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Canopy openness and topographic habitat drive tree seedling recruitment after snow damage in an old-growth subtropical forest

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ABSTRACT

We investigated the relative and combined effect of topography and light environment on the recruitment of seedlings in a subtropical forest after snow damage to the canopy. The tree seedling community in an old-growth subtropical forest was monitored using 500 2 m × 2 m seedling plots at six-month intervals for 2 years. With a focus on recruitment following canopy damage, we related abiotic and biotic environmental variables to seedling dynamics, and we tested if significant topographic and light habitat associations were present for seedlings recruiting via a torus translation test. Then, we used variance partitioning to examine the relative effects of spatial, topographic and light variables on the temporal assemblages of seedlings. A total of 3047 seedlings from 58 species recruited in the first 2 years following snow damage. At the community level, increases in seedling abundance and richness were positively correlated with canopy openness and negatively correlated with elevation. At the species level, both pioneer and late-successional tree species had more recruits in high light environment than in low light environment. 84.3% of the recruiting seedlings were significantly associated to either light environment (35.7%), topography (26.5%) or both (22.1%). Despite this, at the plot level, spatial variables (PCNM) explained the majority of the variability in seedling composition over time. Our results suggest that snow damage to the canopy increases species richness and abundance via light-facilitated seedling recruitment, and that the composition of recruiting seedlings was largely spatially dependent. Topographic habitat filtering acts as a persistent force in determining the recruitment of seedlings and increases in strength with increased light-facilitated seedling recruitment. Our results highlight that, in this subtropical forest, both light requirement and topographic specialization interact over time to play a key role in promoting coexistence of tree species through selection of individuals at the seedling stage. We also suggest exploring the possibilities of management intervention to speed up the recovery of this forest.

1. Introduction

Species differ in their environmental requirements for survival and recruitment (Vandermeer, 1972; Grubb, 1977), which partly explains their coexistence in communities (Wright, 2002; HilleRisLambers et al., 2012). In the context of trees, ecologists have described this concept in relation to the partitioning of the abiotic requirements for germination and subsequently survival, to specific microhabitats (e.g. a set of light and topographic conditions) that are conducive to establishment and growth (Ricklefs, 1977; Harms et al., 2001; Ruger et al., 2009; Metz, 2012). It is understood that there is both a significant degree of variation and a large degree of overlap in microhabitat suitability among species in diverse tropical and subtropical forests (Harms et al., 2001; Kraft et al., 2008; Lai et al., 2009).

Large numbers of tree species have specific light requirements for regeneration (Brokaw, 1985; Laurans et al., 2012; Jin et al., 2018). A classic example is the heliophilic, fast growing pioneer species versus the shade-tolerant, slow growing late successional species (Whitmore, 1990). Tree species with different light requirements filter out in patterns of recruitment along gap-understory gradients based on the amount of light in the understory (Nunezfarfan and Dirzo, 1988; Zhu et al., 2014). However, there were also studies supporting the idea of incomplete filtering, showing that large numbers of tree species are not very sensitive to light conditions (Welden et al., 1991; Lieberman et al., 1995; Dechnik-Vazquez et al., 2016). There is lack of evidence for distinct light niche partitioning within species in forest gaps, and species with similar light requirements often spatially overlap with each other (Midgley et al., 1995; Thompson et al., 1998). Instead, research

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on gap-phase regeneration dynamics in tropical forests suggested that the recruiting species composition of a forest gap largely depends on the species assemblage that exists before gap formation (Brokaw and Scheiner, 1989; Hubbell et al., 1999).

In addition to specificity in light requirement, studies have shown convincing evidence that some tree species have clear topographic preferences (Harms et al., 2001; Kraft et al., 2008; Metz, 2012; Baldeck et al., 2013, Hogan et al., 2016). For instance, in a Neotropical forest in Ecuador, more than 80% of the recruited species demonstrated one or more topographic habitats associations (Metz, 2012). Topography habitat is the proxy for many soil characters that are important in partitioning spatial distributions of tree species (John et al., 2007; Comita and Engelbrecht, 2009; Xia et al., 2016). For example, topographic variation in soil moisture drives habitat associations of tree seedlings significantly (Comita and Engelbrecht, 2009). However, tree species with significant topographic habitat associations oftentimes show large distributional overlap with many other species (Lai et al., 2009). Furthermore, many tree species are reported as habitat generalists or show more-neutral associations with topographic habitats (Wright, 2002; Dechnik-Vazquez et al., 2016). Thus, local topographic specialization contributes only partially to the maintenance of species coexistence in hyper-diverse forests (Wright, 2002).

Although light availability and topographic habitat have been effective but limited in explaining the coexistence of tree species separately, few studies have explicitly focused on the relative and combined effect of light and topography in the regeneration and assemblage of forest (Jin et al., 2018), since gap formation mostly occurs in a stochastically fashion (Brokaw 1985; Brokaw and Scheiner, 1989; Hubbell et al., 1999; Blackburn et al., 2014). This question can be solved by studying forest regeneration after disturbance events that cause the damage of canopy at a large spatial scale. For instance, snow damage reduces tree branch length, canopy crown size and total tree stature, and leaves a matrix of forest gaps of assorted sizes, thus increasing light availability to the forest understory to a varying degree (Rhoads et al., 2002; Olthof et al., 2003; Wu et al., 2011). However, snow damage to the forest canopy is common at mid and high latitudes (Lemon, 1961), but this rarely happens at lower latitudes, especially in subtropical forests (Wu et al., 2011). Such disturbance in subtropical forest can provide an ideal opportunity to study how light availability and topographic habitat interact among species to shape seedling recruitment pattern.

The species composition of a local forest community is assumed to reflect the cumulative effects of both abiotic and biotic filters of the regional species pool (HilleRisLambers et al., 2012). Thus, besides the abiotic factors, such as light and topography, the biotic mechanisms, such as conspecific negative density dependence (CNDD) (Janzen, 1970; Connell, 1978; Comita et al., 2014), interspecific competition (Nasto et al., 2017), and seed dispersal ability (Wright, 2002) of tree species, can also affect the assemblage of forest community.

Therefore, environmental relationships in tree seedling regeneration play a key role in forest dynamics (Bace et al., 2012; Ashton et al., 2018). We examined seedling dynamics for 2 years after snow damage to the canopy of a subtropical forest in southwestern China to study the relative contributions of topography and light in structuring seedling recruitment. We asked: (1) How does seedling recruitment respond to increases in light in canopy gaps created by snow damage? (2) How does recruitment of species vary based on their light and topographic requirements? (3) How does the effect of light, topographic and spatial variables on seedling composition vary over time after the snow damage? We expected that gap formation from snow damage would increase species richness and abundance via seedling recruitment at the community level. At the species level, we expected recruitment dynamics to be dominated by a high frequency of light demanding species. We also expected light and topographic habitat filtering to immediately affect the composition of seedlings after snow damage and then weaken over time.

2. Material and methods

2.1. Study area

The Ailaoshan 20 ha forest dynamics plot (500 m × 400 m) was established in 2014 in the Ailaoshan National Nature Reserve (Fig. A.1). Tree measurement follows the measurement protocols of the Center for Tropical Forest Science (Condit, 1998), where all free standing plant stems ≥ 1 cm diameter at breast height (dbh) are tagged, identified to species and mapped. The elevation of the plot ranges from 2472 m to 2628 m above sea level, and the highest elevation occurs in the eastern part of the plot (see detail environmental variation in Table A.1). The vegetation is characterized as a subtropical evergreen broadleaved forest and it is dominated by three subtropical oak species, *Lithocarpus hancei* (Fagaceae), *Lithocarpus xylocarpus* (Fagaceae) and *Castanopsis wattii* (Fagaceae) (Wen et al., 2018). The forest age is more than 300 years (Song et al., 2015). The annual mean precipitation is 1931 mm with 85% of the annual precipitation falling between May and October (Gong et al., 2011). Snow damage to the canopy occurred between January 9th and 11th 2015, during a rare three-day freeze with a minimum temperature of −2 °C. During this time, roughly 40 cm of snow fell on the plot, damaging the crowns on many canopy trees (Song et al., 2017).

2.2. Data collection

2.2.1. Seedlings census

In February 2015, a total of 500 2 m × 2 m seedling plots was established in the center of each of the 500 20 m × 20 m quadrats in the plot. In each 2 m × 2 m seedling plot, all free-standing woody plants < 1 cm in stem diameter (hereafter referred to as seedlings) were tagged, identified to species, measured for stem height, and number of leaves counted. Species were identified by local botanists, with nomenclature consistent with the Flora of China website (http://foc.eflora.cn/). A total of 4019 individuals of 55 woody plant species was recorded in the first census. Seedling censuses took place in March and November of 2015, and May and November of 2016. During the censuses, new seedlings (defined as recruited seedlings) were tagged, identified to species, measured for leaf numbers and height.

2.2.2. Measuring canopy openness

Using a digital camera (Nikon Coolpix 4500, Nikon Corporation, Japan) with a fisheye lens (Nikon FC-E8 Fisheye Converter, Nikon Corporation, Japan), hemispherical photographs were taken in the center of each seedling plot at 1.3 m height at low light conditions (i.e., during moderate cloud cover or dusk) in November 2015. We used the Gap Light Analyzer software (Version 2.0) (Frazer et al., 1999) to analyze the photographs and calculated the canopy gap fraction for photograph. Canopy openness was then quantified as the fraction of the image not occupied by vegetation cover (Song et al., 2017).

Before snow damage, canopy openness of closed forest at Ailaoshan was 5–11% (Song et al., 2015). Thus, we chose the larger threshold of 11% canopy openness as the low light level and 16% canopy openness as the limit between middle and high light levels, based on the range of light conditions we observed in the field. Therefore, the 500 quadrats were classified in three light levels as follows: low light (135 quadrats, canopy openness < 11%); mid light (220 quadrats, canopy openness ≥ 11% and < 16%); high light (145 quadrats, canopy openness ≥ 16%) (Fig. A.2).

2.2.3. Topography data

For each 20 m × 20 m quadrat, elevation was calculated as the mean of the elevation at its four corners. Slope was the mean angular deviation from horizontal for each of the four triangular planes formed by connecting three corners at a time. Convexity was calculated as the difference between the mean elevation of the focal quadrat and the mean elevation of the eight surrounding quadrats. For edge quadrats, convexity was calculated as the difference between the elevation of the focal quadrat center and the mean elevation of the four corners. Aspect was calculated as: $\left(180-\tan^{-1}\left(\frac{fy}{fx}\right)\right)*\left(\frac{180}{\pi}+90\frac{fy}{fx}\right)$, where *fx* is the elevation difference from east to west in the $20\,m \times 20\,m$ quadrat, is *fy* is that from north to south. All the topographic variables were calculated using the CTFS R package (Condit, 2013). Each $20\,m \times 20\,m$ quadrat was assigned to a habitat category based on its topographic attributes, elevation, slope and convexity, using the methods described in Harms et al., (2001). Therefore, the 500 quadrats were classified in three topographic habitats as follows: flat (140 quadrats, mean elevation < 2500 m and slope $< 15°$); valley (172 quadrats, slope $\geq 15°$ and convexity < 0); ridge (the rest 188 quadrats, slope $\geq 15°$ and convexity ≥ 0 or slope $< 15°$ and elevation ≥ 2500 m) (Fig. A.3).

2.3. Data analysis

2.3.1. Species richness and abundance of recruited seedlings

We first calculated the species richness and abundance of total seedlings and recruited seedlings (the new seedlings that appeared in the seedling plots after snow damage) in each census. We wanted to compare seedling species richness and abundance over time, and the data were not normally distributed. Therefore, we used Friedman's Test, which tests for statistical difference in groups of non-normal data. Then, we used post-hoc pairwise comparisons to detect whether the total and recruiting seedling species richness and abundance changed significantly over time at 6-month intervals. Friedman's Test (Friedman, 1937) is a non-parametric version of a one way ANOVA with repeated measures. Seedling plot was used as the repeated measures factor to account for temporal autocorrelation among seedling plots of each census.

2.3.2. Community wide abundance and richness models of recruited seedlings

To evaluate how seedling recruitment related to abiotic and biotic factors, we explicitly modeled seedling recruitment using two generalized linear mixed models (GLMMs; Bolker et al., 2009), one modeling the species richness of recruits and one modeling the total abundance of recruiting seedlings.

In the first GLMM, the species richness of recruits in each seedling plot during the 2-year monitoring period was modeled as a function of biotic and abiotic variables using a GLMM with a Poisson error structure and log link function. The biotic explanatory variables included species richness of stems ≥ 1 cm diameter in each $20\,m \times 20\,m$ quadrat (SR), and herb coverage in each $2\,m \times 2\,m$ seedling plot (HC, quantified as the fraction of the seedling plot occupied by herb cover); and the abiotic explanatory variables were elevation (EL), slope (SL), convexity (CX), canopy openness (CO) and sin-transformed aspect (AP). A random intercept factor for plot was added to this model as a random effect. To avoid the sample size effect of species richness, we conducted the same analysis using rarefied species richness as the response variable, using six individuals, the average number of recruits per seedling plot, as the rarefied sample size.

For the second model, seedling recruitment for each species was similarly modeled according to abiotic and biotic variables using an identical GLMM framework (Poisson error with log link). The response variable was the abundance of recruits for each species in each seedling plot during the 2 year period. The explanatory variables included biotic variables: total basal area of conspecific stems ≥ 1 cm diameter within a 10 m radius from the center of each seedling plot (BA_{con}), HC, and abiotic variables: EL, SL, CX, CO and AP. Species identity was added to the model as a random factor to account for the different recruitment strategies across species, and plot was added to the model as a cross effect random factor accounting for the potential spatial autocorrelation. In both models, all explanatory variables were standardized by subtracting the mean and dividing by standard deviation prior to modeling. The analysis was performed by R package "lme4" (Bates et al., 2015).

2.3.3. Light and topographic associations test of recruited species

A torus translation test was used to test for associations between seedling recruitment and topographic habitats or light environment (Harms et al., 2001). The torus translation test incorporates the spatial structure of the species abundance distributions across plots and the spatial autocorrelation of the topographic habitats and canopy openness light data. In each test, the topographic habitat map (Fig. A.2) or light map (Fig. A.3) is repeatedly translated in one of four cardinal directions (one at a time), moving the entire topographic habitat map or light map by one quadrat column or row at a time. A further three maps can be generated from each translation: 180° rotation, mirror image and 180° rotation of the mirror image, and the translation procedure is replicated. We translated each of the light and topographic maps 1999 times, simulating 1999 unique light and topographic maps, each differing from the observed, untranslated light and topographic map. The seedling community of each quadrat was not altered as the environmental variables (i.e., topographic habitats or light levels) were shifted (Harms et al., 2001). Of the species that recruited, we defined rare species as those that occurred in less than five quadrats, and they were excluded from this analysis. The number of recruits of each species was counted in each quadrat for each translation, effectively providing an estimate of the expected abundance of each species for each topographic habitat or light level, which were combined to collectively form the null expectation of seedling abundances distributions, given no topographic or light environment association by species. The observed association of a species with a given topographic habitat, on the observed, untranslated topographic habitat or light map, was compared to the frequency distribution of the null expectation (Metz, 2012), using a level of statistical significance (α) of 0.1. Statistically significant associations are those in which the observed level of association (measured by abundance) are less than 0.05 (positive correlated) or greater than 0.95 (negative correlated) of the expected values. A significant positive or negative light or topography association indicated that a species was significantly more or less abundant in a light or topographic habitat than expected by chance. We also calculated Importance Values (IV), which additively summarize the relative abundance and the relative frequency (Curtis and McIntosh, 1951), for each recruited species.

2.3.4. Partitioning the relative contribution of light, topographic and spatial factors on seedling community dynamics

To assess the relative contribution of light and topography variables to the community dynamics of seedlings after snow damage we used canonical distance-based Redundancy Analysis (db-RDA) (Legendre and Anderson, 1999; McArdle and Anderson, 2001). Spatial eigenvectors were constructed using principal coordinate neighbor matrices (PCNMs). We selected only eigenvectors representing significant positive spatial correlation based on Moran's *I* (Dray et al., 2006; Legendre and Legendre, 2012). Forward selection of variables was done for each group (light, topography and PCNM) separately by R package "packfor" (Dray et al., 2013), and the total variation in Hellinger-transformed seedling abundances over time (i.e., in each 6-month census interval) was partitioned with respect to topographic variables (elevation, slope, aspect and convex), canopy openness and PCMM eigenvectors (Legendre and Legendre, 2012). The analysis was performed by R package "vegan" (Oksanen et al., 2018). All analysis was conducted in R 3.3.3 (R Development Core Team, 2015).

3. Results

Extensive damage to the canopy structure by the snow storm increased light availability to the understory (canopy openness: 13.65% ± 0.19%, Table A.1). The canopy openness was greater than 16% in certain areas with more severe damage; less damaged canopies measured around 11% (Fig. A1).

Table 1
Species richness and abundance of total tree seedlings and recruited seedlings following snow damage to canopy (mean ± SE, capital letters indicate significant differences from post-hoc pairwise comparisons following Friedman's Test).

Census	Total species richness	Species richness of recruitment	Total abundance	Abundance of recruitment
2015 March	3.594 ± 0.116 D		8.038 ± 0.458 D	
2015 November	4.030 ± 0.117 C	0.870 ± 0.047 B	8.582 ± 0.417 C	1.480 ± 0.109 B
2016 May	4.598 ± 0.124 B	1.006 ± 0.057 B	9.728 ± 0.438 B	1.794 ± 0.140 B
2016 November	5.326 ± 0.134 A	1.484 ± 0.075 A	11.848 ± 0.540 A	2.820 ± 0.248 A

3.1. Species richness and abundance of recruited seedlings

In the first census in March 2015, the average richness and total abundance of woody seedlings per plot was 3.59 ± 2.60 species and 8.03 ± 10.23 individuals, respectively. From November 2015 to November 2016, we recorded a total of 3047 recruited seedlings from 58 species (including 11 new seedling species not recorded at the first census). Most seedling plots (420 of 500) had recruited seedlings. Friedman's Test found significant difference over time (Table A.2). The average richness and abundance of each seedling plot increased significantly after snow damage (see letters in Table 1). The average species richness and abundance of total recruits in each seedling plot was 2.80 ± 2.21 and 6.09 ± 7.70, respectively.

3.2. Relative importance of factors determining seedling recruitment

Species richness of recruits increased significantly related to more convex topography (coefficient = 0.1792, $P < 0.001$) and increased canopy openness (coefficient = 0.2008, $P < 0.001$) and was significantly reduced by surrounding tree community richness (coefficients = −0.0674, $P = 0.015$) and elevation (coefficients = −0.2856, $P < 0.001$) (Fig. 1). Using rarefied species richness as the response variable, the same pattern was shown (Fig. A.4). The abundance of recruits increased significantly in areas with greater basal area of conspecific adult trees (coefficient = 0.0906, $P < 0.001$), herb coverage (coefficient = 0.0446, $P = 0.023$) and canopy openness (coefficient = 0.1313, $P < 0.001$), but it decreased significantly with elevation (coefficient = −0.1211, $P < 0.001$) (Fig. 2).

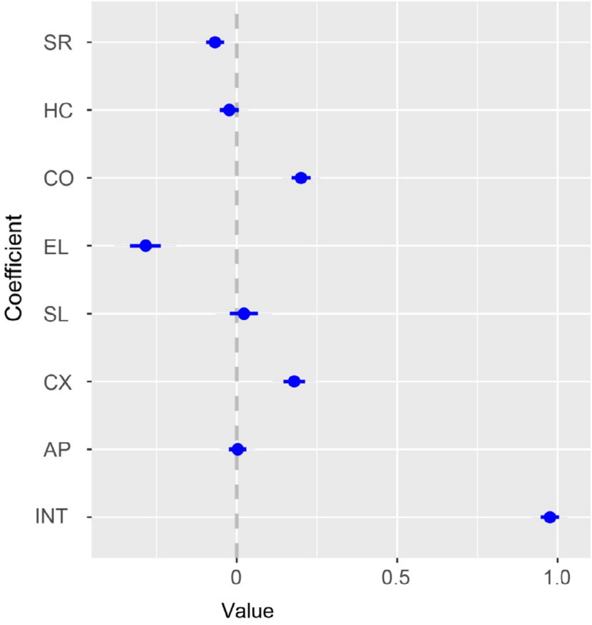

Fig. 1. Coefficient estimates (with 95% confidence intervals) for all explanatory variables (SR: Quadrat Species Richness, HC: Herb Cover, EL: Elevation, SL: Slope, CX: Convexity, CO: Canopy Openness, AP: Sin-translated Aspect, and INT: Intercept) in relation to the species richness of recruited seedlings following snow damage to the canopy.

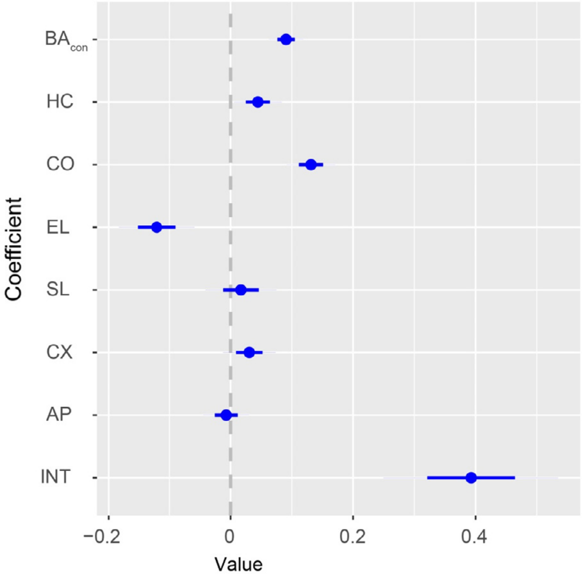

Fig. 2. Coefficient estimates (with 95% confidence intervals) for all explanatory variables (parameter abbreviations on the y-axis are the same as Fig. 1; BA_{con}, Basal Area of Conspecific Trees) in relation to the abundance of recruited seedlings following snow damage to the canopy.

3.3. Variation among species in response to light and topography

Over half of the species (32/58) recruited in 5 or more seedling plots (Fig. 3). Of those species, nine representing 16.5% of all seedlings were significantly associated with one or more topographic habitats. Nine species accounting for 35.7% of all seedlings were significantly associated with high-light environments (i.e. gaps). Five species comprising 22.1% of all seedlings were significantly associated with both topographic habitats and high-light environments. Among the 10 species with highest important values, seven were gap associated (i.e., had

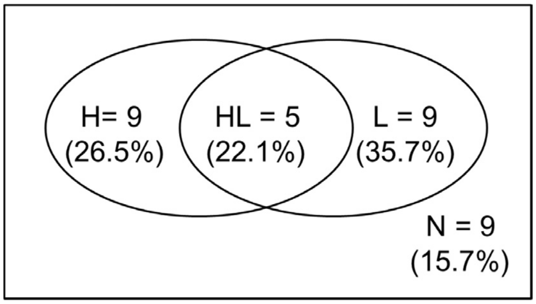

Fig. 3. Results from the Torus translation test: the number of species with significant topographic habitat (H), light environment (L) or topographic habitat and light environment (HL) associations among 32 commonly recruited tree species following snow damage to the canopy. The percentage of total seedling abundance for each group of species is displayed in parentheses.

Table 2

Topographic habitat specialization and light association of 10 species with widespread recruitment following snow damage to the canopy (IV, importance value; +, positive association; −, negative association; blank, no significant association).

Species	Family	Ecological group	IV	Light preference			Topographic preference		
				Low	Mid	High	Valley	Ridge	Flat
Manglietia insignis	Magnoliaceae	Late-successional	0.276	−		+			
Styrax perkinsiae	Styracaceae	Late-successional	0.231						
Viburnum cylindricum	Caprifoliaceae	Pioneer	0.192	−		+	−		
Symplocos ramosissima	Symplocaceae	Late-successional	0.158			+	−		+
Litsea cubeba	Lauraceae	Pioneer	0.138	−		+			
Eriobotrya bengalensis	Rosaceae	Late-successional	0.137					+	−
Machilus gamblei	Lauraceae	Late-successional	0.130						+
Meliosma kirkii	Sabiaceae	Late-successional	0.109			+			
Vaccinium duclouxii	Ericaceae	Late-successional	0.075			+			
Stewartia pteropetiolata	Theaceae	Late-successional	0.062			+	−		+

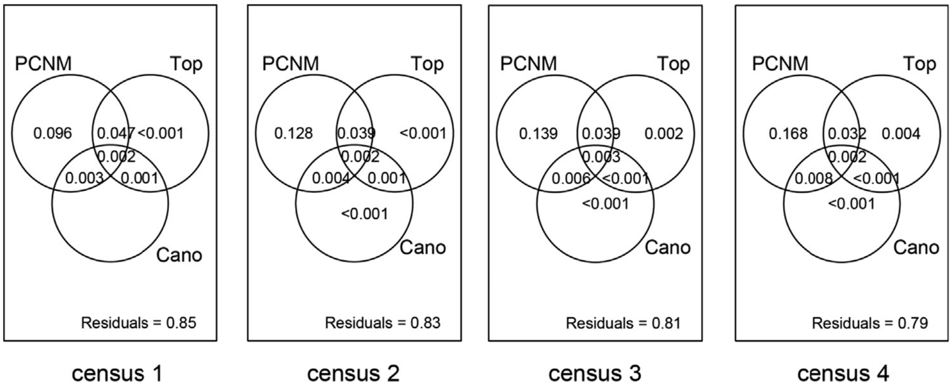

Fig. 4. Individual and interaction effects of spatial (PCNM), topographic (Top), and Canopy openness (Cano) variables explaining the abundance weighted seedling community composition among 500 seedling plots over 4 seedling censuses at 6-month intervals from the db-RDA analysis. Values are adjusted R^2, and values < 0 are not shown.

significant habitat association with high-light environments), and four exhibited significant topographic associations, with three species associated with flat habitats and only one species having significant positive affinity for the ridge areas of the plot (Table 2). We found two pioneer species, *Viburnum cylindricum* (Caprifoliaceae) and *Litsea cubeba* (Lauraceae), which showed statistically-significant associations with light environments. *V. cylindricum* showed significant negative habitat association to valley, but *L. cubeba* showed non-topographic habitat association. *Styrax perkinsiae* (Styracaceae) was the only species that showed no association with either topographic habitat or light.

3.4. *Effects of light, topographic and spatial factors on the composition of recruited seedlings*

Spatial variables (PCNM eigenvectors) explained most of the variation of seedling community composition, which was a trend that strengthened over time (Fig. 4). Light and topographic variables explained very little of the variation in seedling community dynamics, each accounting for < 1% of the variance. The total variability in seedling composition explained by topography increased over time, as did the interaction of spatial variables and the variable characterizing canopy openness (i.e. light condition).

4. Discussion

Using 2 years of seedling monitoring data after a snow damage event in an old-growth subtropical forest, we assessed the relative importance of light and topography in driving the tree seedling recruitment. The species richness and abundance of tree seedlings in the understory increased significantly after snow damage to the canopy. We found strong evidence that both light and topography factors showed significant influence on the species richness and abundance of recruited seedlings. Recruiting tree species varied significantly in light and topographic requirements, which interact over time (Jin et al., 2018) as the seedling community responses to snow damage.

However, there are also other ecological forces that determine the structure and composition of the seedling community. Firstly, dispersal limitation limits the pool of species that regenerate from seed to seedling (Wright, 2002; HilleRisLambers et al., 2012). Secondly, conspecific negative density dependence (CNDD) thins seedlings that recruit in high abundances in either well-suited habitats or near parent trees (Janzen 1970; Connell 1978; Comita et al., 2014; Song et al., 2018). These forces happen at large spatial, in the case of dispersal limitation, or longe temporal, in the case of negative density dependence, scales than we can experimentally test with our data currently.

4.1. *Canopy openness and seedling recruitment*

Gaps are important in maintaining the diversity and regeneration of species within old-growth subtropical forests (Brokaw, 1985; Brokaw and Scheiner, 1989; Hubbell et al., 1999; Barik et al., 1992; Sapkota et al., 2009). In our research, at the community level, canopy openness had a strong positive influence on both species richness and abundance of recruited seedlings (Figs. 1 and 2). This result is congruent with results from previous studies that an increase in light due to canopy damage stimulates the germination of tree seedlings both from the soil seed bank and those dispersing into created gaps (Vazquez-Yanes and Orozco-Segovia, 1990; VazquezYanes et al., 1996; Chen et al., 2013). Comparable results have been found in other tropical and subtropical forests, confirming our understanding that high light conditions in gaps maintain high stem densities and species diversity of seedlings and later saplings (Schnitzer and Carson, 2001; Sharma et al., 2016; Suarez-Esteban et al., 2016).

At the species level, disturbance of the canopy promotes the recruitment of light-demanding pioneer species, which usually do not geminate under a closed canopy with low light condition (Chen et al., 2013). For example, we recorded a large number of recruits of the pioneer species *L. cubeba* and *V. cylindricum* after snow damage that could not regenerate in the primary forest. The large recruitment of pioneer tree species in the understory could possibly speed up the recovery of damaged forests. However, they might also change the future species composition of the forest if the disturbances happen severely and frequently (Vargas et al., 2013). Moreover, our results suggest that increases in light to the understory not only promote the recruitment of pioneer tree species, but they can also facilitate the regeneration of late-succession tree species (Table 2). Thereby, snow damage is an important disturbance that can drive the understory seedling recruitment dynamics of forests, by significantly changing the light environment through the creation of forest gaps (Lafon, 2004; Man et al., 2011).

4.2. Topographic habitat association and seedling recruitment

Topographic habitat filtering among species is one important mechanism in maintaining species coexistence in forest communities (Harms et al., 2001; Kraft et al., 2008; Brown et al., 2013). At the seedling and sapling stages, the topographic habitat associations of tree species are especially variable, for example, 19 of 80 species at Barro Colorado Island (BCI), Panama (Comita et al., 2007), 41 of 60 species at Gutianshan, East China (Lai et al., 2009) and 110 out of 136 of species at Yasuní, Equador (Metz, 2012) had significant species-topographic habitat associations. Likely, there exists a relationship between the degree of topographic habitat heterogeneity and the strength of topographic filtering of species, which may explain less species-topographic habitat association in level forests such as BCI. In our research, of the 32 species we examined, we found half of them to be significantly associated with a topographic habitat (Fig. 3), and more than a quarter of the species showed a positive association to either a ridge or valley habitat (Table A.3). One explanation for this result is that topography is inversely correlated with many soil nutrients, soil oxygen content and soil bulk density, which can allow it to serve as a proxy for many soil characteristics that are important in shaping seedling distributions in space (John et al., 2007; Comita and Engelbrecht, 2009; Baldeck et al., 2013; Xia et al., 2016). Thus, the topographic specialist could be responding to belowground resource partitioning. For instance, the more fertile and moist conditions in low elevation and concave habitats could facilitate seed germination and maintain high species richness (You et al., 2013). So that the species richness and abundance of recruited seedlings were higher in low elevation or valley areas than in high elevation or in ridge areas (Figs. 1 and 2).

4.3. Light specialists vs. topography specialists –above- and below- ground environmental control on seedling recruitment dynamics

We classified the recruitment of species into four categories: mostly light specialists, mostly topographic specialists, have both light and topographic specialization and those that have no specialization to either light or topography environment (Fig. 3). The variation in light and topographic specialization of seedlings illustrates how tree species utilize and partition belowground and aboveground resources differently, and in ways that may promote species coexistence by regulating their recruitment patterns. Therefore, in Ailaoshan, seedling recruitment at the community level is limited by both light and topographic habitat, or by both aboveground and belowground resources (Fig. 3).

The creation of forest gaps resulting from snow damage increased species richness and abundance of the seedling community through facilitating seedling recruitment (Figs. 1 and 2). However, gaps have little effect on composition of seedling community, although the relationship between seedling community composition and light conditions was strengthened. In contrast, spatial variables (PCNM eigenvectors) explained more variation in seedling composition than canopy openness and topography variables, separately or together (Fig. 4). Given that the seeds of most subtropical tree species can only disperse limited distances (Nathan and Muller-Landau, 2000), the seeds of most species are unable to reach all suitable topographic and light habitats within a forest, so dispersal limitation is likely important in determining the spatial distribution of tree species. For example, in our study area, the mean dispersal distance of dominate tree species is less than 15 m (Xiao and Zhang 2012). In relation to seed dispersal and germination, the density of parent trees tends to have a positive effect on the nearby density of conspecific seedlings (Cousens et al., 2008; Lowe and McPeek, 2014). Thus, the abundance of recruited seedlings was positively correlated to the basal area of conspecific trees (Fig. 1) and the composition of recruited seedlings was highly contingent upon the species composition of surrounding adult trees. However, the CNDD mortality may reduce the density of conspecific seedlings near the adult trees, after their germination and establishment (Janzen, 1970; Connell, 1978; Comita et al. 2014). Other biotic factors like the species richness of adult trees and the herb coverage also showed significant influence on the recruitment pattern of tree seedlings (Figs. 1 and 2). These results indicate that biotic mechanisms are also important in driving the recruitment of tree seedlings. The tree seedlings may be filtered by light and topography (biotic factors) at large spatial scale, and then conspecific negative density dependence (abiotic factors) may drive the coexistence of tree seedlings at relatively fine spatial scale (HilleRisLambers et al., 2012). We found that seedling recruitment peaked a year and a half after snow damage. CNDD mortality takes several more years, probably being strongest five to ten years after disturbance (Comita et al., 2009).

4.4. Forest regeneration and canopy damage

With the frequency of extreme climate events increasing (Easterling et al., 2000; Orlowsky and Seneviratne, 2012), forest ecosystems are at increased risk for irreversible changes in community structure and ecosystem function (Gitlin et al., 2006; Elsner et al., 2008; Misson et al., 2011; Lloret et al., 2012). Composition shifts of tree seedlings species in the understory will forecast changes in forest structure (Perez-Ramos and Maranon, 2012) and canopy damage due to increased disturbance frequency or severity under climate change (e.g. ice storms, hurricanes etc.) could accelerate this process in tropical and subtropical forests like Ailaoshan. We show that after the snow damage to the canopy, species that adapted most rapidly to shifts in light environment had increased opportunity to establish. These effects were confounded by topographic habitat filtering, illustrating that multiple processes resulting from temporal and spatial environmental heterogeneity will interact to shape the forest in the future (Buckley and Bridle, 2014).

5. Conclusions

Changes in canopy structure due to snow damage increased the species richness and abundance of tree seedlings in the understory. The majority of the species of recruiting seedling showed higher recruitment in high than in low light environments under canopy gaps and the ability to initially partition habitats across topographies. Over time, topography played an increasing role in filtering recruits, suggesting that in this subtropical forest light requirements and topographic habitat specialization interact to play an important role in regeneration dynamics and the maintenance of species diversity. We suggest that long-term monitoring should be continued to better understand the sustained effects of snow damage on the regeneration of forest community and the community composition alteration following disturbance events. Since the snow damage rarely happens in this subtropical forest, to accelerate the recovery of this forest, management intervention (manual removal of pioneer species seedlings, removal of snags and artificial tending on seedlings based on their light and topographic demanding) may be necessary. However, such efforts should be delayed until strong evidence is obtained that standing dead trees and increasing populations of pioneer species have potentially shifted regeneration dynamics of saplings and adult trees in this forest.

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Appendix

See Tables A1–A3.

Table A1
Environmental variations of topographic and light factor in the 20 ha plot.

Parameter		Mean (± SE)	Range
Topographic factor	Elevation	2521 ± 1.703	2472 to 2628
	Slope	22.75 ± 0.50	3.31 to 49.52
	Convexity	0.087 ± 0.127	−8.48 to 15.11
Light factor	Canopy openness	13.65 ± 0.19	1.53 to 28.58

Table A2
Friedman' Test of species richness and abundance of total and recruited seedlings variation over time.

		F-value	P-vale
Total seedlings	Species richness	239.49	< 0.01
	Abundance	111.93	< 0.01
Recruited seedlings	Species richness	16.60	< 0.01
	Abundance	13.78	< 0.01

Table A3
Torus-translation tests for light and topographic habitat associations of recruited tree species (each species had new records in at least 5 different seedling plots after snow damage; +, positive association; −, negative association).

Habitat type	$P(< 0.05)$	Light type	$P(< 0.05)$
Ridge +	4	High +	9
Valley +	0	Middle +	4
Flat +	9	Low +	0
Ridge −	2	High −	0
Valley −	5	Middle −	0
Flat −	2	Low −	5

See Figs. A1–A4.

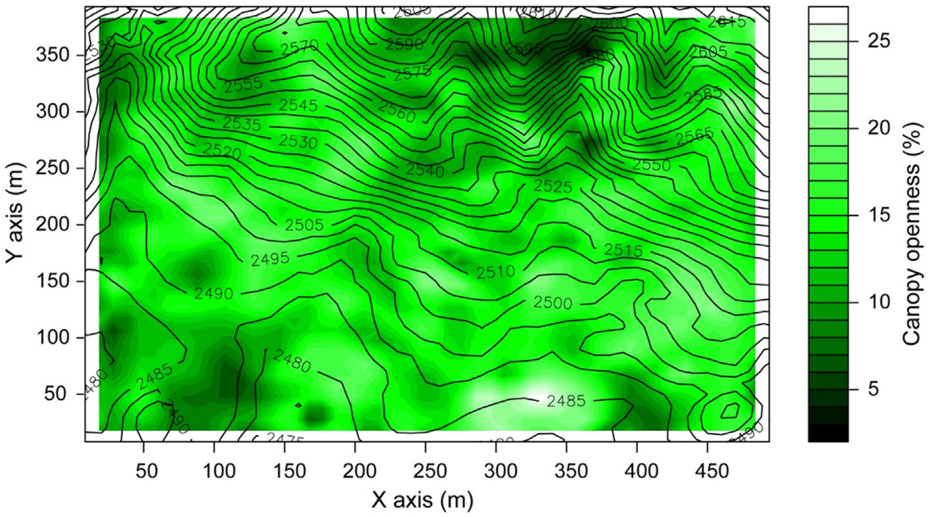

Fig. A1. The Ailaoshan 20 ha forest dynamics plot and canopy openness condition.

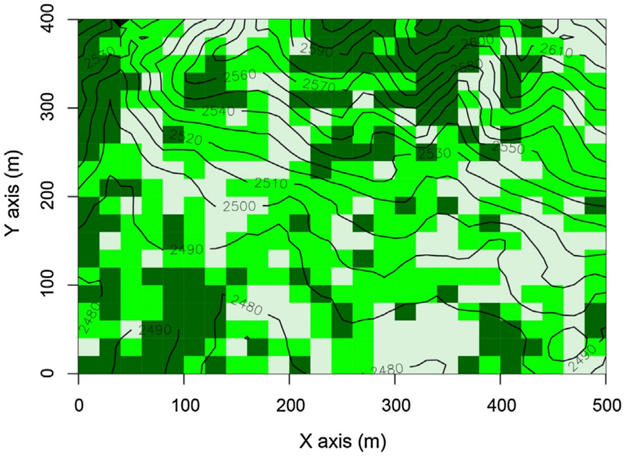

Fig. A2. The Ailaoshan 20 ha forest dynamics plot divided into light habitats assigned to 20 m × 20 m quadrats. Dark green indicates low light environment (135 quadrats, canopy openness < 11%); lime green indicates mid light environment (220 quadrats, canopy openness ≥ 11% and < 16%); light green indicates high light environment (145 quadrats, canopy openness ≥ 16%). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

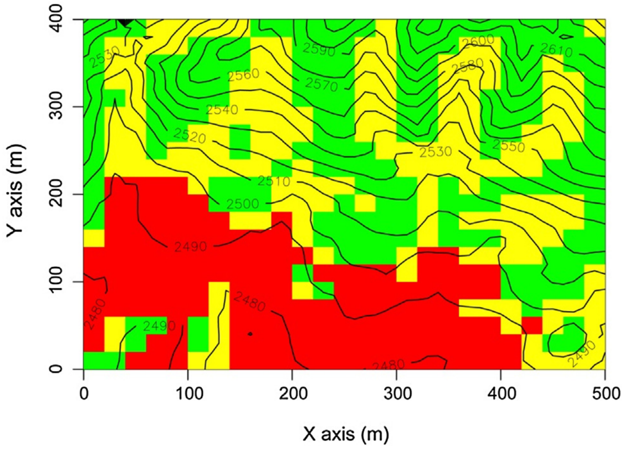

Fig. A3. The Ailaoshan 20 ha forest dynamics plot divided into habitats assigned to 20 m × 20 m quadrats. Red indicates flat habitat (140 quadrats, mean elevation < 2500 m and slope < 15°); yellow indicates valley habitat (172 quadrats, slope ≥ 15° and convexity < 0); green indicates ridge habitat (188 quadrats, slope ≥ 15° and convexity ≥ 0 or slope < 15° and elevation ≥ 2500 m). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

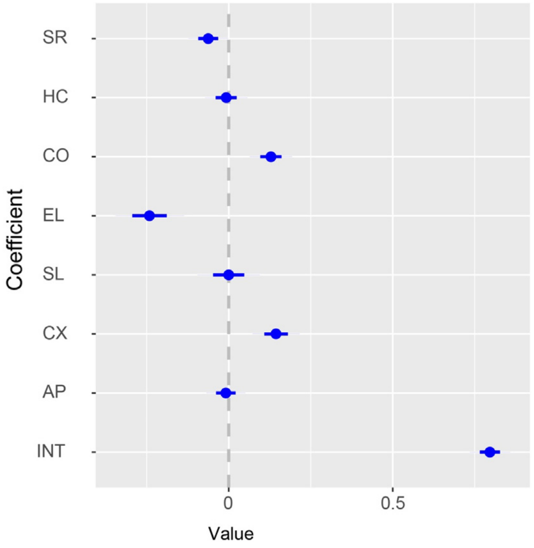

Fig. A4. Coefficient estimates (with 95% confidence intervals) for all explanatory variables (SR, Quadrat Species Richness; HC, Herb Cover; EL, Elevation; SL, Slope; CX, Convexity; CO, Canopy; AP, Sin translated Aspect and INT, Intercept) in relation to the rarified species richness of recruited seedlings following snow damage to the canopy.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.07.038.

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