (EBL) and deciduous broad-leaved (DBL) tree species coexisting under the same climatic regime, raising questions as to the underlying mechanisms. Since EBL and DBL species differ in leaf life span, a key component of resource economic strategies, their coexistence might be attributed to regeneration niche partitioning across habitats varying in resource supply.
2. We investigated the effects of variation in insolation and topography on regeneration of EBL and DBL species in a subtropical EBL forest of eastern China after an ice storm that caused severe canopy disturbance.
3. Using a mixed-effects modelling framework and census data from 2011 to 2014 on 8,548 wild seedlings of 123 species, we quantified habitat preferences of EBL and DBL species during post-disturbance regeneration and how their survival and height relative growth rates varied among habitats.
4. The relative density of DBL seedlings (proportional to all seedlings) was greater in habitats with greater (canopy gaps) compared to habitats with lesser (understorey) insolation and increased with canopy gap size. However, DBL seedlings were not more frequent in higher (valleys) compared to lower (ridges) fertility habitats. Although DBL seedlings exhibited larger differences in growth between higher and lower resource habitats than EBL seedlings, their growth rates did not increase with canopy gap size. Seedlings of EBL species had high survival in all habitats, but larger DBL seedlings survived equally well on ridges. Consequently, the relative density of DBL seedlings declined in valleys, so that by 2014 it became more similar in valley and ridge habitats, whereas it remained higher in gaps than in the understorey, and especially in larger gaps.
5. *Synthesis.* Specialization on contrasting topographic habitats is considered the primary mechanism mediating coexistence between deciduous broad-leaved and evergreen broad-leaved species. Our results, however, suggest this may not always be true, since seedlings of deciduous broad-leaved and evergreen broad-leaved species partitioned regeneration niches based on light more so than topography. We propose that coexistence of deciduous broad-leaved and evergreen broad-leaved species can strongly depend upon canopy disturbance to create a mosaic of

habitat patches, including high light gaps favouring regeneration of deciduous broad-leaved species.

KEYWORDS

forest gap mosaic, Gutianshan 24-ha Subtropical Evergreen Broad-leaved Forest Dynamics Plot, ice storm, leaf habit, leaf life span, seedling height growth, seedling survival

1 | INTRODUCTION

Evergreen broad-leaved (EBL) forest is a common vegetation type of the humid subtropical zone, which covers a large region of eastern Asia and harbours high tree species richness (Bruehlheide et al., 2011; Kira, 1991; Song, 1988, 1995; Wang, Kent, & Fang, 2007). An interesting feature of EBL subtropical forest is that deciduous broad-leaved (DBL) tree species (with leaf life spans less than 1 year and a distinct leafless period) and EBL tree species (with leaf life spans exceeding 1 year) often coexist in the same climatic conditions (Song, 1988). Although the importance of deciduous species often declines during succession (Kröber, Böhnke, Welk, Wirth, & Bruehlheide, 2012), species with contrasting leaf habits coexist in climax EBL subtropical forests (Song, 1988; Zhu et al., 2008). This is somewhat paradoxical because longer growing seasons are thought to favour tree species with longer leaf life spans in order to recoup the costs of long-lived leaves (Givnish, 2002), raising questions as to the mechanisms that allow DBL and EBL species to coexist in the same climatic regime.

Leaf life span not only dictates the proportion of the year over which photosynthetically fixed carbon can be acquired by trees, but also has broad implications for demography and coexistence of tree species (Westoby, Falster, Moles, Vesk, & Wright, 2002). Differences in leaf life span are driven by carbon and nutrient economies in relation to resource availability at the whole-plant level (Chabot & Hicks, 1982; Givnish, 2002; Kikuzawa & Lechowicz, 2011; Reich, Uhl, Walters, & Ellsworth, 1991) and correlate with performance and variations in functional traits, as well as species' light and soil niches (Coley, 1988; Poorter & Bongers, 2006; Russo & Kitajima, 2016). Adult DBL and EBL species often have patchy topographic distributions, with greater basal area of DBL species in valleys and of EBL species on ridges, leading to the hypothesis that topographic habitat filtering and resulting niche partitioning allows species with different leaf habits to coexist at the landscape scale (Fang et al., 2016; Song, 1995; Tang & Ohsawa, 2002). At what life stages this habitat filtering is the most influential and how these spatial patterns are established, however, are not known. Moreover, not all EBL subtropical forests show strong topographic habitat specialization by mature trees of DBL and EBL species (Lai, Mi, Ren, & Ma, 2009), which casts doubt on the necessity and prevalence of topographic specialization as a prerequisite for the coexistence of DBL and EBL species in these forests and begs the question of what other mechanisms that might be involved. Because topographic gradients are complex and vary in different types of resources, as well as canopy disturbance (Nagamatsu, Seiwa, & Sakai, 2002; Yasuhiro, Hirofumi, & Kihachiro, 2004), it is also possible that light availability

may be an important driver of filtering, but most studies have not decoupled these drivers.

The seedling stage is an important demographic filter and establishes the template for subsequent recruitment processes (Harper, 1977). Variation in seedling survival and growth rates linked to leaf habit across resource gradients would lead to different regeneration niches (Grubb, 1977) of DBL and EBL species, which could facilitate the coexistence of species in these groups at landscape scales (Chesson, 2000; MacArthur & Levins, 1967). Since DBL species shed leaves more frequently than do EBL species, and the costs of leaf construction and nutrient losses are higher with faster leaf turnover, DBL species may require habitats with greater availability of both above- and below-ground resources for regeneration (Givnish, 2002; Russo & Kitajima, 2016).

In closed canopy forests, light availability in the understorey is usually low, but occasionally canopy trees die and create canopy gaps that bring high irradiance to the lower strata of the forest. Canopy gaps also vary in size, greater insolation and below-ground resource availability in larger gaps (Denslow, 1987; Denslow, Ellison, & Sanford, 1998). Mature forests can be thought of as consisting of a shifting mosaic of patches varying in time since disturbance, and hence, understorey light availability, that influences tree demography (Clark, 1991; Coomes & Allen, 2007). Compared with seedlings of EBL species, DBL seedlings have greater photosynthetic responsiveness to high light (Böhnke & Bruehlheide, 2013; Cornelissen, 1993; Hu, Guo, Li, & Ma, 2008) and leaf trait values associated with faster leaf economies (Bai, He, Wan, & Jiang, 2015; Reich et al., 1991), whereas seedlings of EBL species are often more shade tolerant (Baldocchi et al., 2010; Kitajima, Cordero, & Wright, 2013; Wang et al., 2007). Since foliage in and around canopy gaps recovers after gap formation, irradiance levels in gaps decline through time, potentially causing gap effects to be transient (Brokaw, 1985; Denslow, 1987). It is therefore expected that, provided gap effects persist, canopy gaps should differentially affect the regeneration of DBL and EBL species, and this effect should depend on canopy gap size. However, the role of canopy disturbance in facilitating the coexistence of DBL and EBL species in EBL forests is poorly understood.

The goal of this study was to test whether, in addition to topography, canopy disturbance contributes to regeneration niche partitioning of DBL and EBL species in a subtropical EBL forest in Gutianshan National Nature Reserve in eastern China. A 24-ha forest dynamics plot (FDP) was established there in 2005 (hereafter, Gutianshan) and contains 69 DBL and 88 EBL species, with EBL species comprising the majority of stems and basal area (Zhu et al., 2008). Gutianshan has

substantial topographic heterogeneity, with more fertile soils having higher concentrations of phosphorus in valleys compared to ridges (Chen et al., 2010; Liu et al., 2012). In January 2008, Gutianshan was hit by a severe ice storm (Man, Mi, & Ma, 2011) that caused dramatic canopy disturbance. The simultaneous formation of many canopy gaps in both valley and ridge habitats afforded the unique opportunity to disentangle how variation in both light availability and topography influenced seedling recruitment of DBL and EBL species and whether species with contrasting leaf habits vary in their regeneration niches. Specifically, we contrasted seedling density and demography between DBL and EBL species in lower (ridge and understorey habitats) vs. higher (valley and gap habitats) resource habitats, and within canopy gaps, as gap size increased, to investigate the relative strength of habitat filtering of DBL and EBL species due to canopy disturbance vs. topography.

Comparing across species with contrasting leaf habits, because EBL species are more conservative in terms of resource use, they should have, on average, slower growth and higher survival rates (Kitajima & Myers, 2008; Wright et al., 2010) than DBL species in all habitats. However, comparing across habitats for species with the same leaf habit, individuals in environments that are favourable for faster growth generally have higher survival rates (Kobe, Pacala, Silander, & Canham, 1995). Given that faster leaf turnover is associated with higher carbon and nutrient costs, we therefore predicted that in habitats supplying more resources, DBL species would grow faster (due to improved carbon and nutrient economy) and have higher survival (due to faster growth) compared to habitats with more limited availability of resources. While all seedlings should usually grow faster with greater insolation and soil fertility, we expected such resource-driven variation in vital rates among habitats to be larger for DBL than for EBL species. As a result, DBL species should achieve higher seedling densities (relative to the total seedling density of the two groups) in higher, compared with lower, resource habitats.

2 | MATERIALS AND METHODS

2.1 | Study site

Our study was conducted in Gutianshan National Nature Reserve (29°10'19"–29°17'41"N, 118°03'50"–118°11'12"E) in Zhejiang Province of subtropical eastern China. Local mean annual temperature is 15.3°C, with minimum of –6.8°C in January and maximum of 38.1°C in July. Mean annual precipitation is 1,964 mm (Yu, Hu, Yu, Ding, & Fang, 2001). Our study site is a 24-ha FDP comprising subtropical EBL forest, which is typical of this region. The Gutianshan FDP was established in 2005 following the protocols of the Center for Tropical Forest Science (Condit, 1998), in which every living, woody stem with diameter at breast height (DBH; 1.3 m) ≥ 1 cm was tagged, mapped, identified to species and its DBH measured. The 2005 plot census recorded 140,676 stems ≥ 1 cm DBH, belonging to 49 families and 159 species (Shen et al., 2009). Deciduous broad-leaved species comprised 69 species and 11.09% of stems and 9.85% of the basal area, whereas EBL species comprised 88 species and 87.31% of stems

and 77.27% of the basal area. Conifers comprised the other two species (i.e., *Pinus massoniana* and *Cunninghamia lanceolata*) in the FDP. The topography of the FDP is rugged, with an elevation range from 446.3 to 714.9 m a.s.l. (Zhu et al., 2008). Five habitat types have been identified within the FDP (Legendre et al., 2009), and this study was conducted within the two largest topographic habitat types (low valleys and low ridges, hereafter referred to as valley and ridge).

2.2 | Canopy gap sampling

In January of 2008, an ice-snow storm severely damaged the FDP (Man et al., 2011), providing an opportunity to quantify regeneration dynamics of DBL and EBL species in new, simultaneously formed canopy gaps. We recorded the locations of canopy openings formed during the ice storm as a part of a tree damage survey conducted immediately after the storm (Man et al., 2011). We identified the gap-makers that were killed during the ice storm and mapped all gaps created by the ice storm in the FDP based on field observation. We defined a canopy gap as an opening in the forest canopy down to an average height of 2 m above ground (Brokaw, 1982) and ≥ 25 m². We estimated the size of each new gap as the area of the polygon formed by the bases of canopy trees surrounding the canopy opening, which comprised the area directly and indirectly affected by the canopy opening (Runkle, 1981; Figure S1).

Among the 207 new gaps formed during the ice storm, we selected gaps using a stratified random sampling design. First, we stratified sites according to topographic habitat type (valley vs. ridge) and then into four gap size classes (25–100 m², 100–200 m², 200–300 m² and 300–500 m²; Römer, Kneeshaw, & Bergeron, 2007). From these, we randomly selected four gaps of each size class from each topographic habitat type, for a total of 32 gaps. We defined the gap centre as the intersection of the two lines formed by the longest canopy opening dimension (gap length) and the longest line perpendicular to it (gap width). We demarcated an area of closed canopy forest that had minimal storm damage within a 30-m-radius circle centred at the canopy gap centre. We refer to the gap and its paired understorey area as a site, for a total of 32 sites across valley and ridge habitats (Figure S1). Pairing gap and understorey areas near each other within a site helped ensure similar seed arrival to each.

2.3 | Seedling sampling

At each site, we established 1 × 1 m seedling quadrats every 5 m on a grid covering the entire gap and understorey, with quadrats set at the grid intersections (Figure S1). Each seedling quadrat was classified as either gap or understorey. For gaps <100 m² in size, quadrats were spaced every 2.5 m due to small gap size. Irradiance was quantified for each site with hemispherical photographs taken at 1.3 m above five to eight randomly selected seedling quadrats in the gap and understorey areas of each site. The images were taken by CANON EOS 50D digital camera connected to Sigma 4.5-mm fisheye lens mounted on a tripod, and then, photographs were processed by HemiView v. 2.1 software. Seedling quadrats in gaps received significantly higher insolation

than quadrats in the understorey (Figure S2), but hemispherical photographs did not detect significantly greater insolation in larger vs. smaller gaps ($p > .05$, $df = 28$, linear mixed-effects model). Further, insolation did not differ between valleys and ridges in either canopy gaps of the same size ($p > .05$, $df = 28$, linear mixed-effects model) or the understorey ($p > .05$, $df = 30$, linear mixed-effects model).

Seedlings were defined as woody plants of any height with DBH < 1 cm (Dalling, Muller-Landau, Wright, & Hubbell, 2002) and therefore included individuals that recruited before and after gap formation. We tagged, identified and measured the height of every seedling in each quadrat initially in August 2011, and then 1, 2 and 3 years later in August of 2012, 2013 and 2014, respectively. The difference in inter-census intervals across all quadrats was less than 1 month. There were two fruiting seasons after the ice storm and prior to our initial seedling census, allowing us to capture post-disturbance regeneration dynamics in our censuses. In the first census, 8,548 broad-leaved seedlings belonging to 123 species were recorded in 905 quadrats (Appendix S1). Based on the descriptions in Zheng (2005) and Fang and Chen (2013), we categorized these seedlings as DBL or EBL, representing 6,655 seedlings of 75 EBL and 1,893 seedlings of 48 DBL species. In the first census, seedlings of the coniferous species *P. massoniana* were recorded. They were excluded because our focus was on broad-leaved tree species, which comprise the old-growth EBL forests of this region (Song, 2013). In the 2014 census, 7,300 seedlings were recorded in the 905 quadrats. Of these, 4,009 were seedlings recorded in the 2011 census, and 3,291 were seedlings that recruited between 2011 and 2014.

Of the 123 study species in our data, the phylogenetic relationships of 113 species were resolved based on the sequences of three commonly used barcode genes *rbcL*, *matK* and *trnH-psbA* from trees in the Gutianshan FDP (Liu, Swenson, Zhang, & Ma, 2013). Refer to Liu et al. (2013) for the detailed description of the phylogeny construction. The other ten species (indicated in Appendix S1) were manually added to the phylogeny as polytomies based on taxonomic relationships (Jin, Qian, & Yu, 2015).

2.4 | Statistical analyses

In our sampling scheme, seedlings were nested in quadrats (905 quadrats), quadrats, which could have a canopy status of either gap or understorey, were nested in sites (32 sites), and sites were nested in topographic habitat (valley or ridge; Figure S1). We used mixed-effects models to account for this hierarchical error structure (Bolker et al., 2009; McMahon & Diez, 2007; see Appendix S2 for the detailed descriptions of the statistical models). All analyses were performed in the statistical software, R version 3.2.4 (R Core Team, 2016).

To evaluate our predictions that DBL species should achieve higher seedling densities in habitats with higher compared with lower resource supply, we examined a variation in the relative densities of DBL seedlings, considering all seedlings present in 2011 and 2014 and seedlings recruited between 2011 and 2014, across habitat types and canopy gap size gradient using generalized linear mixed-effects models (GLMMs) as implemented in the “glmer” function in the *lme4*

package (Bates, Maechler, Bolker, & Walker, 2015). Species were categorized as either DBL or EBL. Whether or not seedling i in quadrat j at site k of species l was a DBL species was assumed to be distributed as a Bernoulli random variable as $D_{ijkl} \sim \text{Bernoulli}(p_{ijkl})$, where p_{ijkl} is the probability of the seedling being a DBL species. Using a logit link function, we hierarchically modelled variation in p_{ijkl} with topographic habitat (valley vs. ridge), canopy status (gaps vs. understorey) and their interaction in the full model. We included random terms for canopy status nested within site identity to reflect the fact that gap and understorey quadrats were nested within sites, which were either on ridges or in valleys. We also included random terms for species, since the number of individuals of each species varied in the dataset. Random terms were assumed to be normally distributed with a mean of zero and estimated standard deviations. To estimate how the relative DBL seedling densities changed through time, we ran the model separately for the 2011 and 2014 censuses. To test the effects of canopy gap size on the relative density of all and newly recruited DBL seedlings in gaps, we fitted similar models, but with a continuous predictor for gap size and its interaction with topographic habitat. Summary statistics for fixed effects in the most supported GLMM were estimated using the “ANOVA” function in the *car* package based on type III Wald chi-squared tests (Fox & Weisberg, 2011). Student's t tests were used for post hoc pairwise comparisons.

We examined whether leaf habit was a phylogenetically conserved trait among the 123 broad-leaved species included in our dataset using the approach described in Cadotte and Davies (2016). Specifically, we used a likelihood ratio test to compare whether the evolution of leaf habit was better explained by a macroevolutionary model fitted using the resolved phylogenetic relationships vs. a null model fitted using a star phylogeny, performed using the “fitDiscrete” function with the “ER” model in the *geiger* package (Harmon, Weir, Brock, Glor, & Challenger, 2008). We found statistically significant phylogenetic conservatism in leaf habit (Pagel's $\lambda = 0.899$, $p < .001$). We used the “phylosig” function in the *phytools* package (Revell, 2012) to extract the species-level random intercepts from the results of the most supported for the survival and height relative growth rate models. We found these residuals to be phylogenetically conserved (survival: Pagel's $\lambda = 1.01$, $p < .001$; growth: Pagel's $\lambda = 1.01$, $p < .001$). We therefore modelled residuals as correlated due to phylogenetic relationships in our seedling survival and growth models (Appendix S2).

Whether seedling i in quadrat j at site k of species l survived from the 2011 to 2014 census was assumed to be distributed as a Bernoulli random variable as $V_{ijkl} \sim \text{Bernoulli}(s_{ijkl})$, where s_{ijkl} is the probability of a seedling alive in the August 2011 census (total of 8,548 seedlings) surviving until the August 2014 census. Using a logit link function, we hierarchically modelled variation in s_{ijkl} as described below. Seedling relative growth rate was calculated as $(\log(H_2) - \log(H_1)) / (t_2 - t_1)$, where H_2 and H_1 are the heights at times t_2 and t_1 , respectively, of each seedling alive in the August 2014 and August 2011 censuses (total of 4,009 seedlings). The relative growth rate (g_{ijkl}) of seedling i in quadrat j at site k of species l was assumed to be normally distributed with standard deviation σ_g . We hierarchically modelled variation in g_{ijkl} as described below.

Survival and growth models had the same full fixed-effects and random-effects models (Appendix S2). The full fixed-effects models included seedling height in 2011, leaf habit (DBL vs. EBL), topographic habitat, canopy status and all interactions. The random-effects models included random intercepts for species and for quadrat nested within site and a random slope for species-specific height-dependent survival (or growth). To test the effects of canopy gap size on the survival and growth of seedlings in gaps, we fitted similar models, but with a continuous predictor for gap area and its interaction with topographic habitat. The parameter estimates were therefore averaged over all species in each leaf habit category and over all quadrats and sites within habitats, enabling us to examine the overall differences between DBL and EBL species in factors determining their habitat-dependent regeneration dynamics.

Survival and growth models were fitted as GLMMs using Markov chain Monte Carlo (MCMC) simulation as implemented in the “MCMCglmm” package (Hadfield, 2010) and using a distance matrix (Hadfield & Nakagawa, 2010) constructed based on the phylogenetic relationships of species in the dataset (Liu et al., 2013; Appendix S2). In all models, a weakly informative Wishart prior was used for the residual structure (R-side effects for correlated residuals due to phylogenetic similarity), and a parameter-expanded prior was used for the random effect (G-side effects for correlations due to group membership) structure (Bolker, 2013; Hadfield, 2010; McCarthy, 2013). Weakly informative R-side and parameter-expanded G-side priors improve MCMC convergence and chain mixing, especially for parameter-rich models, while allowing the data to dominate inference (Bolker, 2013; Gelman, 2006; McCarthy, 2013). The number of MCMC iterations was set as 510,000, with a thinning

interval of 500 and a burn-in of 10,000 iterations. All continuous predictor variables were standardized by subtracting the mean and dividing by the standard deviation before analysis (Table 1).

We used backwards selection of fixed-effect terms based on the deviance information criterion (DIC; Gelman, Carlin, Stern, & Rubin, 2004), starting with the full model, to select the most supported survival and growth models. The fixed terms that produced the largest drop in the DIC value were sequentially deleted, starting from the highest level interaction terms, and the model with the lowest DIC was considered the most supported model (Tables S1–S4). In the most supported survival and growth GLMMs, inference was based on the mean and 95% credible intervals estimated from the posterior distribution for each parameter and *p*MCMC value, which represents a test of whether the posterior parameter estimate is different from zero. Specifically, *p*MCMC is two times the smaller of two MCMC probability estimates: that the parameter value is either less or greater than zero (Lajeunesse & Fox, 2013). For relative growth rate, diagnostic frequency histograms showed that the model residuals were approximately normally distributed.

3 | RESULTS

3.1 | Variation in seedling densities of DBL and EBL species among habitats

The relative density of seedlings of DBL species across sites within habitat types averaged <0.5, indicating that seedlings of EBL species generally achieved higher densities in all habitats (Figure 1 and Figure S3), as expected based on the greater basal area of species with an evergreen leaf habit in this forest. In both 2011 and 2014, the relative density of seedlings of DBL species was higher in gap

TABLE 1 Summary of the response and predictor variables in the fixed-effects portions of the linear mixed-effects models examining variation in regeneration dynamics of deciduous and evergreen broad-leaved (EBL) tree species in a Chinese subtropical EBL forest. The relative density of deciduous broad-leaved (DBL) seedlings was calculated as the number of DBL seedlings divided by the total number of seedlings in each 1-m² quadrat

| Predictor variables | | | |
|---|-------------------------|-------------------|-----------|
| Categorical | Levels | | |
| Topographic habitat | Valley, ridge | | |
| Canopy status | Canopy gap, understorey | | |
| Leaf habit | DBL, EBL | | |
| Continuous | Range | Mean (<i>M</i>) | <i>SD</i> |
| Seedling height in 2011 (cm) | 1–360 | 24.72 | 35.38 |
| Canopy gap size (m ²) | 28–282 | 143.00 | 77.29 |
| Response variables | | | |
| Categorical | Levels | | |
| Seedling survival probability (2011–2014) | Alive, dead | | |
| Continuous | Range | Mean (<i>M</i>) | <i>SD</i> |
| Relative density of DBL seedlings in 2011 (per m ²) | 0–1 | 0.21 | 0.24 |
| Relative density of DBL seedlings in 2014 (per m ²) | 0–1 | 0.14 | 0.23 |
| Relative density of DBL seedling recruits in 2014 (per m ²) | 0–1 | 0.13 | 0.26 |
| Seedling height relative growth rate in 2011–2014 | –1.00 to 4.77 | 0.37 | 0.49 |

habitats with greater light availability, as compared to the understorey (Table 2, Figure 1 and Figure S3). While the relative density tended to be higher in valleys compared to ridges, this difference was statistically significant not in 2011 nor in 2014 (Table 2, Figure 1 and Figure S3). In neither year was there a significant interaction between canopy status and topographic habitat (Table 2). The densities of all seedlings declined from 2011 ($M = 9.48$, $SD = 11.46$) to 2014 ($M = 4.44$, $SD = 5.18$). This decline was larger for DBL ($p < .001$, Student's t test) but not EBL ($p = .286$, Student's t test) seedlings in valleys, causing DBL relative density to become even more similar in 2014 across topographic habitats, whereas the relative density of DBL species remained higher in gaps than in understorey habitats. The relative density of DBL seedlings recruiting into the 2014 census was higher in canopy gaps compared to the understorey and in valleys compared to ridges, but the difference was only statistically significant between the gap vs. understorey habitat (Table S5, Figure 2). In gaps, the relative density of DBL species did not significantly increase with canopy gap size in 2011. However, in 2014, the increase in density of DBL species with gap size was statistically significant (Table 3, Figure S4), even though the relative density of DBL seedlings recruiting between 2011 and 2014 did not increase with canopy gap size (Table S6, Figure S5).

3.2 | Variation in survival and growth of DBL and EBL seedlings across habitats

The most supported seedling survival model included the three-way interaction between seedling height, leaf habit and topographic habitat, as well as the two-way interaction between canopy status and leaf

habit (Tables S1 and S7). The three-way interaction between height, leaf habit and topographic habitat indicated that the survival–height relationship of EBL seedlings was similar in valleys and on ridges and was usually higher than for DBL seedlings, except on ridges, where larger DBL seedlings achieved survival rates comparable to larger EBL seedlings (Figure 3). While there was no significant habitat-related variation in survival for EBL seedlings, for DBL seedlings, the survival–height relationship depended significantly on topographic habitat. Survival of the smallest DBL seedlings was similar in valleys and on ridges, but diverged so that larger seedlings survived better on ridges than in valleys (Figure 3). The interaction between leaf habit and canopy status arose due to slight differences in survival of DBL vs. EBL seedlings to gap vs. understorey habitats, but most survival variation was across topographic habitats (Table S7, Figure S6).

In gaps, the most supported seedling survival model included a three-way interaction between seedling height, leaf habit and canopy gap size (Tables S2 and S8). This interaction showed that in gaps, the smallest seedlings had the lowest survival, with survival of EBL seedlings exceeding that of DBL seedlings. However, for larger seedlings, DBL seedlings maintained higher survival across all gap sizes, although survival of DBL and EBL seedlings eventually converged as canopy gaps grew larger (Figure 4).

The most supported model for seedling height relative growth rate included two-way interactions between leaf habit and topographic habitat and between leaf habit and canopy status (Tables S3 and S9). Both DBL and EBL seedlings grew significantly faster in valleys than on ridges, but this difference was substantially larger for DBL than for EBL species, with DBL seedlings growing faster than EBL seedlings in

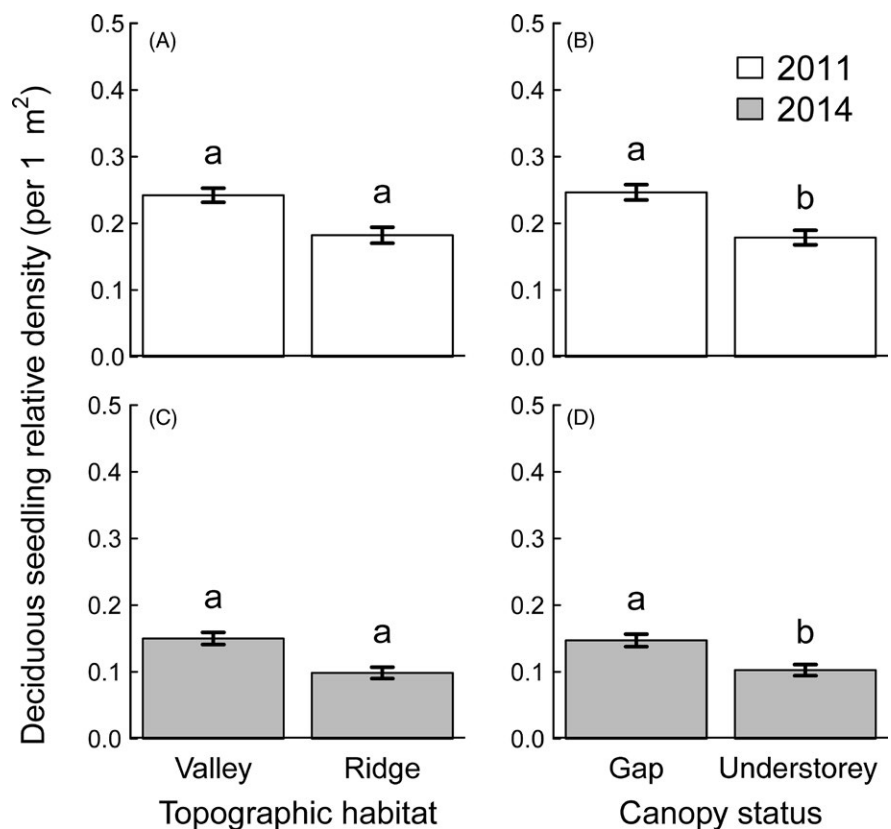


FIGURE 1 Variation in the relative density of seedlings of deciduous broad-leaved tree species among habitat types in 2011 (A and B) and 2014 (C and D) in a Chinese subtropical evergreen broad-leaved forest. Relative density was calculated as the number of deciduous broad-leaved seedlings divided by the total number of seedlings in each 1-m² quadrat. In each panel, bars with different letters are significantly different from each other based on generalized linear mixed-effects models (Table 2). Error bars indicate one standard error of the mean

TABLE 2 Analysis of deviance table for a generalized linear mixed-effects model examining variation in the relative density of deciduous broad-leaved tree species between habitats differing in topography and canopy closure in a Chinese subtropical evergreen broad-leaved forest in 2011 and 2014. Wald type III test statistics are shown

| | <i>df</i> | χ^2 | <i>p</i> |
|-------------------------------------|-----------|----------|----------|
| 2011 | | | |
| Topographic habitat | 1 | 2.57 | .109 |
| Canopy status | 1 | 14.38 | <.001 |
| Topographic habitat × Canopy status | 1 | 1.27 | .261 |
| 2014 | | | |
| Topographic habitat | 1 | 3.16 | .075 |
| Canopy status | 1 | 10.72 | .001 |
| Topographic habitat × Canopy status | 1 | 0.97 | .324 |

df, degree of freedom number; χ^2 , value of χ^2 statistic; *p*, probability.

valleys (Figure 5, Figure S7). The interaction involving leaf habit and canopy status showed that, comparing gap vs. understorey habitats, DBL seedlings grew slightly faster in gaps, but that EBL seedlings grew at similar rates in gaps and the understorey (Figure 5, Figure S8). In gaps, the most supported model for seedling height relative growth rate included a two-way interaction between leaf habit and canopy gap size (Tables S4 and S10). In the smallest gaps, the relative growth rate of DBL species exceeded that of EBL species, but growth declined for DBL species, whereas that of EBL species showed little variation, with canopy gap size (Figure 6).

4 | DISCUSSION

In many subtropical forests of eastern Asia, DBL and EBL tree species coexist in the same forest (Song, 1988), despite predictions from

TABLE 3 Analysis of deviance table for a generalized linear mixed-effects model examining variation in the relative density of deciduous broad-leaved tree species in canopy gaps with respect to topography and canopy gap size in a Chinese subtropical evergreen broad-leaved forest in 2011 and 2014. Wald type III test statistics are shown

| | <i>df</i> | χ^2 | <i>p</i> |
|---------------------------------------|-----------|----------|----------|
| 2011 | | | |
| Topographic habitat | 1 | 1.37 | .243 |
| Canopy gap size | 1 | 3.62 | .057 |
| Topographic habitat × Canopy gap size | 1 | 0.03 | .874 |
| 2014 | | | |
| Topographic habitat | 1 | 1.61 | .205 |
| Canopy gap size | 1 | 4.35 | .037 |
| Topographic habitat × Canopy gap size | 1 | 1.20 | .274 |

df, degree of freedom number; χ^2 , value of χ^2 statistic; *p*, probability.

models that species with contrasting leaf habits should dominate ecoregions with different growing season length and availability of soil resources (Givnish, 2002). To explain this paradox, previous studies have emphasized the contrasting topographic distributions of mature DBL and EBL trees as evidence of coexistence mediated by niche partitioning, but the joint effects of canopy disturbance and topography on seedling establishment patterns and dynamics have not been examined. As expected from their greater resource demand due to faster leaf turnover, the densities of DBL seedlings were higher in the more fertile valleys and in larger canopy gaps. However, in this EBL forest, canopy gaps preferentially facilitated the regeneration of DBL species more strongly, whereas the effect of topography on differential regeneration of DBL vs. EBL species was weaker. Thus, while DBL and EBL species in Gutianshan differed in their regeneration niches with respect to both canopy status and topography, the extent to which these differences facilitate

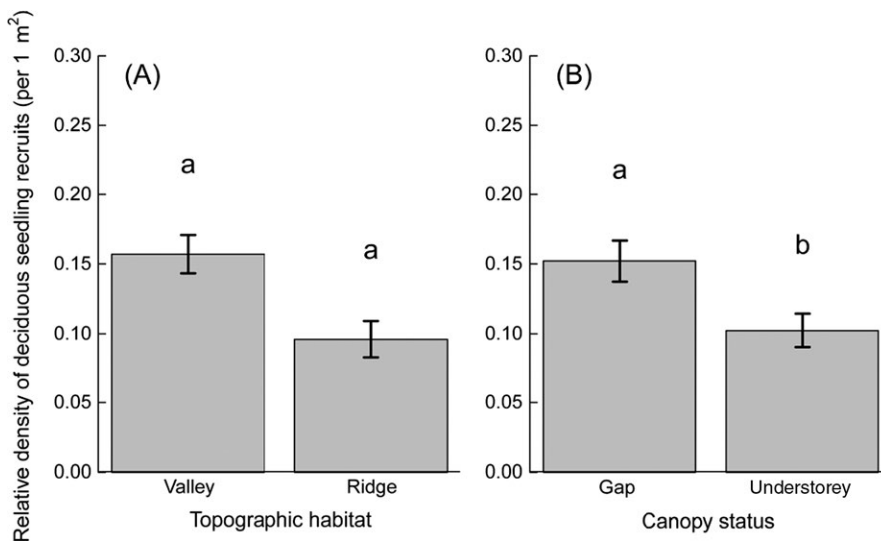


FIGURE 2 Variation in the relative density of seedlings of deciduous broad-leaved tree species recruiting between 2011 and 2014 among habitat types varying in topography (A) and canopy status (B) in a Chinese subtropical evergreen broad-leaved forest. Relative density of recruits was calculated as the number of deciduous broad-leaved seedlings divided by the total of recruited seedlings in each 1-m² quadrat for seedlings recruiting between the 2011 and 2014 censuses. In each panel, bars with different letters are significantly different from each other based on generalized linear mixed-effects model (Table S5). Error bars indicate one standard error of the mean

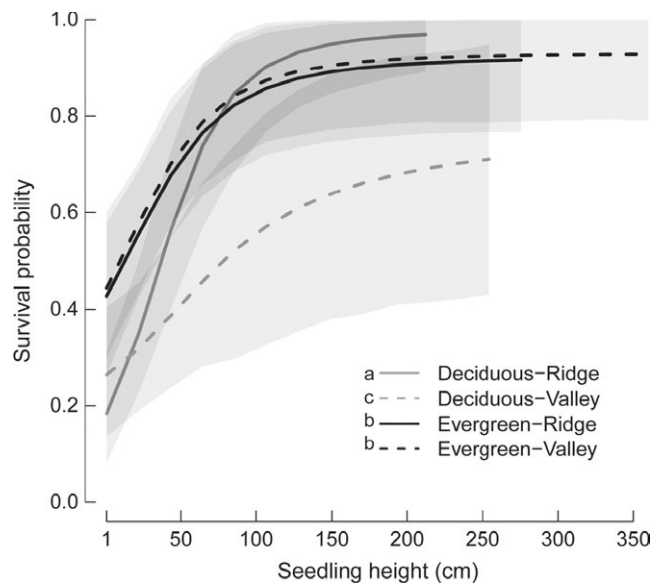


FIGURE 3 Variation in seedling survival probability of deciduous and evergreen broad-leaved tree species with respect to seedling height, tree species' leaf habit and topographic habitat from 2011 to 2014 in a Chinese subtropical evergreen broad-leaved forest as predicted by a generalized linear mixed-effects model. Different line types in the legend show survival for seedlings of deciduous (grey) or evergreen (black) broad-leaved species on ridges (solid) and in valleys (dashed). Letters on the left side of the legend indicate post hoc tests of the difference in slopes between each habitat combination, with different letters indicating significantly different slopes. Shaded regions show 95% confidence regions for the predicted relationship for each habitat combination

coexistence between these groups of species at the seedling stage may be stronger for gap vs. understorey, compared to topographic, habitats.

Although the relative density of DBL seedlings was consistent with our predictions that DBL species should prefer environments with greater resource supply during regeneration, habitat-related patterns of growth and survival did not always perfectly align with our expectations. The magnitude of variation in growth and survival across contrasting habitats was generally smaller for EBL, compared to DBL, seedlings, consistent with the more conservative resource-use strategy of evergreen species (Reich, 1998). Although DBL seedlings grew faster in gaps than in the understorey, their faster growth did not result in significantly higher survival in gaps. Likewise, significantly faster growth of DBL seedlings in the more fertile valleys did not translate into higher survival there, and instead, DBL seedlings survived better on the less fertile ridges. Survival of larger DBL seedlings in gaps was high across all gap sizes, but their fast growth rates in smaller gaps declined with increasing gap size. While faster individual growth generally is associated with higher individual survival probability, often driven by variation in insolation (Kobe et al., 1995), one explanation for the patterns we observed is that within-species survival-growth relationships may vary among habitats, as has been found for the between-species trade-off between growth and survival (Russo, Brown, Tan, & Davies, 2008).

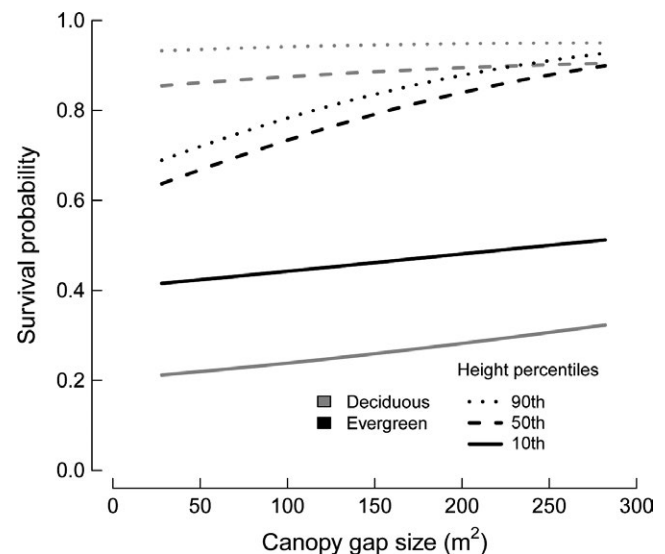


FIGURE 4 Variation in seedling survival probability of deciduous and evergreen broad-leaved tree species with respect to seedling height, tree species' leaf habit and canopy gap size from 2011 to 2014 in a Chinese subtropical evergreen broad-leaved forest as predicted by a generalized linear mixed-effects model. The different lines show survival for seedlings of the 10th (solid), 50th (dashed) and 90th (dotted) percentiles of seedling height, which represent 14, 107 and 212 cm, respectively. Black lines are for evergreen, and grey lines are for deciduous, broad-leaved species

Results from previous experimental studies are inconsistent with respect to the effect of insolation on growth of seedlings of DBL vs. EBL species. Both Cornelissen (1993) and Guo and Werger (1999) found that in high light, first-year DBL seedlings grew faster in height than EBL seedlings in subtropical forests in Southwest China. In contrast, Böhnke and Bruehlheide (2013) did not find a difference in height growth rate with respect to light for first-year DBL and EBL seedlings.

Given that adults surrounding a site contribute seeds to both gap and understorey habitats, we would expect approximately proportional seed arrival of DBL and EBL species to be similar for gap and understorey quadrats within a site. It is therefore likely that the observed variation in density between gaps and understorey may have been established very soon after the ice storm, as a result of light-related performance variation, and ensuing habitat filtering, operating during the early stages of post-disturbance seedling establishment. This interpretation is supported by the facts that although gaps always harboured greater relative density of DBL seedlings than the understorey, this difference was larger in 2011 than in 2014 and that the relative density of DBL seedlings increased with gap size. By 2014, 6 years after the ice storm, relative densities of seedlings of DBL species had declined everywhere. This might be due to the recovery of tree crown and lower-strata foliage at the whole-forest level, which would reduce light levels and be expected to limit seedling regeneration of DBL, more so than EBL, species (Kröber et al., 2012). However, DBL seedlings continued to be preferentially recruited in gaps even up to 2014. Thus, the observed seedling distribution patterns of DBL and EBL species in gaps and understorey were probably formed during

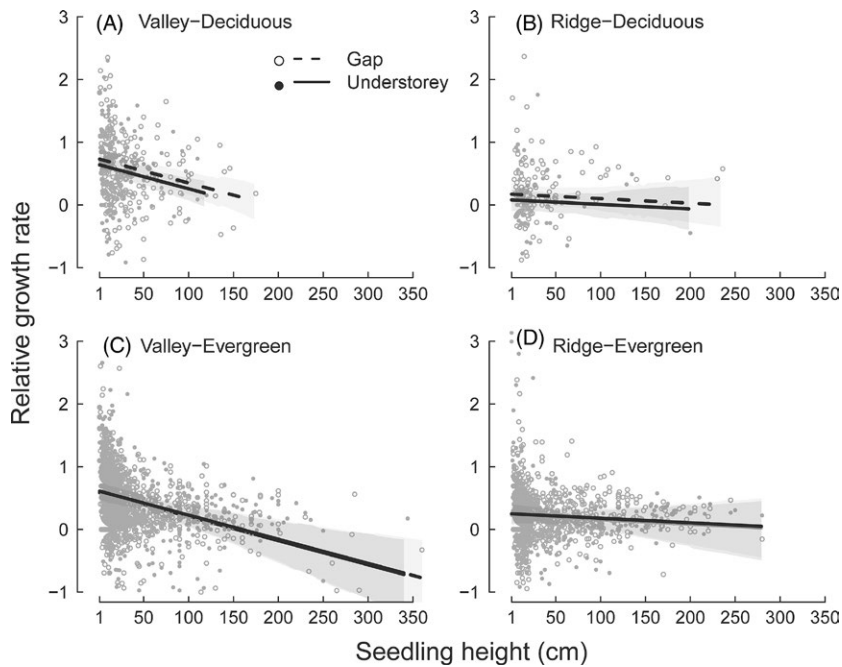


FIGURE 5 Variation in height relative growth rate of seedlings of deciduous (A) and (B) and evergreen (C) and (D) broad-leaved tree species as a function of initial height in four habitats varying in topography (valley vs. ridge) and canopy status (canopy gap vs. understorey) from 2011 to 2014 in a Chinese subtropical evergreen broad-leaved forest. Different line and symbol types in the legend show relative growth rate for seedlings of deciduous or evergreen broad-leaved species in gaps (dashed line, open circle) and understorey (solid line, solid circle). Shaded regions show 95% confidence regions for the predicted relationship for each habitat combination

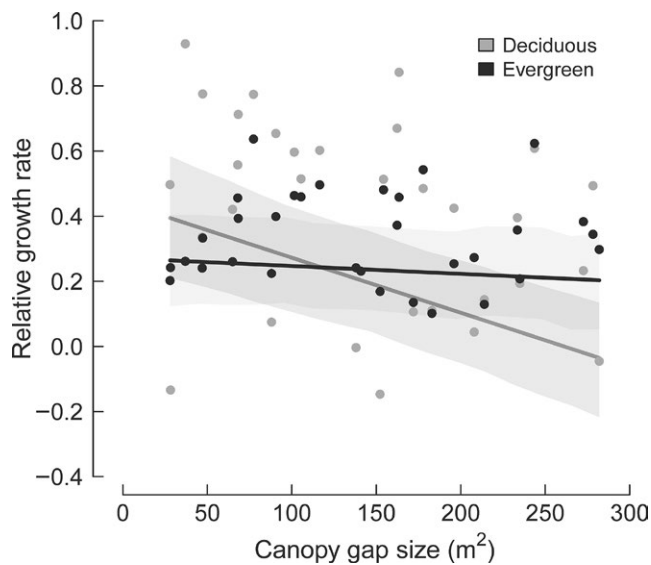


FIGURE 6 Variation in height relative growth rate of seedlings of deciduous and evergreen broad-leaved tree species in canopy gaps with respect to canopy gap size from 2011 to 2014 in a Chinese subtropical evergreen broad-leaved forest. Black and grey circles are the observed mean relative growth rates for evergreen and deciduous broad-leaved species, respectively. Black and grey lines show the predicted relationships for evergreen and deciduous broad-leaved species, respectively. Shaded area indicates 95% confidence interval of the mean.

the first few years after canopy gap formation, which is considered to be the most influential stage of the canopy gap disturbance cycle (Brokaw, 1985). Indeed, saplings of DBL, but not EBL, species were restricted to open canopy gaps in a Japanese EBL forest (Miura, Manabe, Nishimura, & Yamamoto, 2001). We argue that canopy gaps, and in particular episodic, severe canopy disturbances, appear to be critical

for the regeneration of DBL species (Nagamatsu et al., 2002) and, hence, their coexistence with EBL species, in mature forest consisting of a shifting mosaic of patches varying in time since disturbance (Clark, 1991; Coomes & Allen, 2007).

With respect to topographic habitats, we did not observe DBL species to achieve significantly higher relative densities in the more fertile valleys than on ridges. Topographic gradients encompass complex variation in the availability of many types of resources. Our finding does not agree with previous studies in other EBL forests in subtropical China that found DBL and EBL species distributions to be differentially associated with habitats varying in topography and soil fertility (Fang et al., 2016; Tang & Ohsawa, 2002). In addition, our prediction that the survival and growth of DBL species should be greater in valleys than on ridges was only partially supported. Growth in valleys was faster than on ridges for both DBL and EBL seedlings, but the difference was much greater for DBL seedlings, as predicted. This, combined with slightly faster height growth of DBL seedlings in gaps, might increase the chance of DBL seedlings reaching higher forest strata and becoming reproductive sooner than EBL seedlings in gaps located in valleys, thereby facilitating long-run recruitment of DBL species and their coexistence with EBL species. However, seedlings of DBL species almost always had lower survival in valleys than on ridges, which would presumably operate to reduce their relative densities in valleys over time. This filtering process appears to be already underway, since the average decline in the density of DBL species relative to the sum of DBL and EBL species from 2011 to 2014 tended to be greater in valleys than on ridges (mean decline of 0.06 in valleys vs. 0.03 on ridges, $p = .055$, Student's t test). While soils in valleys are more fertile for most nutrients and moister than soils on ridges, we did not find these two topographic habitats to differ in light availability, suggesting that the observed differences in performance were more related to below-, than above-ground, resource availability.

It may be that the more fertile and moist conditions in valleys facilitate seed germination and early seedling growth, but are also associated with greater pathogen hazards (Gao et al., 2016). Since DBL species are considered less well defended than EBL species (Coley & Barone, 1996; Schuldt et al., 2012), stronger effects of natural enemies could reduce the survival of DBL, more so than EBL, seedlings in valleys. Evergreen broad-leaved seedlings nearly always had higher survival than DBL seedlings, regardless of habitat. Given that the relative density of seedlings of DBL species was similar in valleys and on ridges throughout our study, any effect of topographic habitat on promoting coexistence of DBL and EBL species appeared to be weak. This finding is consistent with a study of the habitat preferences of the 59 most common broad-leaved tree species in Gutianshan. Lai et al. (2009) found that at neither juvenile nor adult stages did DBL species show any strong habitat preferences: at the adult stage, the distributions of only three of the 18 DBL species were aggregated in valleys, and none was aggregated on ridges. In contrast, adults of EBL species showed stronger habitat preferences, with 19 of 41 species aggregated in valleys and three aggregated on ridges. Thus, topographic niche partitioning alone might not be a strong determinant of coexistence between DBL and EBL species in Gutianshan.

5 | CONCLUSIONS

In this subtropical EBL forest, canopy gaps more strongly facilitated the regeneration of seedlings of DBL, compared to EBL, species, whereas niche partitioning across topographic habitats was weak. If differential performance of species with contrasting leaf habits initially establishes strong habitat distribution patterns during the first several years after a major disturbance, those patterns may persist to larger size classes, as appears to be the case for gap vs. understorey habitats in Gutianshan after the ice storm. While a common set of physiological processes regulates the carbon and nutrient economies of both DBL and EBL species, their differences in leaf life span create shifting competitive dynamics across resource gradients. Competition for light, rather than for below-ground resources, at least to the extent that the latter is correlated with topographic habitats, may more strongly influence coexistence of species with contrasting leaf habits in Gutianshan at the seedling stage. Thus, topographic habitat specialization may not be required for coexistence of DBL and EBL species in all EBL subtropical forests. We propose that their coexistence depends upon canopy disturbances to create a mosaic of habitat patches in which early regeneration of DBL species is favoured. The extent to which these patches persist through forest development, or are obscured by other habitat filtering processes, requires further investigation.

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AUTHORS' CONTRIBUTIONS

Y.J., M.Y. and S.E.R. conceived and designed the study; Y.J. and M.Y. performed the experiments and collected the data; Y.J. and S.E.R. analysed the data; Y.J., S.E.R. and M.Y. wrote the paper. All authors gave final approval for publication.

DATA ACCESSIBILITY

The study species descriptions are included in Appendix S1. Seedling density, survival and growth data are archived in Dryad Digital Repository: <https://doi.org/10.5061/dryad.67nd5> (Jin, Russo, & Yu, 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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