



Response of community diversity and productivity to canopy gap disturbance in subtropical forests

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ABSTRACT

Forest ecosystem productivity is crucial for regulating global climate change and carbon budget. Previous studies have shown that community diversity (such as species, functional and structural diversity) promotes forest productivity. However, species, functional, and structural diversity are often affected by canopy gap disturbance. In the context of global change, increases in canopy gap disturbance can augment the uncertainty in these relationships. Here, we used forest inventory, functional traits, and environmental data from a 20-ha subtropical forest plot located in the Zhejiang Province of China. We applied spatial synchronous autoregressive error modeling and structural equation models (SEMs) to analyze the effects of environmental factors (topography and soil properties), canopy gap disturbance (with and without the inclusion of the effect), community diversity variables on productivity. Results showed that stand structural diversity explained the largest amount of variation in productivity, followed by initial above-ground biomass and stand density. For canopy disturbed quadrats, stand structural explained the largest amount of variation in productivity, followed by stand density and species richness. For canopy non-disturbed quadrats, initial above-ground biomass explained the largest amount of variation in productivity, followed by stand density and stand structural diversity. Canopy gap disturbance enhanced the effect of stand structural diversity on productivity and reduced the effect of initial above-ground biomass. Our results provide strong evidence for the effect of canopy gap disturbance on the relationship between biodiversity and productivity in a subtropical forest. We argue that canopy gap disturbance reduces competition and promotes complementary utilization of resources, thus enhancing the impact of niche complementarity on productivity through species richness, stand density, and tree DBH diversity in forests.

1. Introduction

The loss of species and homogenization of stand structure may reduce the productivity and services of forest ecosystems (Naeem et al., 2012; Liang et al., 2016). It is, therefore, important to understand the relationships among species, functional, and structural diversity and how they affect forest productivity to better predict the impact of biodiversity loss on forest function (Ali and Yan, 2017; Poorter et al., 2017; Yuan et al., 2018b). There is strong evidence for the independent effects of species, functional, and structural diversity on ecosystem functions; however, in natural forest ecosystems, these effects are routinely perturbed by other coupling factors (such as stand age and disturbance), increasing the uncertainty of their interrelationships

(reviewed by Adair et al., 2018; van der Plas, 2019). In most empirical studies, canopy gap disturbance effects on community diversity and productivity interactions are often ignored, making overarching patterns difficult to decipher (Pedro et al., 2016; Ali, 2019). Therefore, it is necessary to understand the patterns, magnitude, and mechanisms of community diversity-productivity relationships in response to canopy gap disturbance (Fig. 1).

Canopy gap disturbance has negative (the initial stage of canopy gap formation) and positive (recovery phases) effects on ecosystem functions (Pedro et al., 2016; Thom and Seidl, 2016). Canopy tree death caused by canopy gap disturbance initially reduces carbon absorption and has a negative impact on forest productivity (Lindroth et al., 2009; Peters et al., 2013). However, canopy gap disturbance also affects

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changes in species and functional diversity, while higher species and functional diversity increase productivity (Wright et al., 2010; Rissanen et al., 2019). Moreover, the recovery of productivity is related to structural diversity (Gough et al., 2013). After canopy gap disturbance, structural diversity could change, enhancing light and temperature inside the forest and promoting soil nutrient circulation, thus, promoting the growth of trees (Terborgh et al., 2017a). Therefore, it is possible that canopy gap disturbance affects productivity directly and indirectly via modulating effects on species, functional and structural diversity in forest ecosystems. For example, after canopy gap disturbance, the surviving trees, regeneration trees, and gap edge trees could form different forest layers. Canopy gap disturbance is conducive to lateral expansion of the canopy of these trees, increasing the space-filling of different forest layers (Jucker et al., 2014; Juchheim et al., 2017). The horizontal and vertical structural heterogeneity of the community changes to form multiple allocations of trees in space and improve the utilization efficiency of light resources (Rissanen et al., 2019; Haber et al., 2020). Canopy gap disturbance can reduce asymmetric competition between canopy trees and the understory (Fahey et al., 2016; Riutta et al., 2018). For example, canopy gap disturbance increases the light intensity within the forest and increases the light capture ability of understory trees. Therefore, canopy gap disturbance increases the horizontal and vertical niche complementarity effects of the forest to a certain extent (Haber et al., 2020).

The main hypotheses for linking species, functional and structural diversity with productivity are the niche complementarity, the selection effect, and the mass ratio interrelationships (reviewed by Barrufol et al., 2013; Ruiz-Benito et al., 2014; Poorter et al., 2015; Liang et al., 2016; van der Plas, 2019). The niche complementary hypothesis states that the increase of species, stand structure and functional diversity improves forest productivity through niche differentiation and facilitation (Tilman and Knops, 1997). The selection effect hypothesizes that higher species diversity increases the probability of high-functioning species, thereby increases community productivity (Hooper et al., 2005). The mass ratio hypothesis predicts that ecosystem function is driven by the traits of the most dominant species in the plant community (Grime,

1998), and hence, a community dominated by plants with a single resource utilization strategy could have higher productivity. The selection (or mass ratio effect) and the niche complementary effects are not necessarily mutually exclusive—they both play a joint role in natural ecosystems but have different relative importance in different situations (Hooper et al., 2005; Chiang et al., 2016; Sullivan and Sullivan, 2016). However, the increased species, structural and functional diversity caused by canopy gap disturbance could further enhance the complementarity and promotional effects of different species on resource utilization (Morin et al., 2011; Lasky et al., 2014a). But, the selection or mass ratio effect could be enhanced when a canopy gap disturbance has a great promotional effect on the regeneration and growth of a dominant species (Carreño-Rocabado et al., 2012), otherwise, it could be weakened. For example, canopy gap disturbance also modulates the ecological impact of structural diversity, as structural diversity not only reflects the light absorption level of different forest layers but also reflects changes in stand structure after canopy gap disturbance (Xiangdong et al., 2009; Dănescu et al., 2016). However, the complementarity effect caused by canopy gap disturbances may be countered by other effects. Carreño-rocabado et al (2012) found that species diversity responded most significantly to canopy gap disturbance. When the forest environment change was conducive to the convergence and evolution of dominant traits, productivity changes dominated by mass ratio effects mask the complementarity effects caused by structural diversity (Suding et al., 2008; Falster et al., 2011). Additionally, the effects of canopy gap disturbance on species, functional, and structural diversity were synchronous (Pedro et al., 2017). Thus, the effects of species, functional, and structural diversity on productivity should be considered together when studying the effects of canopy gap disturbance on productivity.

The relationship among species, functional, structural diversity, and productivity is constrained by initial above-ground biomass and environmental factors (Chen et al., 2015). Some studies have suggested that initial above-ground biomass of forest stands is a key driving factor of forest productivity, which indicates that vegetation quantity (i.e., initial above-ground biomass) rather than vegetation quality (i.e., species, functional diversity and structural diversity) plays a major role in

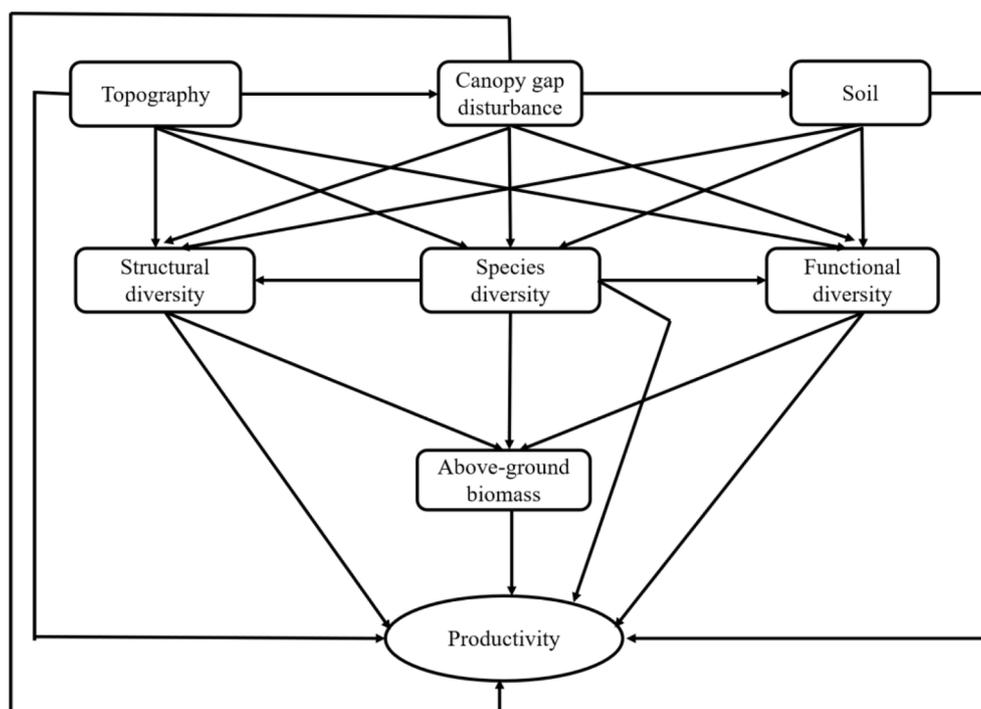


Fig. 1. A conceptual model for linking environmental factors (topography and soil properties), canopy gap disturbance, community diversity variables (species, functional and structural diversity) and productivity in a subtropical evergreen broadleaf forest.

productivity changes (Lohbeck et al., 2015). Environmental change is also a key regulatory factor of forest productivity. Forests in areas with low soil fertility have stronger effects on species diversity than those with high soil fertility (Pretzsch et al., 2013; Toigo et al., 2015). Individual diameter class differences in regions with low soil fertility are small (Ali and Yan, 2017). Terrain heterogeneity of elevation, slope, and aspect directly affect the growth, distribution, and abundance of species (Boerner, 2006; Murphy et al., 2015). To explore the effects of gap disturbance on these relationships, it is necessary to consider initial above-ground biomass, soil nutrients, and terrain.

To explore the effects of canopy gap disturbance on the relationship between community diversity (species, functional, and structural diversity) and productivity, we examined a 20-ha subtropical evergreen broad-leaf forest (EBLF) plot in eastern China. We divided the plot into a canopy gap disturbed quadrat and non-disturbed quadrat and asked (see Fig. 1): (1) whether canopy gap disturbance had significant effects on species, functional, and structural diversity, (2) whether canopy gap disturbance mediated species, functional, or structural diversity that then affected productivity and (3) whether the main drivers of productivity in canopy gap disturbed and non-disturbed quadrats changed.

2. Materials and methods

2.1. Study area and forest inventory

This study was performed in a 20-ha permanent forest plot (500 m × 400 m), located in Tiantong National Forest Park, Zhejiang Province, China (121.78° E, 29.80° N; Fig. 2), which is an evergreen broad-leafed forest dominated by *Fagaceae* and *Theaceae*. The mean annual temperature in this region is 16.2 °C, where the mean temperature of the warmest and coldest months is 28.1 °C in July and 4.2 °C in January, respectively. The mean annual precipitation is 1374.7 mm, which

mostly falls between May and August (Yang et al., 2011). Soils are developed on mesozoic sediments and acidic intrusive rocks, such as quartzite and granite (Wang et al., 2007). In 2008, the snow disaster in China caused a rare natural disturbance in this area, which resulted in many tree crowns breaking and uprooting, and thus, caused multiple canopy gaps.

Following the field protocol of the forest Global Earth Observation (forest GEO) (Condit, 1998), the plot was divided into 500 quadrats (20 m × 20 m). For each quadrat, topographic variables (elevation, slope, and aspect) and soil variables (depth, pH, and nutrient content) were collected (Yang et al., 2011). All free-standing trees and shrubs, with a diameter at breast height (DBH) ≥ 1 cm, were tagged, mapped, measured, and identified to species. The first and second census of the plots were carried out in 2010 and 2015, respectively. In total, two sets of data for 82,406 living individuals (DBH ≥ 1 cm) and 58,500 recruiting individuals (DBH ≥ 1 cm) were analyzed in this study, representing 108 species, 76 genera and 43 families.

2.2. Experimental design for assessing canopy gap

We defined and measured the canopy gap using useful suggestions for specific types of studies (Brokaw, 1982; Popma et al., 1988). Considering that there are two layers of trees in the EBLF plot, the coverage of the second layer of trees is greater than that of the first layer of trees (Song et al., 2011). The first and second layers of trees are treated as boundary trees when determining canopy gaps. In the EBLF plot, 25 transects (dotted line in Fig. 3) were evenly set in the north-south direction every 20 m. Gaps were investigated along the transects. The number of boundary trees, the height of gap (the height of canopy in the gap), and the number and status of the gap forming trees (DBH > 10 cm) were recorded (including overturned trees, dead trees, middle broken trees, and base broken trees) (Zhang et al., 2013). According to

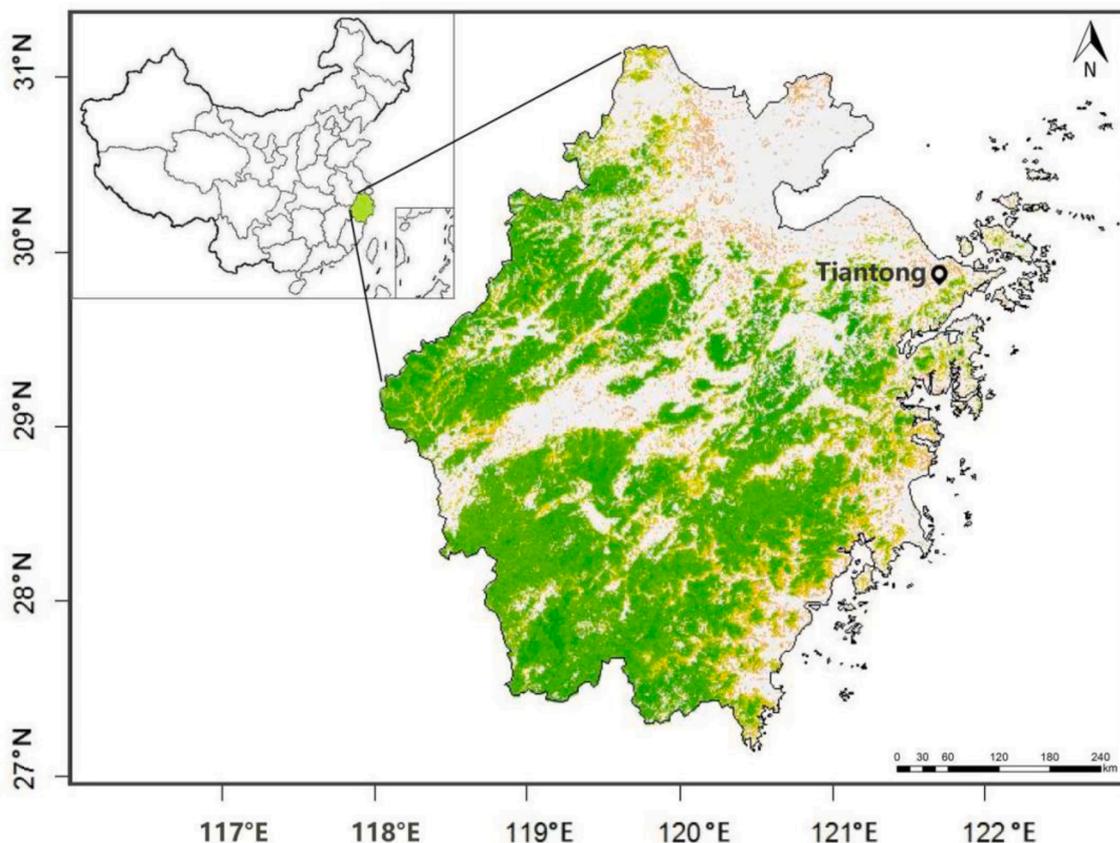


Fig. 2. Location of the study site in Tiantong National Forest Park, Zhejiang Province, China.

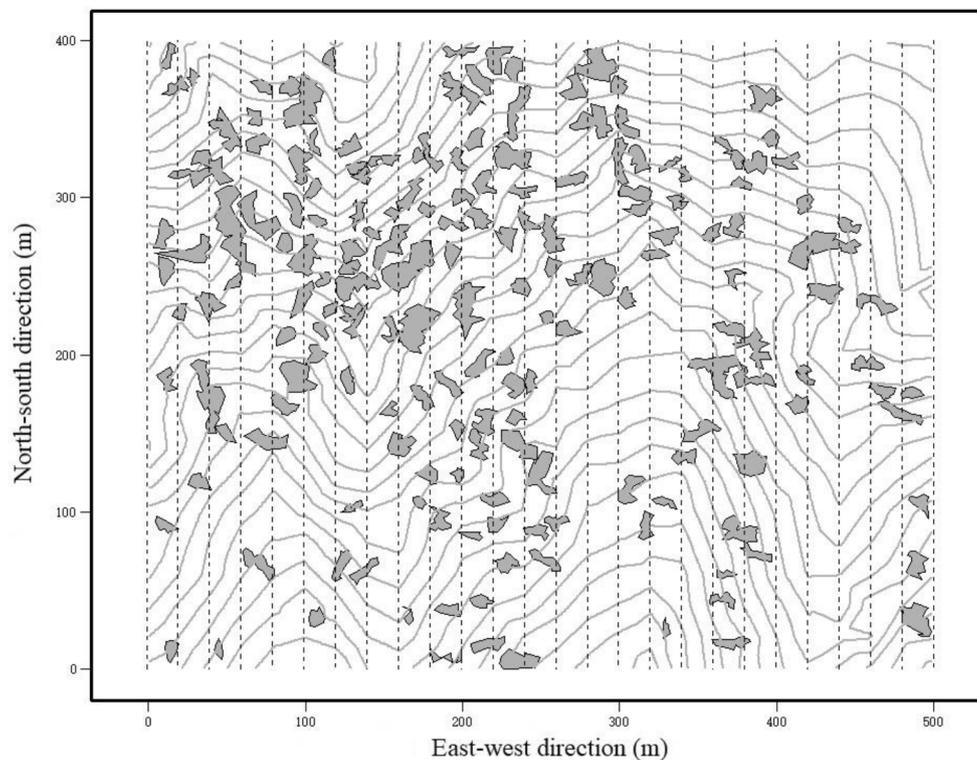


Fig. 3. The distribution of sample lines and gaps in studied forests. Note: Dashed lines represent sample lines, gray shapes represent gaps, and curved lines represent contours.

the coordinates of the boundary trees, combined with ArcGIS 10.0 software, the area of the expanded gaps were drawn. Compared with the expanded gaps, light conditions inside the canopy gap were significantly different from those in the closed stands, and the influence on the growth and regeneration of tree species in the gap was more representative. Therefore, we choose canopy gaps as our research objective (Zhang et al., 2013; Liu et al., 2015). Previous studies showed canopy gap area accounted for about 35.4% of the expanded gap in this region (Jiang et al., 2007; Liu et al., 2015). According to this result, without changing the shape of the gaps, equal proportions of the expanded gaps were retracted to a certain distance from the center, and the canopy gap accounting for 35.4% of the expanded gap was obtained. According to previous research in this region, the minimum area of canopy gap was defined as 45 m² (Jiang et al., 2007).

Changes in diversity indices inside the gap mainly reflect renewal species (Liu et al., 2015; Terborgh et al., 2017a). Only by comprehensively considering changes in diversity indices inside and outside the gap can we reflect the impact of canopy gap disturbance on the community (Seidl et al., 2014; Yuan et al., 2018b). When gap area accounts for more than 10% of the community area (experimental plot), the soil and light in the plot will change significantly, which is conducive to the regeneration of pioneer species, and the growth of trees in the plot will have a significantly different before and after assemblage (Muscolo et al., 2014; Yuan et al., 2018b; Zhao et al., 2020). Previous studies on canopy gap disturbance in this region have obtained similar results (Song et al., 2011).

We classified 500 quadrats (400 m²) into two groups, i.e., (1) quadrat having total gap area more than or equal to 40 m² was defined as the canopy gap disturbed quadrat (DQ), and used "1" to calibrate, and (2) quadrat having total gap area more than 40 m² was defined as the non-disturbed quadrat (NDQ), and used "0" to calibrate. To avoid biases caused by rocks and streams, where trees are permanently absent because of unsuitable habitats, we avoided those quadrats across those locations. By doing so, we used a total of 470 quadrats in the study area

(i.e., 230 DQ and 240 NDQ).

2.3. Aboveground biomass and forest productivity calculation

For the calculation of aboveground biomass (AGB) of each tree, we used species-specific allometric equations for biomass estimation of trees in Gutian Mountain (Lin et al., 2012). We considered that site-specific allometric biomass equations should be used in order to account for the influence of climate (Brown, 2002). In addition, we also showed that AGB calculated using the species-specific equations (Table S2) was nearly equal to the AGB calculated using the pantropical allometric biomass equation (Chave et al., 2014) ($R^2 = 0.95$; Figure S1). The initial above-ground biomass was used to assess the vegetation quantity effects on productivity (Lohbeck et al., 2015; Yuan et al., 2019), which was represented by the sum of biomass of all trees within each quadrat during the first inventory.

We calculated coarse woody productivity (productivity, henceforth, is coarse woody productivity) as the increase in above-ground biomass (AGB) of each tree (DBH \geq 5 cm) during two forest inventories (Eq. (1)), and then summed the productivity values of all trees within a quadrat (Eq. (2)) and scaled-up to Mg ha⁻¹ year⁻¹ (Yuan et al., 2018a).

$$CWP_i = \frac{AGB_{2015i} - AGB_{2010i}}{t_{2015} - t_{2010}} \quad (1)$$

$$CWP_{jk} = \sum_{i=1}^n CWP_i \quad (2)$$

where CWP_i is coarse woody productivity of the i th individual tree in j th quadrat, AGB_{2015i} and AGB_{2010i} is the AGB of the i th individual tree in j th quadrat measured in 2015 and 2010, respectively, where k stands for either DQ or NDQ.

2.4. Species, functional, and stand structural diversity

Species diversity was quantified using species richness and species composition within each quadrat. Species richness was defined as the total number of observed species within each quadrat (Oksanen et al., 2015). Species composition was obtained by non-metric multidimensional scaling analysis (NMDS) (Fortin and Dale, 2008). The first axes of NMDS (NMDS1) were used to maximize the logarithmic transformation correlation with productivity (Figure S2). We calculated NMDS using the R package “Vegan” (Oksanen et al., 2015).

For the quantification of multi-trait functional diversity and community-weighted mean (CWM) trait values, we extracted the functional trait data from existing databases in the study area (Yan et al., 2013). The obtained functional traits were leaf dry mass content (LDMC), specific leaf area (SLA), wood density (WD), and potential maximum DBH of species (max DBH) (Table S3). By doing so, we quantified multi-trait functional diversity indices within each quadrat, i.e., functional evenness (FEve) and functional divergence (FDiv) (Mason et al., 2005; Villéger et al., 2008; Laliberté and Legendre, 2010). The CWM of each functional trait within each quadrat was calculated based on basal-area-weighted averages to represent the functional identity or composition of each species within a quadrat (Díaz et al., 2007). Before the quantification of functional trait diversity indices, we standardized the values of functional traits to a mean of 0 and a standard deviation of 1. The functional trait diversity and CWM indices were calculated using the R package “FD” (Laliberté and Legendre, 2010).

Structural diversity variables used in this study included stand density, DBH layers (DBHs) and DBH Shannon’s diversity index (DBHsi) for each quadrat. Stand density was the number of individual trees in a quadrat, representing the intensity of the plant-plant interactions (Forrester and Bauhus, 2016). DBHs represents quantified structural complexity as the number of the DBH layers in a given quadrat and has a good correlation with tree height and canopy size (Fahey et al., 2015). In this study, DBH classes were divided into 19 grades: [1, 5), [5, 10), [10, 15), [15, 20) [90, ∞). Lastly, DBHsi was tree DBH diversity calculated by Shannon-Wiener biodiversity index (Eq. (3)) (Yuan et al., 2018b), which is commonly used in structural diversity-productivity studies (Ali and Yan, 2017). Calculations of DBHsi were performed using the R package ‘Vegan’.

$$H_d = - \sum_{i=1}^d P_i \times \ln(P_i) \quad (3)$$

where P_i is the proportion of the basal area of i th DBH classes while d is the number of DBH classes within each quadrat.

2.5. Environmental factors

In this study, we considered the effects of topography and soil properties on species, functional, and stand structural diversity as well as on productivity. Topographic factors included elevation, slope, and aspect of quadrats. Specifically, elevation was measured at the four corners of each 20 m × 20 m quadrat using an Electronic Total Station, and the elevation of each quadrat was then defined as the mean value of the four corners of each quadrat (Harms et al., 2001). The slope was defined as the mean angular deviation from the horizontal of each of the four triangular planes formed by connecting three of the corners of each 20 m × 20 m quadrat (Harms et al., 2001; Lai et al., 2009). The aspect was referred to the direction in which the slope faced (Wang et al., 2007). The mean elevation ranged between 304.2 m and 602.8 m, and the mean slope varied from 13.8° to 50.3°.

For the collection of soil samples, we followed standard field protocols (John et al., 2007). More specifically, in March 2011, we selected the southwest corner intersection of each quadrat as the sampling base point, and we then randomly selected one direction from the east, west, south, north, southeast, southwest, northwest, and northeast of each

base point for extended soil sampling. We randomly selected two sampling points at 2 m, 5 m, and 8 m from the base point in the selected direction. By doing so, we established a total of 1310 sampling points with a soil depth of 0–10 cm. We used a 1 m long steel drill rod to measure the thickness of the soil layer at each sampling point. All soil samples were air-dried after collection and passed through a 0.149 mm sieve. Each sieved soil sample was divided into two subsamples. One subsample of 10 mg was used to analyze total carbon (TC) and total nitrogen (TN) by the elemental analyzer (vario MICRO cube, Elementar, Germany). Another subsample of 350 mg was used to analyze total phosphorus (TP) using a flow-injection auto-analyzer (SAN++, Skalar, Netherlands). The soil pH of each soil sample was determined by Mettler Toledo pH meter (1:2, H₂O). Soil values for each 20 × 20 m quadrat were calculated using ordinary kriging.

We performed principal component analysis (PCA) on topographic factors (Figure S3) and soil properties (Figure S4), separately, and then used the first two axes (PC1 and PC2) of PCA in statistical analyses in order to avoid complexity and multicollinearity issues in the models, as suggested by a previous study in this area (Ali and Yan, 2017). A summary of the productivity, AGB, species diversity, functional diversity, structural diversity, and environmental factors used in this paper is provided in Table S1.

2.6. Statistical analyses

First, we used one-way ANOVA to examine the differences for species diversity, functional diversity, structural diversity, initial above-ground biomass, and productivity between DQ and NDQ. In addition, we used simple linear regression analysis to evaluate the bivariate relationships amongst species diversity, functional diversity, structural diversity, initial above-ground biomass, soil nutrients, topography, and productivity (Figure S5). Pearson correlations amongst tested variables are provided in Table S4.

Second, we used multiple regression models to model the influences of all predictors on productivity. To increase normality of the data and to compare the regression coefficients of predictors on productivity, all continuous predictors variables were standardized by the Z-score method (Average = 0, SD = 1), and the response variable or variable of interest (i.e., productivity) was natural-logarithm transformed, following a standard statistical protocol for multiple regression models (Zuur et al., 2009). By doing so, we tested the confounding influences of spatial autocorrelation in productivity among subplots for each of DQ and NDQ by fitting generalized least-square (GLS) models with and without spherical autocorrelation structure for the relationship between each predictor and productivity. We compared the GLS models (spatial and non-spatial) using the Akaike Information Criterion (AIC), and we found that models with spatial autocorrelation structures always had the lowest AIC values (Tables S5-S7). Therefore, we used a spatial synchronous autoregression error model (SARs) (Kissling and Baudoin, 2008) as our multiple regression model. To find the most important drivers of productivity, we tested a full model containing all individual predictor variables. Model selection was then conducted by comparing all possible subsets of models based on corrected Akaike information criterion (AICc) (Table S8-S11), and we considered models having a difference in AICc values less than 2 units equally (Burnham et al., 2010). In the case of multiple model selection, we used a weighted averaging procedure. Model comparison and averaging were conducted using the “MuMIn” R package (Bartoń, 2016). We also evaluated multicollinearity using the variance inflation factor (VIF) for each predictor.

Finally, we used structural equation models (SEMs) to evaluate multiple multivariate relationships amongst canopy gap disturbance, soil nutrients, topographic factors, species diversity, functional diversity, structural diversity, initial above-ground biomass, and productivity. We tested three SEMs based on pooled data from DQ and NDQ, i.e., (1) SEM based on the effects of canopy gap disturbance, as a categorical variable, on predictors and productivity; (2) SEM for DQ; and (3)

SEM for NDQ. In the model structure of the SEM, we evaluated the following main summarized direct paths: i.e., the influences of (1) topography on canopy gap disturbance; (2) canopy gap disturbance on soil nutrients; (3) topography, canopy gap disturbance, and soil nutrients on species diversity, functional diversity, and structural diversity; (4) topography, canopy gap disturbance, soil nutrients, species diversity, functional diversity, and structural diversity on initial above-ground biomass; and (5) topography, canopy gap disturbance, soil nutrients, species diversity, functional diversity, structural diversity, and initial above-ground biomass on productivity. Through this model structure, we also evaluated the direct and indirect effects of predictors on response variables via corresponding mediator(s). We considered the influences of some diversity variables on each other to improve model fit. To evaluate the model-fit to data, we used Chi-square tests with associated P-values (i.e., $P > 0.05$ indicates accepted model), Comparative Fit Indices (CFI, i.e., $CFI > 0.90$ indicates good fit), Goodness of Fit Indices (GFI, i.e., $GFI > 0.90$ indicates good fit), and standardized root mean square residuals (SRMR, i.e., $SRMR < 0.08$ indicates good fit) (Hoyle, 2012). The SEMs were tested using the “lavaan” R package (Rosseel, 2012). All ecological and statistical analyses were conducted in R. 3.6.0 (R Development Core Team, 2019).

3. Results

One hundred seventy-four gaps (irregular polygon in Fig. 3) were found in the ELBF plot, with a combined total area of 23980.87 m². The maximum gap area was 664.04 m², and the minimum gap area was 46.18 m². The gap porosity was 13.1%, and the gap density was 9.5/ha. Among them, 80.1% of the total area and 94.2% of the total number of

gaps were between 45–300 m². The gap density and void fraction in high altitudes (≥ 500 m) were significantly higher than those in middle and low altitudes (< 500 m). The gap density and porosity of the valley was significantly larger than that of the side slope, and the gap area was also significantly larger than that of the ridge and steep slope (Fig. 3).

The average productivity value (5.2 Mg ha⁻¹.year⁻¹) in the canopy gap disturbed quadrats was significantly higher compared to non-disturbed quadrats (4.1 Mg·ha⁻¹.year⁻¹) (Fig. 4A). The average values of species richness (Fig. 4C), CWM of specific leaf area (Fig. 4G) and stand density (Fig. 4K) in canopy gap disturbed quadrats were significantly higher than those in non-disturbed quadrats. Tree DBH diversity (Fig. 4L) in canopy gap disturbed quadrats were significantly lower compared to non-disturbed quadrats. The species composition value was significantly different between canopy gap disturbed (positive value) and non-disturbed (negative value) quadrats (Fig. 4D). There were no significant differences for FEve (Fig. 4F), FDiv (Fig. 4E), CWM of maxdbh (Fig. 4I), CWM of leaf dry mass content (Fig. 4J), CWM of wood density (Fig. 4H) and the number of DBH classes (Fig. 4M) between canopy gap disturbed and non-disturbed quadrats.

Among recruiting individuals, the average values of species richness (Fig. 5A) and stand density (Fig. 5B) in canopy gap disturbed quadrats were significantly higher than those in non-disturbed quadrats. The average productivity value (0.51 Mg ha⁻¹.year⁻¹) in the canopy gap disturbed quadrats was significantly higher compared to non-disturbed quadrats (0.38 Mg·ha⁻¹.year⁻¹) (Fig. 5C). In canopy gap disturbed quadrats, the values of species richness (Fig. 6A), stand density (Fig. 6B) and productivity (Fig. 6C) of the pioneer species in recruiting individuals were significantly higher than those of the non-pioneer species. In non-disturbed quadrats, the species richness (Fig. 6D) of the

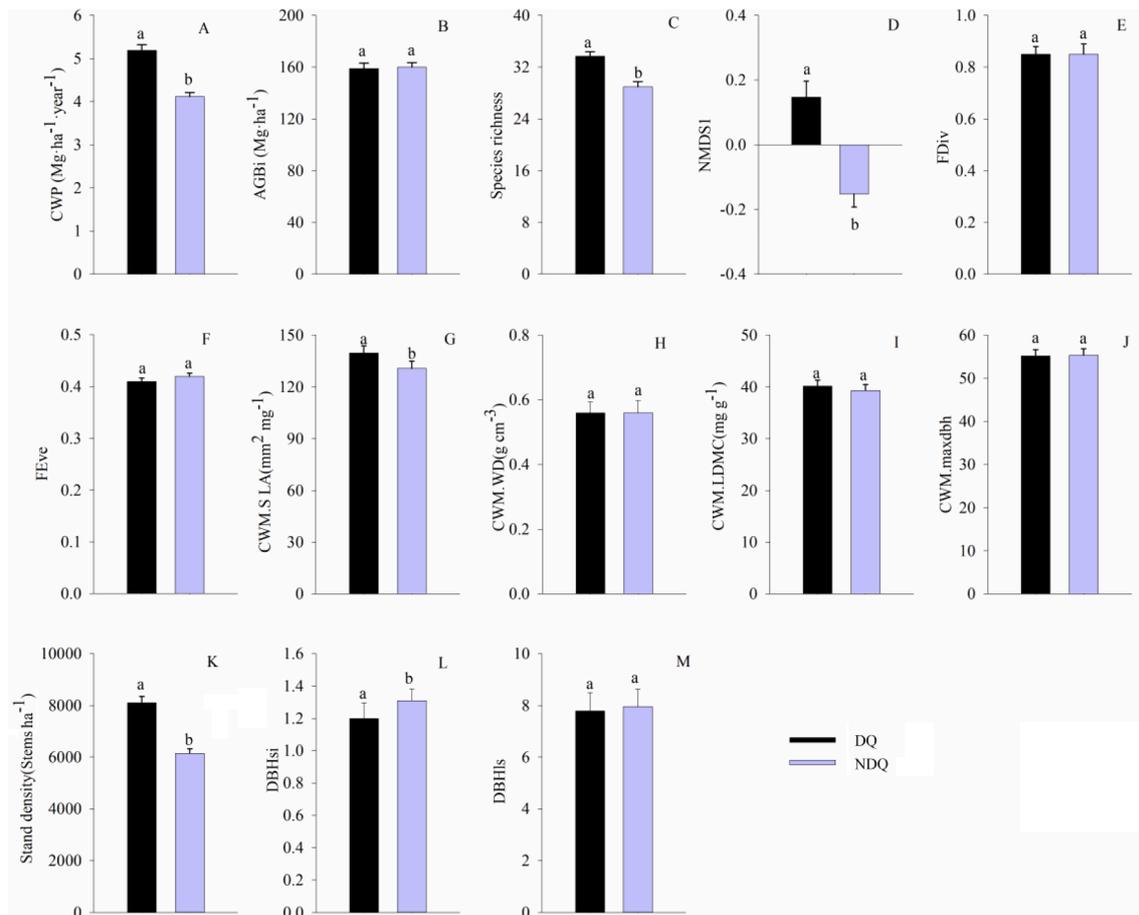


Fig. 4. Comparison of mean values of productivity, initial above-ground biomass, species diversity, functional diversity, and structural diversity between canopy gap disturbed quadrats (black bars) and non-disturbed quadrats (lilac bars).

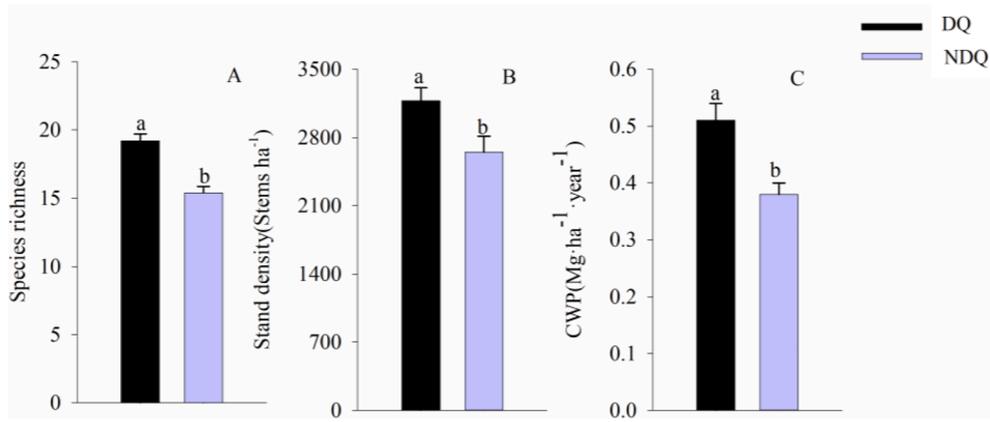


Fig. 5. Comparison of mean values of species richness, stand density, productivity of regenerators between canopy gap disturbed quadrats (black) and non-disturbed quadrats (lilac).

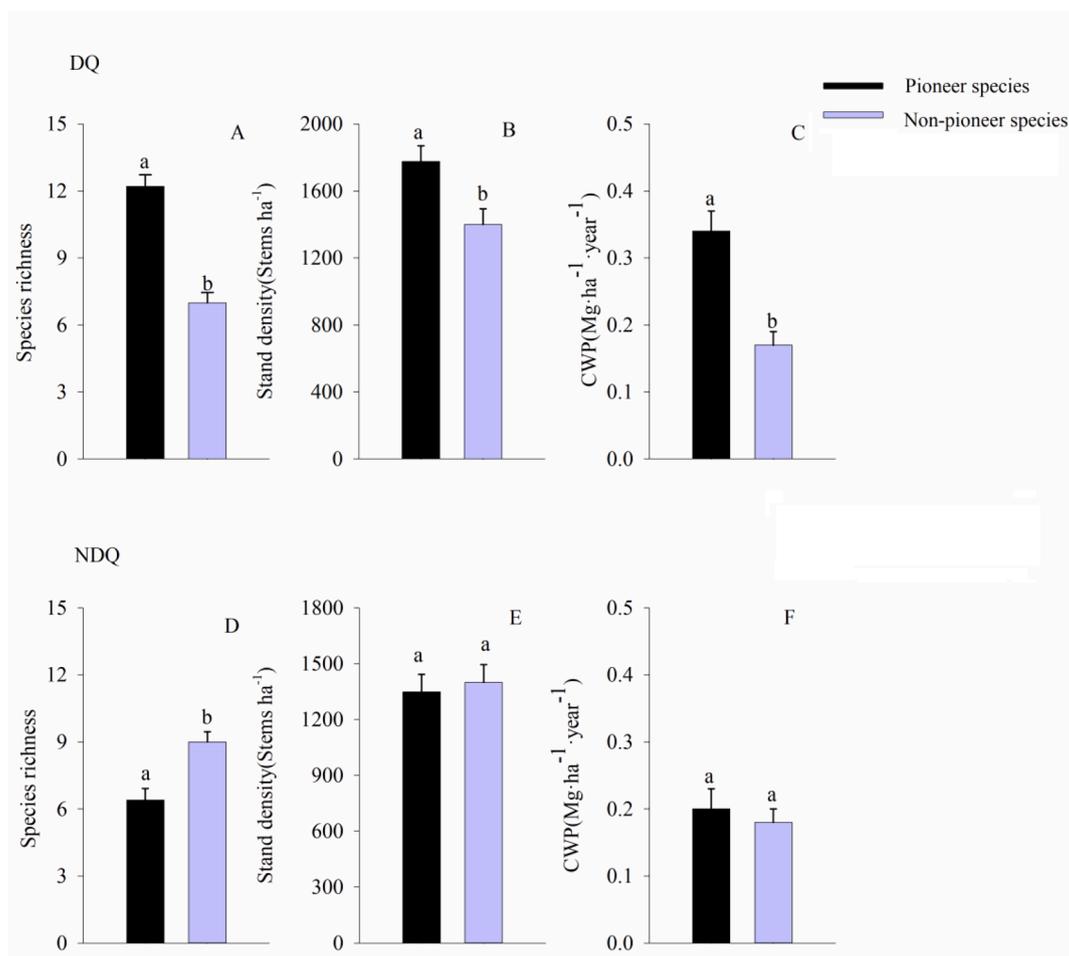


Fig. 6. Comparison of mean values of species richness, stand density and productivity of pioneer (black) and non-pioneer species (lilac). A, B and C are canopy gap disturbed quadrats (DQ); D, E and F are non-disturbed quadrats (NDQ).

pioneer species in recruiting individuals was significantly higher than those of the non-pioneer species, but there were no significant differences for values of species richness (Fig. 6E) and productivity (Fig. 6F) between pioneer species and non-pioneer species.

The SEM for pooled data for testing the direct and indirect effects of canopy gap disturbance on variables showed that all predictor variables together explained 44% of the variance in productivity (Fig. 7A). Canopy gap disturbance had a positive direct effect on productivity ($\beta =$

0.10, $P < 0.001$), and an indirect positive impact on productivity through stand density ($\beta = 0.09$, $P < 0.001$), and an indirect negative impact on productivity through tree DBH diversity ($\beta = -0.03$, $P < 0.001$). The SEMs for canopy disturbed (Fig. 8A) and non-disturbed (Fig. 8B) quadrats showed that all predictor variables together explained 38% and 42% of the variance in productivity, respectively. Across the tested SEMs, stand density increased productivity directly. However, the direct effects of tree DBH diversity, CWM of specific leaf

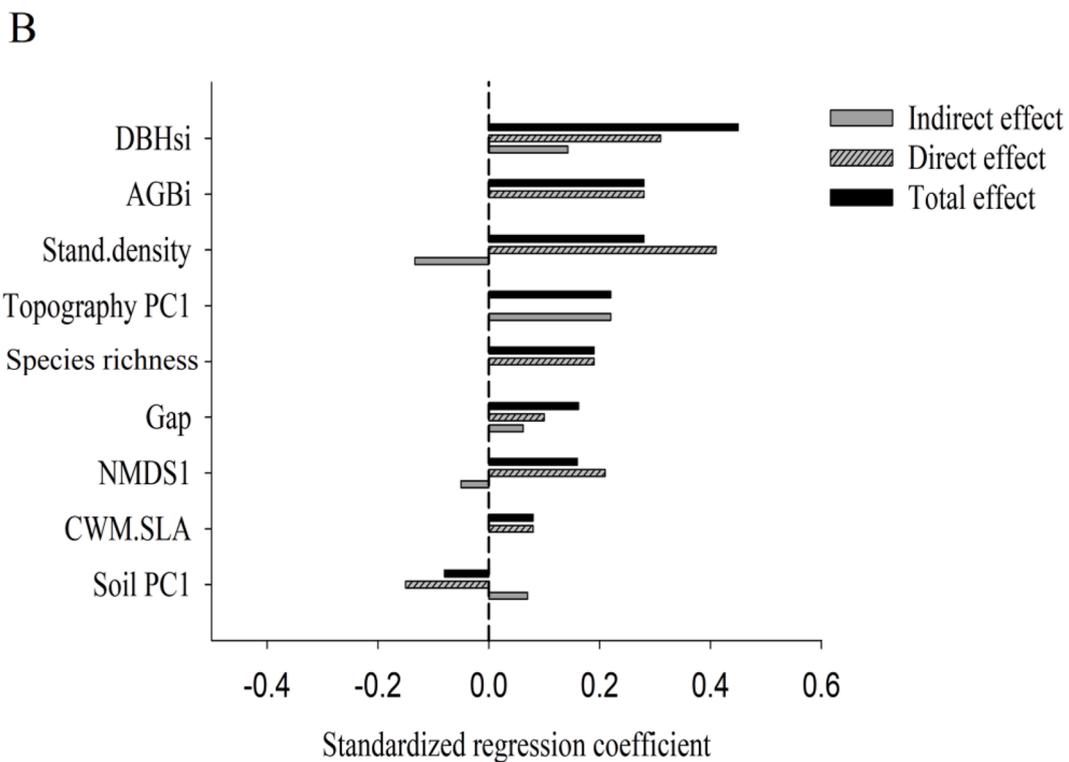
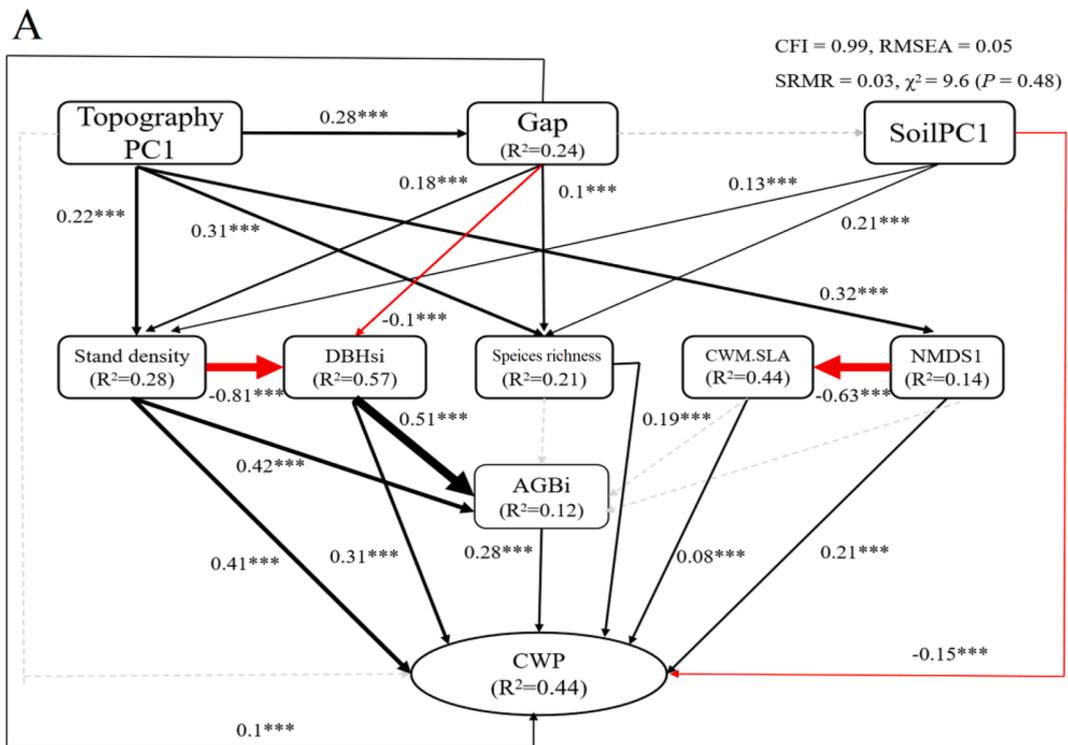


Fig. 7. Structural equation model (A) and standardized effects (B) for overall quadrats. In panel A, solid black arrows represent positive whereas solid red arrows represent negative direct effects. Width of the solid line indicates the strength of the direct effect. The dotted arrows indicate a non-significant effect. Number and its associated asterisks are standardized path coefficient and significance level (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$) for each path. Model-fit statistics are shown in Table S12. In panel B, black hash bar is the direct effect, gray is the indirect effect, and black is the total effect.

area, and species richness and species composition as well as initial above-ground biomass on productivity changed across canopy disturbed and non-disturbed quadrats. More specifically, SEM for pooled data showed that tree DBH diversity increased productivity directly, followed by positive effects of initial above-ground biomass, stand density,

species richness, canopy gap disturbance, species composition, and CWM of specific leaf area. However, SEM for canopy disturbed quadrats showed that productivity was positively controlled by species richness, stand density, and tree DBH diversity only. SEM for canopy non-disturbed quadrats showed that stand density, species compositions,

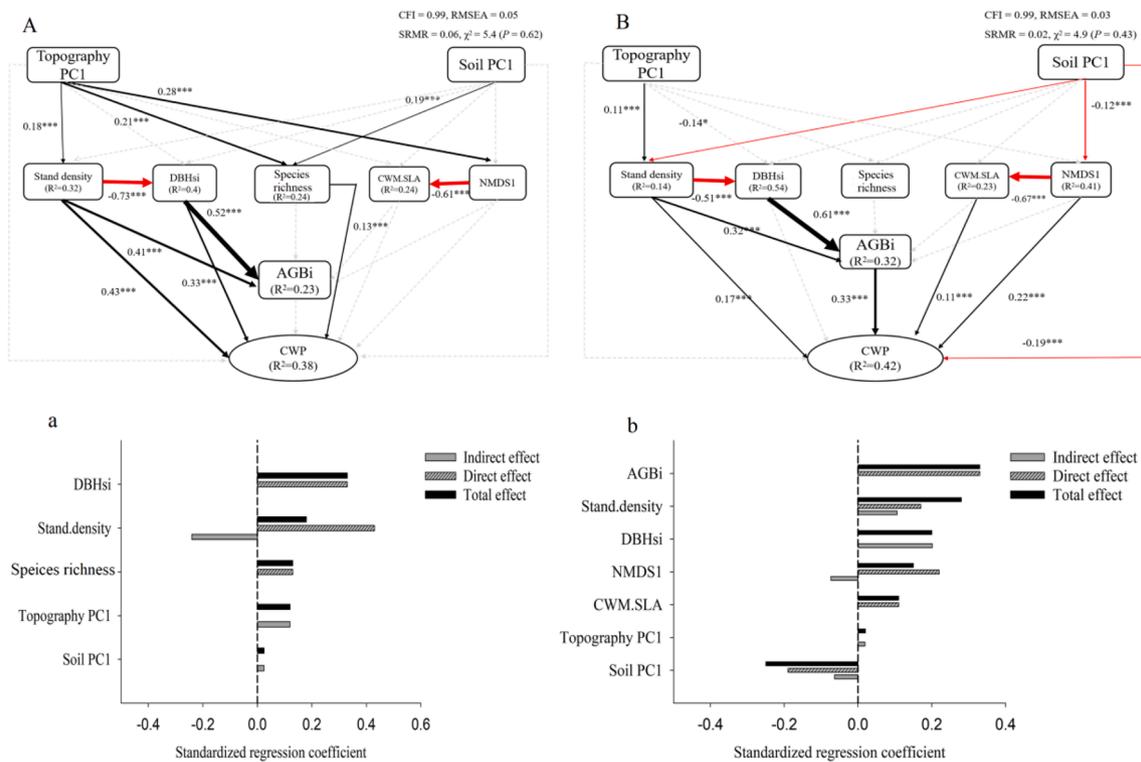


Fig. 8. Structural equation models (A, B) and standardized effects (a, b) in canopy gap disturbed quadrats (A, a) and non-disturbed quadrats (B, b). In panels A and B, solid black arrows represent the positive direct effects whereas the solid red arrows represent negative direct effects. Width of the solid line indicates the strength of the direct effect. The dotted arrows indicate non-significant direct effects. Number and its associated asterisks are standardized path coefficients and significance level ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$) for each path. Model-fit statistics are shown in Table S12. In panels a and b, black hash bar is the direct effect, gray is the indirect effect, and black is the total effect.

initial above-ground biomass and CWM of specific leaf area increased productivity directly. These results indicated that canopy disturbances decreased tree DBH diversity directly, which, in turn, increased productivity more than species composition and CWM of specific leaf area in canopy disturbed quadrats rather than non-disturbed quadrats.

Stand density and tree DBH diversity rather than species composition and CWM of specific leaf area increased initial above-ground biomass across tested SEMs. Stand density decreased tree DBH diversity and, as such, species composition decreased CWM of specific leaf area, despite tested SEMs. Thus, positive and negative indirect effects of tree DBH diversity and species composition on productivity were of additional importance, but these indirect effects changed dramatically in the SEMs for canopy disturbed and non-disturbed quadrats. In addition, the direct effects of topography on productivity were non-significant, but, the direct negative effect of soil nutrients on productivity was significant. Also, the indirect effects of topography and soil nutrients on productivity via multiple mediator predictors were significant.

4. Discussion

We investigated the effects of canopy gap disturbance on the relationships between community diversity and productivity in a subtropical forest. We found that canopy gap disturbance increased species richness, stand density, and productivity and also caused changes in species composition yet decreased tree DBH diversity and CWM of specific leaf area. The SEM for pooled data showed that species richness, species composition, CWM of specific leaf area, stand density, tree DBH diversity, initial above-ground biomass, and canopy gap disturbance had significant effects on productivity. But, the SEM for canopy gap disturbed quadrats showed that productivity was positively correlated to species richness, stand density, and tree DBH diversity only. The SEM for canopy non-disturbed quadrats showed that stand density, species

compositions, initial above-ground biomass, and CWM of specific leaf area increased productivity directly. This indicates that the relationship between community diversity and productivity is strongly responsive to canopy gap disturbance.

4.1. Species, functional, and structural diversity changes in response to canopy gap disturbance

We found that canopy gap disturbance increased species richness and altered species composition. An increase in species richness caused by canopy gap disturbance was related to a large number of pioneer species supplementation because canopy gap disturbance changes the micro-environment in the forest in favor of the growth of pioneer species (Pedro et al., 2017). The increase of species richness will inevitably lead to changes in species composition (Schnitzer and Carson, 2001; Terborgh et al., 2017b). In addition, canopy gap disturbance in this study resulted in a decrease in the CWM of specific leaf area. This may be related to the CWM changes from conservative traits toward more acquisitive traits. Canopy gap disturbance intensities promoted species with low leaf construction costs (i.e. high LDMC), poorly-defended leaves (i.e. low leaf toughness), and short leaf life span (Kitajima and Poorter, 2010; Onoda et al., 2011). Such species also had high SLA and leaf nitrogen concentrations (Carreño-Rocabado et al., 2012).

The decrease of tree DBH diversity in the canopy gap disturbed quadrats was related to an increase in stand density. Regeneration caused by canopy gap disturbance promotes increases in stand density (Terborgh et al., 2017a), and we obtained similar results. However, regeneration trees (DBH is smaller) reduces the evenness of the diameter class, which leads to decreases in tree DBH diversity (Forrester, 2019). But, the regeneration of small trees improves the canopy filling in the understory (Chiang et al., 2016). Therefore, the decrease of tree DBH diversity caused by canopy gap disturbance can be understood to

optimize light resources in the understory and promote the complementarity effect of light resources in the overstory and understory (Fahey et al., 2015; Ali, 2019).

4.2. Structural diversity mediates the effects of canopy gap disturbance on productivity

Interestingly, canopy gap disturbances had an indirect effect on productivity but only through species richness and structural diversity (stand density and tree DBH diversity). This indicates that the effect of canopy gap disturbance on the relationship between community diversity and productivity mainly depends on the effect of canopy gap disturbance on species richness and structural diversity. Generally, in later stages of successional development, superior competitive species dominate the ecosystem and strongly limit the relative abundance of other species, i.e., competitive exclusion occurs (Paquette and Messier, 2011; Lasky et al., 2014b). Canopy gap disturbances, here, acted as a disruption of the exclusion processes, freeing up resources for other species, and, consequently, increased species richness and structural diversity (Franklin et al., 2002; Shea et al., 2004). This indicates that canopy gap disturbance can promote species niche differentiation, improve resource utilization, and enhance the impact of niche complementarity on productivity.

4.3. Main drivers of productivity in canopy gap disturbed and non-disturbed quadrats

We found that the initial above-ground biomass dominated changes in productivity in non-disturbed quadrats, but there were non-significant relationships between initial above-ground biomass and productivity in the canopy gap disturbed quadrats. This may be related to the canopy gap disturbance breaking the asymmetric competition dominated by large-diameter trees (Fahey et al., 2015). Generally, biomass increases (productivity) exponentially with tree diameter at the tree scale, and large trees in overstory strata, thus, contribute disproportionately to productivity compared with small trees in natural forests (Poorter et al., 2015). In high-density canopy forests, the growth of understory trees is often suppressed by canopy trees due to lack of light (Gough et al., 2013; Ali and Yan, 2017). Thus, productivity is often controlled by large-diameter trees (Fahey et al., 2015). However, in the canopy gap disturbance quadrat, gaps enhanced the light intensity of the understory, promoted the growth of the understory trees, and made the understory and upper forest form complementary utilization of light resources. Thus, the effect of asymmetric competition on productivity was reduced, and the effect of initial above-ground biomass on productivity was non-significant.

4.4. Effects of environmental factors on canopy gap disturbance, community diversity, and productivity

Topography had significant effects on canopy gap disturbance, stand density, and species richness, which indirectly affected productivity. However, the effect of topography on stand density and species richness mainly occurred in the canopy gap disturbed quadrats. This may be due to the complex terrain conditions of the ELBF plot, which not only affected the distribution of forest gaps but also affected the spatial distribution of regenerators. Good site conditions indicated favorable resource supply (e.g. soil fertility and water availability) (Toigo et al., 2015; Forrester and Bausch, 2016). This indicates that the canopy gap disturbed quadrats provides better growth environments for small trees and regenerators, thus, improving the productivity at the stand level (Muscolo et al., 2014).

The soil fertility hypothesis predicts that productivity increases with increasing soil nutrient availability and that plants grow faster when resource availability is high (Wright et al., 2011; Quesada et al., 2012). However, high nutrient availability may also lead to increased

competition, and, thereby, higher mortality and biomass turnover rates of plants (Prado-Junior et al., 2016). Consequently, high productivity in subtropical forests is often associated with nutrient-poor soils (Poorter et al., 2015; Chiang et al., 2016). In this study, we also found that nutrient enhancements decreased species composition and stand density in non-disturbed quadrats. This mismatch between the soil fertility hypothesis and the empirical pattern is potentially due to an interaction between tree size and niche overlap among canopy tree species (Prado-Junior et al., 2016). Large diameter class trees in overstory strata may integrate available resources by increasing niche overlap with functionally similar tree species and by reducing the niche complementarity with functionally dissimilar tree species (Ali and Yan, 2017).

5. Concluding remarks

Our results provide strong evidence for the effect of canopy gap disturbance on the relationship between biodiversity and productivity in a subtropical forest. In the late-successional forest, understory trees are generally long suppressed, which leads to forest productivity dominated by individuals with a large diameter in the overstory. However, canopy gap disturbance provides a good growth environment for suppressed trees in the understory and reduces the impact of large-diameter trees on productivity. We argue that canopy gap disturbance reduces competition and promotes complementary utilization of resources, thus enhancing the impact of niche complementarity on productivity through species richness, stand density, and structural diversity.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119740>.

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