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

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A B S T R A C T

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

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,