Effect of Gap Size And Elevation On The Regeneration And Coexistence of Three Tree Species In A Subalpine Coniferous Forest

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Research

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Abstract

Background: Gap size and environmental gradient have fundamental influence on the tree species coexistence and community assembly. We studied the regeneration and coexistence of three co-dominant tree species in three different gap size (large gap, 201-402 m²; medium gap, 101-200 m²; small gap, 38.8-100 m²) along an elevation gradient (between 3000m and 3500m) in an old-growth forest, on Mount Nadu in southwest China.

Results: We found that the photosynthetic photon flux density (PPFD) was positively affected by gap size during the growing season. All three species had a higher regeneration density in large gaps, but the detailed response to treatments for each species depended on its stem size. Gap size had a significant positive effect on the regeneration density of *Abies faxoniana* small trees and *Betula utilis* saplings, but had no significant effect on *Acer maximowiczii* regeneration density. Saplings regeneration density is more sensitive to elevation compared to small trees regeneration density. Large gaps magnified the negative effects of elevation on regeneration density. Our findings indicated that *Abies* may maintain its regeneration advantage with low-intensity canopy disturbance, and large gap may provide excellent opportunities for broadleaf species (*Betula* and *Acer*) establishment and regeneration in this subalpine coniferous forest.

Conclusion: Microhabitats heterogeneity controlled by characteristics of forest gaps along an elevation affected regeneration niche difference of tree species, which contributed to species coexistence and community assembly processes.

Background

Gap creation not only increase the heterogeneity of environment but also promote the regeneration and coexistence of species in forest understory (Muscolo et al. 2014). Gap formation has long been an effective way to achieve continuous forest regeneration and succession (Wang et al. 2017). Compared with traditional silviculture policy, close-to-nature forest managements highlight the importance of gap disturbance (Zhu et al. 2014). As an important gap characteristic, gap size, which reflects the disturbance degree, can strongly influence microclimate species regeneration, and other ecological processes (Muscolo et al. 2014, Chen et al. 2018). Thus, understanding how gap size affect species regeneration and coexistence has been an important theme in forest ecology and management (Lang and Knight 1983, Dirzo et al. 1992, Barberis and Tanner 2005, Lu et al. 2018).

Most studies on canopy gaps have been focused on gap regeneration on a temporal scale (Lang and Knight 1983, Tamura and Nakajima 2017). Little attention, however, has been directed to gap regeneration on a spatial scale, especially along an elevation gradient (Chen et al. 2018). As an important geographical factor, elevation drives the environment factors and tree species regeneration, survival and coexistence (Cole et al. 2014, Sizonenko and Dubrovskiy 2018). For example, a study on Atlantic Rainforest gaps suggested that low altitude (at approximately 350 m a.s.l.) is more conducive to plant regeneration and coexistence (Eisenlohr et al. 2013). Another study in subalpine *Abies fabri* suggested in mountainous regions, air temperature is more sensitive to disturbance at high elevation areas than that at low elevation areas (Sun et al. 2017). In addition, the underground environment factors also exhibited significant difference along the elevation gradients from 2800 to 3600 m in a subalpine forest (Luo et al. 2015). These studies investigated the effects of elevation on plant generation and environment factors, but changes in regeneration and environment factors may be related to gap size along the elevation gradient. Given the complexity of the ecological mechanism underlying gap regeneration, a combined investigation may be required to better understand species regeneration and coexistence along the gradients of gap sizes and elevation.

Studies on plant regeneration and coexistence mechanism of different species have been widely studied (Tang and Ohsawa 2002, Masaki et al. 2007, Jin et al. 2018). The sapling-to-small tree stage is often a critical phase during the life history of plants in determining the distribution of adults (Masaki et al. 2007). The sapling stage is an important demographic, and it establishes the template for later regeneration process (Jin et al. 2018). Variation of regeneration density from sapling stage to small trees linked to the different regeneration niche and species response to microenvironmental resources (Tang and Ohsawa 2002, Jin et al. 2018). Moreover, regeneration density is an imperative knowledge to develop sustainable forest management (Padilha and De Marco 2018), and density dependence has been also hypothesized as one of the most prominent mechanism in species coexistence (Chen et al. 2010). Consequently, the species regeneration and coexistence mechanism of density dependence and habitat association becomes essential for better understanding gap species regeneration and its appropriate management strategy.

The subalpine coniferous forest is the second largest forest area in China (Sun et al. 2017). It plays an important role in ecosystem services (e.g. water resources, timber supply and tourism services) in southwestern China (Bossard et al. 2015). Meanwhile, the subalpine coniferous forest in mountainous area is highly sensitive to climate change (Sun et al. 2017). Historically, at elevations greater than 3000 m, the old growth forest canopy was dominated by *Abies* in Wolong National Nature Reserve (Taylor and Qin 1998, Chen et al. 2018). A recent study showed broadleaf species (e.g. *Betula*) have increased in the subalpine coniferous forest (Bossard et al. 2015). Therefore, it may be a challenge to the development of forest managements in the future.

Abies, *Betula* and *Acer* are major component tree species in most subalpine coniferous gaps from 3000 m to 3500 m. Changes in sunlight, precipitation, temperature and soil properties often improve growth conditions for *Betula* and *Acer* establishment in gaps. To further understand potential changes in future subalpine forest composition (Bossard et al. 2015), we determined the three species regeneration density in different size gaps at the same elevation and examined the three species regeneration density in the same size gap along the elevation. We also studied how environment factors varied across different habitat gradients and their effects on the regeneration and coexistence of different tree species at different life history stages.

Methods

2.1 Study site

This study was carried out in a subalpine coniferous forest, an old-growth forest on Mount Nadu of the Wolong Nature Reserve (30°45'–31°25' N, 102°52'–103°24' E), Sichuan Province, southwestern China. The study area has a subtropical inland and mountainous climate, with a strong solar radiation and cold temperature. The ultraviolet radiation (365 nm, UV-A 365) ranges from 1621 $\mu\text{W cm}^{-2}$ to 549 $\mu\text{W cm}^{-2}$ in the growing season and the mean annual temperature is between 4.1°C and 5.1°C. The mean annual rainfall is between 861 mm and 1800 mm, with the highest precipitation month of August averaging 340 mm. The soil is brown coniferous forest soil and the pH is between 3.9 to 5.0 (Chen et al. 2018). The majority of the snowfall occurs from October to February at high elevation. More detailed information on the study area could be found in our earlier publications (Chen et al. 2018, Liu et al. 2018, Chen et al. 2019).

Our field study was conducted in a coniferous forest with few human disturbance at the elevation span of 3000–3500 m. Historically, snowstorm and other natural disturbances were the main causes of forest gap formation. In this old-growth forest, the conifer tree of *Abies faxoniana* is found mostly from 2000 m to 3800 m and considered as a shade-tolerant species. At the elevation range from 3000 m to 3500 m, the subalpine coniferous forest also include *Betula utilis* and *Acer maximowiczii*, two broadleaf, shade-intolerant tree species. The three dominant tree species make up 95% of trees at this range of elevation and they were natural regeneration. The shrub species mainly included *Rhododendron faberisp*, *Rhododendron phaeochrysum* and *Fargesia nitida*. The herb layer was dominated by *Circaea alpine*, *Oxalis acetosrlla* and *Parasencio deltophyllus*.

2.2 Gap selection and experiment design

A randomized design was used to sample gaps in each 100 m intervals during 2015–2018. At each elevation level, three gaps in each size class were selected. The three gap size class were: small gap ($n = 3$, area range: 38.5–100 m^2), medium gap ($n = 3$, area range: 101–200 m^2) and large gap ($n = 3$, area range: 201–402 m^2), which were determined for as the expanded gaps (Wang et al. 2017). In total, we sampled 45 gaps with similar age, with an elevation range from 3000 m a.s.l. to 3500 m a.s.l.. We measured the longest canopy opening dimension as gap length and the perpendicular to gap length across the gap center as gap width, and then used these data to calculate the gap area using the formula of $A = \pi ab$ with a and b being half the gap length and width if gap was more similar to oval. If gap was more similar to circular, the formula of $A = \pi r^2$ was used, with $r = (a + b)/2$.

2.3 Data collection

2.3.1 Regeneration characteristics

Within each gap, all saplings and small trees of the three tree species (repeat the names here) were censused during the growing season, and their species, height and ground line diameter (GLD) were recorded. Considering the difference in their growth among the three species, we divided these two different regeneration stage (sapling and small tree) based on our previous studies (Chen et al. 2018). The sapling stage was defined as “0.1 m < stems < 1 m in height and 0.1 cm < GLD < 1.5 cm” (Kneeshaw and Bergeron

1998). The regeneration stage of small tree was defined as “either stems ≥ 1 m in height or GLD ≥ 1.5 cm”. Stems with height > 5 m or diameter at breast height (DBH) > 10 cm were removed from regeneration datasets because they were considered as adult. There were fewer regeneration especially for *Betula* and *Acer* regeneration in small gaps and at high elevation gaps.

2.3.2 Environment factors

The aboveground and underground environment factors that could affect seedling establishment, growth and survival were measured in each gap along the elevation gradient, which include solar radiation, air temperature, air humidity, soil temperature and soil nutrient (Zhu et al. 2014). Generally, the photosynthetic photon flux density (PPFD) determine the species distribution and different life stage's growth of woody plants (Chen et al. 2018). Under overcast sky condition, PPFD was stable and have a good correlation with the growing season PPFD (Messier and Comeau 1998). Moreover, the PPFD in sunny days during the growing season may have the lowest restriction on the establishment of shade-intolerant species. In our study, PPFD (LI-190, Li-Cor Inc) was measured 1 m above ground level. Within each gap, the mean daily PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) datasets were recorded continuously as 2-hour averages from 8:00 am to 6:00 pm on cloudless days and overcast days during the growing season (June– September, 2015–2018) (Parent and Messier 1996). Temperature and precipitation conditions were significantly and positively affected by the creation of canopy gaps (Zhu et al. 2014, Buajan et al. 2018). Therefore, we measured the annual mean air temperature (AMAT, °C), air relative humidity (RH, %) and soil temperature (ST, °C) (Chen et al. 2018). We also measured and calculated annual average temperature difference between day and night (ΔT_{AMT} , °C), annual mean temperature of growing/non-growing season (GST/NGST, °C), soil temperature in the upper layer (0–10 cm, ST_1 , °C) and deep layer (10–20 cm, ST_2 , °C).

These datasets were measured by button thermometer (iButton, DS1923-F5#, USA) and recorded every 2-hour for one year at least. For the above-ground environment factors, two iButton recorders were fixed separately in the gap center and gap edge in each gap. The soil temperature datasets were monitored in the gap center at the depth of 0–10 cm and 10–20 cm. Three random soil sample were collected beneath the litter layer in each gap and stored in a clean bags. All soil samples were air dried at room temperature. Stones, roots and debris were removed and then sieved through 2-mm mesh screen (Chen et al. 2019). Soil total carbon (STC, %), Soil total nitrogen (STN, %) and carbon to nitrogen ratio (C/N, %) were measured in each sampling quadrat using a Vario EL III analyser (Elementar Analy- sensysteme GmbH, Germany).

2.4 Data analysis

The regeneration data of all plots were averaged in each gap before analysis. We used one-way analysis of variance (ANOVA) to test the difference of regeneration density among three tree species in the same gap size and elevation gradient. The multivariate analysis of variance (MANOVA) analysis was then used to determine the effect of gap size or elevation on three species regeneration density of sapling and small tree. Two-way ANOVAs was used to test the effects of gap size and elevation on the environment factors. Each p -value less than 0.05 was regarded as the evidence of statistically significant. Tukey's post hoc tests were used to further exam the difference among treatment levels. Bonferroni-adjusted test was applied for multiple testing, a p -value less than 0.01 indicated significant difference. To assess the relationship of regeneration density with environment factors, we used the Pearson correlation analyses based on all treatment data. Data were performed using R version 3.3.3 (R Core Team, 2017). Multcomp package was used for descriptive statistics, one-way ANOVA, two-way ANOVA and Tukey's post hoc tests. MASS package was used for MANOVA analysis. Psych package was used for correlation analyses.

Results

3.1 Variation in regeneration density of three species and environment factors among gaps

Saplings had a higher density than small trees within each habitat type (Table 1). As expected, regeneration density increased with increasing gap size but declined with increasing elevation (Fig. 1). In small gaps, *Abies* saplings density was significantly greater than *Betula* and *Acer* saplings density, but the three tree species were similar for the small tree density regardless of gap size. Moreover, these regeneration density and gap size relationships did not change with elevation (Fig. 1A).

In medium and large gaps, *Betula* sapling and small tree density were significantly higher than *Abies* and *Acer* (Fig. 1B and C), while *Abies* regeneration density will predominate at the higher elevation gradients (Fig. 1B and C). These results indicated that small gaps

were conducive to *Abies* sapling. Moreover, the dominance of species regeneration density changed in large and medium gaps with increasing elevation, but the sapling regeneration density in small gaps did not.

The PPFD was mainly affected by gap size on overcast days during the growing season ($F = 27.57, p < 0.001$). Besides GST was not significantly affected by gap size ($F = 2.09, p = 0.141$), the AMAT, ΔT_{AMT} and NGST were significantly affected by elevation and gap size ($p < 0.001$). Soil temperature showed no difference among different sizes gaps ($ST_1: F = 0.09, p = 0.914$; $ST_2: F = 1.86, p = 0.173$), while significantly affected by elevation ($ST_1: F = 127.26, p < 0.001$; $ST_2: F = 106.56, p < 0.001$). Our result showed a significant interaction effect between elevation and gap size on soil C/N ratio (0–10 cm: $F = 2.36, p = 0.042$; 10–20 cm: $F = 6.47, p < 0.001$), though it is similar in all treatments (elevation: $F = 2.48, p = 0.065$; gap size: $F = 1.68, p = 0.204$). Otherwise, in our study, the other below-ground environment factors were significantly affected by elevation and gap size ($p < 0.001$). In conclusion, the improvement of understory illumination mainly comes from canopy gaps opening, and elevation has a relatively wider influence on environmental factors than forest gap (Table 2).

3.2 Effect of gap size and elevation on regeneration density of three species

Abies sapling regeneration density was significantly higher in small gaps than in medium gaps and large gaps along the elevation gradients (Fig. 2A and Table 3). In the same elevation gradient, these three tree species small trees regeneration density were positively affected by the gap size, while *Betula* small tree regeneration density was not significantly affected by gap size at the elevation gradient of 3400 m – 3500 m and *Acer* small tree regeneration density was not significantly affected by gap size from 3200 m a.s.l to 3500 m a.s.l (Fig. 2B). These results meant that the gap size most affected *Betula* sapling regeneration density, followed by *Abies* and *Acer* saplings density. However, for the small trees, the gap size affected the *Abies* small trees regeneration density more obvious than *Betula* and *Acer* regeneration density (Table 3) .

In small gaps (Fig. 3 A₁ and B₁), three species saplings regeneration density were significantly and negatively affected by the elevation (*Abies*: $F = 40.06, p < 0.001$; *Betula*: $F = 29.25, p < 0.001$; *Acer*: $F = 4.48, p = 0.025$), while their small trees regeneration density was similar among different elevation gradients. In medium gaps (Fig. 3 A₂ and B₂), the *Betula* small trees regeneration density was not significantly affect by the elevation ($F = 5.10, p = 0.017$), other regeneration density was significantly affected by elevation. In large gaps (Fig. 3 A₃ and B₃), both three species saplings regeneration density, and their small trees regeneration density was significantly affected by elevation (Table 4). These results indicated that elevationshowed a greater impact on saplings regeneration density than small trees regeneration density, and the effect of elevation on their regeneration density was more obvious in large gap size than in small gap.

3.3 Relationship between regeneration density and environment factors

Correlation analysis revealed thatthe relationships between *Abies* regeneration density and environment factors differed between the two life history stages (Table 5). For *Abies* saplings, there were significant and positive correlation between regeneration density and air temperature, ST and STN (0–10 cm). For *Abies* small trees, the ΔT_{AMT} , PPFD, RH and more soil properties had a significant and positive correlation with regeneration density (Table 5). The other two species (*Acer* and *Betula*) showed similar relationships between regeneration density and environment factors for the two life history stages (Table 5), suggesting *Acer* and *Betula* likely have similar life habits. For each species (*Acer* and *Betula*), the results also revealed that the regeneration density at two life stages have the similar relationships with environment factors (Table 5). More below-ground environment factors showed significant positive correlations with *Acer* and *Betula* sapling regeneration density than with *Abies* sapling regeneration density.

Discussion

4.1 Effect of gap size on environment filtering for species regeneration

In forest gaps, gap size can affect the microenvironment in gaps, and the two factors combined together then affecting vegetation regeneration (Denslow et al. 1998, He et al. 2019). Our results confirmed that the PPFD is mainly affected by gap size on overcast day during growing season, and it has positive and significant correlation with *Acer* and *Betula* saplings regeneration density and the three species small trees regeneration density in subalpine gaps. However, *Abies* sapling regeneration density shows insignificant correlation with PPFD during growing season. Since *Abies* is a common shade tolerance species, and the small gaps with lower

PPFD provided a more superior habitat for *Abies* saplings (Miao et al. 2014). In order to meet the growth, light demanding also increased in the *Abies* small tree life stage (Chen et al. 2018, Jin et al. 2018). However, in small gaps, there are still several *Abies* small trees survived in these relatively low-light environment. Some studies suggested (Wang et al. 2017, Lu et al. 2018) that the center of small gaps with higher light was one of the most reasons allowing shade-tolerance species to be established. We speculate that the previous regeneration might be attribute to *Abies* small trees survival in small gaps, because several *Abies* saplings may have established in understory and they will grow rapidly once the gaps formed.

With respect to *Acer* and *Betula* regeneration in different size gaps compared with *Abies*, the correlation analysis results suggested the regeneration density exhibited greater similar between regeneration density and aboveground environment factors (e.g. AMAT and RH) which were affected by gap size. As mentioned by Gray and Spies (1998) (Gray and Spies 1998), establishment and regeneration of different species was related to the tolerance of environmental and utilization of resources in gaps. Moreover, in the medium gaps and large gaps, the *Betula* regeneration density was significant higher than *Acer* regeneration density. Thus, we speculate that the *Betula* has stronger competitiveness and more effective regeneration strategy in sapling life stage than *Acer* in the suitable microsite in our study area.

A study on Calabrian pine (*Pinus laricio*) showed no significant differences in GST between gaps of different sizes (Muscolo et al. 2007). Similarly, several studies in conifer forest reported GST was not significant affect by gap size (Muscolo et al. 2014, Gray et al. 2002). Our study also did not detect a significant difference in GST among different size gaps. But, *Abies*, *Acer* and *Betula* regeneration were significantly correlated with GST. Further study showed that the interact effects of elevation and gap size significantly influenced the GST. Our results suggested that the concurrent effects of elevation and gap size on some environment factors, such as GST, may be also important drivers on the establishment, regeneration and survival of vegetations, and their interaction effects should not be neglected in future researches.

Many studies of gap regeneration have focused on the relationships among gap size, soil properties and regeneration success. According to Scharenbroch and Bockheim (2008) the surface C efflux was significantly higher in gaps, likely in response to solar radiation and soil temperature which, in turn, generally positively related tree regeneration successful. In a former research, C/N ratio was negatively and significantly related with gap size (Muscolo A and R. 2011). In our study, soil temperature in two soil layers were not significantly affected by the gap size. While STC, STN and C/N ratio were significantly and positively affected by gap size or influenced by the interact effects of elevation and gap size. For the saplings regeneration, *Betula* and *Acer* was more significantly related to fertile soil nutrients in large gap than *Abies* (Muscolo et al. 2014). These findings therefore suggested the view that during early-successional, natural regeneration of pioneer tree species as *Betula* restricted by soil nutrition besides solar radiation and demands large gaps in the subalpine coniferous forest.

4.2 Effect of elevation on environment filtering for species regeneration

Elevation is a strong driver of spatial variation in environment factors (e.g. temperature, precipitation and soil properties), and it may therefore have large consequences for species distribution and plant regeneration (Korner 1992, Chen et al. 2018). Sanchez et al. (2013) suggested that soil characteristics of the altitudinal gradient determines the distribution of plants pattern. In a rainforest, Eisenlohr et al. (2013) found that disturbances, topography and spatial proximity drive vegetation patterns along an elevation gradient. Moreover, some previous studies (Scarano 2002, Rezende et al. 2015) have shown that low temperature is the particularly important stressful factor for plant species subject near mountaintops. In our study, almost all of the underground and belowground environment factors were significantly affect by elevation, except for PPFD. Moreover, except for soil temperature, few belowground environment factors showed significantly correlation with *Abies* saplings regeneration density. For *Betula* regeneration, PPFD, air temperature, RH and soil properties were significantly correlated with saplings density. These facts, which restrictive environmental factors invalidated from belowground, may partly explain why *Abies* saplings occupied regeneration advantage in gaps with the elevation increasing, while *Betula* saplings regeneration is more dominant at lower elevation gradients.

Forest gaps are commonly formed by canopy tree fall, which partly resembles to the early successional forest habitats in old-growth forest (Jin et al. 2015). We found that in large gaps, the effect of elevation on our observed species regeneration density was more obvious. For the canopy opening area, Denslow (1987) (Denslow 1987), point out that, the environment factors in gaps would be more sensitive from harsh weather conditions without the canopy protection. Considering the extensive influence of elevation on environmental factors, the filtration capacity from elevation for plant establish and regeneration may be enlarged with gap size increased.

4.3 Community assembly processes along gap and elevation gradient

Species coexistence in communities is due to different ecological strategies for species occupying different niches. Environmental heterogeneity affecting niche space is a primary factor on species coexistence (Adler et al., 2013, Stein et al., 2014). Bergholz et al. (2017) showed that environmental heterogeneity resulted from environmental filtering within microhabitats had a main influence on community assembly (Bergholz et al., 2017). The microhabitats heterogeneity controlled by characteristics of forest gaps affected trees regeneration. Our study demonstrated that *Betula* saplings regeneration dominated as a shade intolerant species in large and medium gaps, and the regeneration advantage could be extended to the small trees stage in large gaps at lower elevation gradients (3000m-3300m).

The three pioneer species of subalpine coniferous forest in the study area have different regeneration ecology. The conifer *Abies* is long-living climax species and could endure the competitive disadvantage with lower regeneration density in relatively resource-rich gaps in early stages of succession (Tang and Ohsawa 2002). As mentioned by Jin et al. (2018), light radiation limit shade tolerance species regeneration in large gaps. In addition, the slow allocation to height growth of *Abies* results in tall and hard stems, which appears to be a long-term competitive strategy to tolerant shading (Taylor and Qin 1998). However, *Betula* as a shade intolerant species grow fast under full sunlight, resulting in tall young trees with slender trunks and narrow crowns (Miao et al., 2014). *Betula* grow rapidly under full sunlight, and becomes a pioneer species in the early stages of succession. This competitive strategy results a higher rates of mortality from sapling to small trees stage (Mori and Takeda 2004). With the increase of the continuous canopy cover in later stages of succession, *Betula* is replaced by shade-tolerant species such *Abies*. Thus, *Abies* is more representative of k-selected species compared to r-selected species like *Betula* (Miao et al. 2014). For deciduous *Acer* regeneration, it survives as a fugitive with lowest saplings and small trees regeneration density. This species seems to avoid competition with *Abies* and *Betula*, and adapt a relatively narrow niche even though insuitable habitat (e.g. large gaps and medium gaps) (Tang and Ohsawa 2002). Light radiation limit shade tolerance species regeneration in large gaps, as mentioned by Jin et al. (2018). If *Betula* and *Acer* trees want to be canopy trees, the large gaps may provide excellent opportunities and places (Brokaw 1987, Hoffman, Bataineh et al. 2018). Environmental conditions including soil conditions and light intensity controlled by topographic features affect the saplings regeneration of these three tree species and the processes of community assembly.

Conclusion And Management Implication

In conclusion, we tested the effect of forest gap size on three tree species regeneration density along an elevation gradient, and each species have shown different regeneration and coexistence ecology strategy. This study reveals that the large gap could enlarged the effects of elevation on species regeneration density. In addition, mountain regions are particularly sensitive to climate change, and current climate change favors broadleaf species rather than conifer species (Bossard et al. 2015, Fourcade et al. 2019). Moreover, a related study reveals elevation shifts can locally reshape species competitive (Alexander et al. 2015). Thus, low-intensity canopy treatments could be applied in future forest management plants if we want maintain *Abies* dominance regeneration along the elevation gradients.

Unlike the old-growth forests with few human disturbance in core zone in natural reserve, a large area of coniferous forests in Wolong National Nature Reserve play an important role in tourist and timber supply. The broadleaf tree species, especially *Betula* and *Acer*, play a vital role in forming the "color forest" in fall (Bossard et al. 2015). In addition, long-term monoculture *Abies* plantation may lead more vulnerable to disease, pest insect disturbance, or facing reduced soil fertility and other potential ecological problems (Lu et al. 2018). We suggest creating large or medium gaps examined in our study in these forests that aims to promote broadleaf species regeneration improving ecological function and sustainability.

Although, our study exploratory analysis only implemented along a section of elevation gradient at a regional scale in Wolong National Nature Reserve. We found clear evidence of species regeneration and coexistence potential ecological mechanism with typical habitat gradients in a subalpine coniferous forest. Our study indicates that (1) gap size had largely and significantly affected on the *Abies* small trees regeneration density and *Betula* saplings regeneration density but limited influence on *Acer* regeneration density. (2) For these three tree species, saplings regeneration density were more sensitively influenced by elevation than small trees regeneration density, and gap size can positively enlarged the effects of elevation on the three species regeneration density. (3) Based on the underlying ecological mechanism of species regeneration and coexistence of density dependence and habitat association, we also put forward different forest management measures according to forest ecosystem service functions in our

study area. However, since multiple environment factors were associated with gap size and elevation, many direct and indirect effects among gap size and/or elevation, environment factors and species regeneration remain unknown. In the future, continuous monitoring and additional treatments would be required to disentangle their inner links between gap size, environment variables and species regeneration along elevation gradients.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

The dataset used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

W.-Y.H., L.C. designed the study, analyzed the data and wrote the manuscript. D.L. organized and analyzed the data. G.-G.W., G.-H.L. modified article structure. All the authors contributed discussion to improve the manuscript.

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Tables

Table 1 Descriptive statistic for three species regeneration density and environment factors in our gap study of a subalpine coniferous forest (mean $\pm$ SE). PPFD: photosynthetic photon flux density; GST: annual mean temperature of growing season; NGST: annual mean temperature of non-growing season; ΔT_{AMT} : annual average temperature difference between day and night.

Variables			
Regeneration density	sapling	small tree	total
<i>Abies faxoniana</i> (N m ⁻²)	0.91 $\pm$ 0.19	0.37 $\pm$ 0.26	0.64 $\pm$ 0.35
<i>Betula utilis</i> (N m ⁻²)	0.94 $\pm$ 0.86	0.42 $\pm$ 0.49	0.68 $\pm$ 0.86
<i>Acer maximowiczii</i> (N m ⁻²)	0.27 $\pm$ 0.20	0.19 $\pm$ 0.12	0.23 $\pm$ 0.17
Light radiation	Cloudless	Overcast	total
PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	464.56 $\pm$ 88.48	261.4 $\pm$ 15.7	362.95 $\pm$ 120.13
air temperature	GST	NGST	Annual
Mean temperature ($^{\circ}\text{C}$)	15.73 $\pm$ 1.80	-7.96 $\pm$ 1.36	3.71 $\pm$ 0.43
ΔT_{AMT} ($^{\circ}\text{C}$)	-	-	4.19 $\pm$ 0.60
air relative humidity			
Mean humidity (%)	-	-	93.12 $\pm$ 1.15
Soil properties	0-10 cm	10-20 cm	total
Soil temperature ($^{\circ}\text{C}$)	2.48 $\pm$ 0.70	2.63 $\pm$ 0.76	2.56 $\pm$ 0.73
Soil total C (%)	9.15 $\pm$ 5.18	6.88 $\pm$ 1.51	8.02 $\pm$ 3.96
Soil total N (%)	0.45 $\pm$ 0.14	0.38 $\pm$ 0.06	0.41 $\pm$ 0.11
Soil C/N ratio	20.14 $\pm$ 6.99	0.27 $\pm$ 1.83	19.05 $\pm$ 5.20

Table 2 Two-way ANOVAs for the effects of elevation and gap size on environment factors. Significant effects ($p < 0.05$) are bolded.

	Elevation		Gap size		Elevation*size	
	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>
PPFD ($\mu\text{ mol m}^{-2} \text{ s}^{-1}$)						
Cloudless	0.50	0.485	1.49	0.229	0.75	0.393
Overcast	0.68	0.615	27.57	<0.001	0.27	0.971
Air Temperature ($^{\circ}\text{C}$)						
Annual mean temperature	134.52	<0.001	13.59	<0.001	5.07	<0.001
ΔT_{AMT}	139.05	<0.001	510.80	<0.001	50.97	<0.001
temperature in growing season	151.53	<0.001	2.09	0.141	5.87	<0.001
temperature in non-growing season	44.82	<0.001	85.31	<0.001	39.98	<0.001
Air Humidity (%)						
Annual mean humidity	7.39	<0.001	51.40	<0.001	15.15	<0.001
Soil property						
Soil temperature ($^{\circ}\text{C}$) 0-10 cm	127.26	<0.001	0.09	0.914	0.51	0.836
10-20 cm	106.56	<0.001	1.86	0.173	0.82	0.588
Soil total C (%) 0-10 cm	11.68	<0.001	8.54	0.0016	2.33	0.044
10-20 cm	371.40	<0.001	298.50	<0.001	21.80	<0.001
Soil total N (%) 0-10 cm	31.93	<0.001	12.23	<0.001	1.17	0.3469
10-20 cm	155.63	<0.001	134.36	<0.001	22.49	<0.001
Soil C/N ratio (%) 0-10 cm	2.48	0.0653	1.68	0.2038	2.36	0.042
10-20 cm	26.16	<0.001	29.73	<0.001	6.47	<0.001

Table 3 MANOVA analysis of the effects of gap size on three species regeneration density at each elevation intervals. Significant effects ($p<0.01$) are bolded.

Elevation	<i>Abies faxoniana</i>				<i>Betula utilis</i>				<i>Acer maximowiczii</i>			
	sapling		small tree		sapling		small tree		sapling		small tree	
	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>
3000-3100m	18.08	0.003	109.35	<0.001	1123.70	<0.001	289.64	<0.001	32.39	<0.001	14.49	0.005
3100-3200 m	34.40	<0.001	129.53	<0.001	468.09	<0.001	68.05	<0.001	28.11	<0.001	21.94	0.002
3200-3300 m	20.21	0.002	123.15	<0.001	416.58	<0.001	30.65	<0.001	25.53	0.001	3.45	0.101
3300-3400 m	7.51	0.003	89.24	<0.001	65.67	<0.001	20.08	0.002	1.13	0.383	1.30	0.340
3400-3500 m	14.95	0.005	68.85	<0.001	8.60	0.017	0.94	0.442	1.20	0.364	0.95	0.438

Table 4 MANOVA analysis of the effects of elevation on three species regeneration density in the same size gaps. Significant effects ($p<0.01$) are bolded.

Speices		Large gap		Medium gap		Small gap	
		F	<i>p</i>	F	<i>p</i>	F	<i>p</i>
<i>Abies faxoniana</i>	sapling	22.43	<0.001	17.22	<0.001	40.06	<0.001
	small tree	25.06	<0.001	25.36	<0.001	2.63	0.098
<i>Betula utilis</i>	sapling	339.97	<0.001	99.05	<0.001	29.25	<0.001
	small tree	59.28	<0.001	34.42	<0.001	1.83	0.200
<i>Acer maximowiczii</i>	sapling	56.30	<0.001	8.91	0.002	4.48	0.025
	small tree	14.31	<0.001	5.10	0.017	3.59	0.046

Table 5 The relationship between environment factors and species regeneration density at sapling and small tree life stage. Significant relationships ($p < 0.05$) are bolded.

Environment variable	<i>Abies faxoniana</i>				<i>Betula utilis</i>				<i>Acer maximowiczii</i>			
	sapling		small tree		sapling		small tree		sapling		small tree	
	r	p	r	p	r	p	r	p	r	p	r	p
PPFD												
Overcast	-0.16	0.349	0.72	<0.001	0.59	<0.001	0.55	<0.001	0.45	0.004	0.46	0.003
Cloudless	0.09	0.609	0.26	0.129	0.26	0.131	0.22	0.206	0.24	0.154	0.21	0.225
Air Temperature												
Annual mean temperature	0.80	<0.001	0.25	0.149	0.50	0.001	0.50	0.001	0.60	<0.001	0.54	<0.001
ΔT_{AMT}	0.58	<0.001	-0.42	0.008	-0.20	0.246	-0.23	0.185	-0.09	0.600	-0.12	0.508
GST	0.65	<0.001	0.30	0.071	0.53	<0.001	0.46	0.003	0.58	<0.001	0.52	0.001
NGST	0.41	0.010	-0.26	0.125	-0.19	0.271	-0.32	0.052	-0.13	0.45	-0.16	0.349
Air Humidity												
Annual mean humidity	-0.12	0.476	-0.37	0.021	-0.39	0.015	-0.49	0.001	-0.45	0.004	-0.42	0.008
Soil property												
Soil temperature 0-10 cm	0.67	<0.001	0.33	0.045	0.59	<0.001	0.54	<0.001	0.64	<0.001	0.60	<0.001
10-20 cm	0.62	<0.001	0.41	0.010	0.65	<0.001	0.60	<0.001	0.69	<0.001	0.66	<0.001
Soil total C (%) 0-10 cm	0.19	0.285	0.54	<0.001	0.71	<0.001	0.71	<0.001	0.69	<0.001	0.68	<0.001
10-20 cm	0.27	0.103	0.51	<0.001	0.60	<0.001	0.43	0.007	0.54	<0.001	0.52	<0.001
Soil total N (%) 0-10 cm	0.38	0.017	0.61	<0.001	0.76	<0.001	0.68	<0.001	0.72	<0.001	0.63	<0.001
10-20 cm	0.32	0.050	0.58	<0.001	0.61	<0.001	0.48	0.002	0.55	<0.001	0.54	<0.001
Soil C/N ratio(%) 0-10 cm	-0.11	0.549	0.22	0.198	0.32	0.050	0.39	0.016	0.33	0.048	0.37	0.023
10-20 cm	0.09	0.588	0.24	0.160	0.37	0.022	0.21	0.231	0.33	0.042	0.30	0.071

Figures

Figure 1

The results of one-way ANOVA analysis for three species sapling and small tree regeneration density in different size gaps at each elevation intervals. Different letters indicate significant difference ($p < 0.05$) among treatments.

Figure 2

The MANOVA analysis for sapling and small tree regeneration density in different size gaps at each elevation intervals. Different letters indicate significant difference ($p < 0.01$) among treatments.

Figure 3

The MANOVA analysis for sapling and small tree regeneration density in same size gaps along the elevation gradients. Different letters indicate significant difference (p<0.01) among treatments.