# Changes in biotic and abiotic drivers of seedling species composition during forest recovery following shifting cultivation on Hainan Island, China

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## ABSTRACT

Seedlings play an important role in the processes of plant community succession. We compared seedling (dbh  $\leq 1$  cm) species composition and diversity over a chronosequence (18-, 30-, 60-year-old second growth and old growth forest) after shifting cultivation in a tropical lowland rain forest area on Hainan Island, China. Seedling diversity reached a maximum in the 60-year-old second growth forest, which is consistent with the intermediate disturbance hypothesis. With the progression of secondary succession, canopy openness (CO), soil organic matter, soil phosphorus content, and tree abundance showed a general decreasing trend; soil water content and tree basal area showed a general trend of increase, while soil pH and other nutrients reached maximum values and tree richness reached a minimum value at intermediate stages of succession. Seedling composition and diversity were significantly affected by soil water, pH, soil nutrient content, and biotic factors in the 18-year-old second growth forests; by soil pH, soil nutrient content, and biotic factors in the old growth forests. At earlier stages of succession, the effect of the proportion of old growth forest in the surrounding landscape on seedling diversity was greater than that of land-use history, but the importance of these drivers was reversed at later stages of succession.

Key words: abiotic factors; biotic factors; landscape; seedlings; tropical secondary forest.

THE KNOWLEDGE OF THE RECOVERY DYNAMICS OF PLANT COMMUNITIES IS ESSENTIAL for understanding the underlying processes that govern the future direction of forest succession and restoration. There is a general consensus that landscape changes are among the key drivers of local species and community dynamics (Jakovac *et al.* 2015). Landscape patterns determine the general environmental conditions and connections between different vegetation types and thus greatly influence seed dispersal and other related regeneration dynamics of plant communities (Martínez-Ramos *et al.* 2016). Landscape structure and juxtaposition could significantly affect the composition and succession of different patch types within a forest area (Hernández-Stefanoni *et al.* 2011). Seedling dynamics are major drivers of successional trajectories and can reflect both dispersal (as influenced by the landscape) and local environmental conditions (Chazdon & Guariguata 2016).

In tropical regions, forest landscape patterns have dramatically changed due to extensive, high-intensity anthropogenic activities and climate change (Chazdon 2003). Most primary forest landscapes have been fragmented into mosaics composed of forest patches that vary in size, shape, and disturbance history. Landscape fragmentation can have dramatic impacts on seedling dynamics, which can determine the future species composition, community structure, and long-term dynamics of forest

Received 7 April 2016; revision accepted 16 August 2016. <sup>3</sup>Corresponding author; e-mail: zangrung@caf.ac.cn ecosystems (Alvarez-Buylla & Martínez-Ramos 1990, Benitez-Malvido 1998, Comita *et al.* 2010). Fragmentation increases the fraction of edge zones, creating environmental conditions that could promote the establishment of pioneer and light-demanding species (Hernández-Stefanoni & Dupuy 2008). Some studies suggest that the interactive effects of landscape changes may influence seedling recruitment and composition.

In contrast, seedling dynamics can influence and contribute to the structure and mosaic dynamics of forest landscapes. For example, Comita *et al.* (2010) monitored seedlings in a humanand hurricane-impacted forest in northeastern Puerto Rico over an approximately 10-year period and found that the composition and diversity of seedlings were significantly related to land-use history and landscape changes. In mixed temperate forests, canopy-seedling feedback could contribute to the maintenance of a stable landscape structure (Catovsky & Bazzaz 2002).

A number of studies on changes in species composition and diversity have been carried out to explain the mechanisms of forest succession (Chazdon 2008b). Forest succession is a stochastic process resulting from the behavior of component populations and species (Chazdon 2008a). Most of the current knowledge regarding the dynamics of diversity during succession is based on chronosequence studies, in which plots at different times since abandonment are used to represent different stages of similar successional development (van Breugel 2007). This 'space-fortime' approach allows studies to be conducted in a year or two that would otherwise take decades or longer. Although drawbacks exist, this approach has provided extensive information on successional patterns in plant species composition, plant functional traits, and functional diversity in tropical forests (Purschke et al. 2013, Laliberté et al. 2014, Helsen et al. 2015, Laughlin et al. 2015). Species diversity may vary considerably during succession, depending on biophysical conditions, landscape context, and other factors. Through the course of succession, attributes of secondary forests are gradually recovered to those of old growth forests, such as high species diversity, structural complexity, and a balance between community production and respiration, although changes in these attributes do not occur at the same rates (Chazdon 2014). Seedling dynamics in tropical forests are driven by many abiotic and biotic factors, including light availability, soil nutrients, and interactions with enemies (Comita et al. 2009, Vandecar et al. 2009, Jurinitz et al. 2013). During early successional stages, light is not as limiting, and, therefore, other factors, such as the tree species present and the availability of soil nutrients and water, are more important; however, later in succession, light becomes more limiting than soil factors or the abundance of trees (Lebrija-Trejos et al. 2011). Among the biotic processes related to seedling performance during succession, several are related to the density of neighboring adult trees. It is hypothesized that negative density dependent mortality could promote coexistence by reducing the abundance of competitive dominants (Jurinitz et al. 2013, Shuai et al. 2014).

Seedling establishment is generally the most important stage in the regeneration of trees. Species composition and diversity studies at the seedling stage-the most vulnerable stage of the plant life cycle-can provide a useful way to obtain an overview of the potential community shifts in species diversity (Pérez-Ramos et al. 2012). Several studies highlight the importance of seedlings in plant community assembly and landscape restoration. Capers et al. (2005) analyzed changes in woody seedling communities over 5 yrs in four second growth forests in Costa Rica, and the results demonstrate the importance of seedling recruitment and mortality in determining the course of succession. Ceccon et al. (2004) found that the effects of low nutrient availability combined with low light availability determine forest succession in Yucatán, Mexico. Comita et al. (2010) explored the effects of land-use history on seedling dynamics and found that land-use history had significant effects on the composition and diversity of seedlings. Seedling regeneration patterns can determine the future species composition, community structure, and long-term succession patterns in forest ecosystems. The seedling pool is the most important component of any vegetation development process across a heterogeneous landscape (Lu et al. 2014). Studies of seedling regeneration will be useful in assessing the quality and rate of forest regeneration in different vegetation patches, so information on seedling dynamics might be used in activities and strategies for large-scale landscape restoration. Previous findings on changes in species diversity during forest succession have come almost exclusively from saplings and adult plants. Little knowledge exists regarding the patterns of changes in species diversity for small seedlings (dbh < 1 cm) during tropical forest succession, although their role in the maintenance of diversity has been widely recognized (Potter & Woodall 2012, Muscarella et al. 2013, Dhakal et al. 2015).

In this study, we report the differences in the species diversity of tree seedlings during succession in a tropical lowland rain forest on Hainan Island, South China. On Hainan Island, shifting cultivation has been the main land-use type in lowland (<800 m) areas (Ding et al. 2012). Due to long-term intensive agricultural land use, the area of primary forests has been greatly reduced, resulting in landscape mosaics of a few old growth forest patches dispersed in the large matrix of secondary forests at various stages of recovery. The area where our investigation plots were located has been mainly used for cultivating Manihot esculenta. After about five cycles of shifting cultivation, the soil lost a great proportion of its nutrients, and shifting cultivation was no longer profitable for the local people (Hu & Li 1992). The establishment of the Bawangling National Nature Reserve in 1980 protected large areas of the shifting cultivated lands, which are currently undergoing a natural recovery process. These lands were abandoned after the last shifting cultivation ended in 1999, which allowed most of the lands to naturally recover, so there are extensive areas of second growth forests in the lowland areas of the reserve. We address the following questions: (1) What are the patterns of variation in the abiotic and biotic conditions in the forest understory during shifting cultivation in the tropical lowland rain forest? (2) Do seedling composition and diversity change significantly during the recovery process? (3) Which abiotic and biotic factors control seedling composition and diversity at each stage of recovery? (4) Are landscape features correlated with seedling richness and diversity?

We hypothesize that the environment changed from hot, sunny, and dry during initial stages of fallow regrowth to cooler, shady, and moist conditions decades later. We further expect that the tree diversity increased first and then decreased during succession following the intermediate disturbance hypothesis (IDH; Connell 1978). We considered the IDH to apply if seedling diversity (richness and abundance) shows a peak in the middle successional stage. We hypothesize that different environmental factors play different roles in determining seedling diversity during the different stages of succession. In early succession, seedling diversity may be closely related to soil water content (SWC), which is a limiting factor in this successional stage. However, later in succession, light becomes more limiting than other factors, so seedling diversity may be affected by light conditions. We hypothesize that seedling regeneration is confined by the landscape context around the second growth and old growth forests due to the effects on seed dispersal. We considered that land-use history and the proportion of old growth forest would determine the rate of forest recovery and the species diversity of secondary forests.

#### METHODS

STUDY SITES.—The study site is located in tropical lowland rain forest (<800 m asl) in the Bawangling National Nature Reserve (18°52′–19°12′ N, 108°53′–109°20′ E) on Hainan Island, China, which is at the northern edge of the Asian tropical forest zone.

The study area receives a mean of 1677 mm of rainfall per year, most of which falls during the 7-month wet season from April to October. The mean annual temperature is 23.6°C. The lowland area of the study site is mainly dominated by secondary forest recovering from shifting cultivation and logging, while some fragments of old growth forest are scattered across the landscape in low elevation areas. In the lowland areas of the reserve, tropical lowland rain forest is the major vegetation type, dominated by species from the families of Dipterocarpaceae, Fagaceae, and Lauraceae. This study areas were covered by tropical lowland rain forest of different recovery stages.

The landscape of the Bawangling National Nature Reserve is a mosaic of natural vegetation and plantations, in which natural tropical forests occupy a greater area. Most of the primary forest landscapes have been fragmented into mosaics composed of secondary forest patches at different stages of recovery. Prior to 1960, deforestation occurred primarily owing to hurricanes, insects, and traditional low-intensity shifting cultivation by the indigenous people. Starting in 1960, commercial timber harvesting became the major mode of deforestation. In the 1980s, due to decreased tropical forest resources, timber harvesting changed from clearcutting to selective logging. Due to severe and repeated human disturbances over the past 40 yrs, the forest landscapes in the Bawangling National Nature Reserve became increasingly fragmented, and the old growth forests were replaced by secondary forests at different stages of recovery. Since 1994, timber harvesting was banned to protect and restore the degraded forests. Following the logging ban, second growth forests in the Bawangling National Nature Reserve have been naturally recovering. At present, most of the forests in the study region are secondary forests at different stages of recovery, and only a few areas of primary vegetation types have been preserved.

FIELD INVESTIGATION.-The field investigation was conducted in tropical lowland rain forest that has naturally recovered after shifting cultivation in areas at four different stages of succession (18-year-old second growth forest, 30-year-old second growth forest, 60-year-old second growth forest, and old growth forest). In the lowland rain forest area of our study region, approximately 70 percent is secondary forest that has regenerated on abandoned shifting cultivation land, 25 percent is secondary forest that has regenerated from commercially logged forest (mainly through clearcutting), and 5 percent remain as old-growth forest fragments (Zang personal estimation after discussion with local foresters). All of the disturbed forests were allowed to follow their natural successional trajectories. Our earlier studies have measured tree species data from the same chronosequence of forests (Ding 2006, Bu et al. 2014), in which two replicate sites were selected from each of the four successional stages. In the present study, 25 seedling plots  $(2 \times 2 \text{ m})$  were randomly sampled near the tree investigation plots at each site. At each site, plots were separated by more than 20 m. All of the plots were surrounded by secondary or old growth tropical lowland rain forest. Information on the history of land-use for the plots was obtained from the management records of the Bawangling National Nature

Reserve. All of the plots are located on low hills with slopes of approximately  $15^{\circ}$ , and their elevations range from 412 to 626 m. Earlier studies indicated that only a few families, genera, and species dominated the early stages of vegetation recovery on the abandoned lands of shifting cultivation and that deciduous species occurred at a rather high percentage in the community during the early recovery stages compared with the older secondary or old growth forests (Ding *et al.* 2006, Bu *et al.* 2014). All woody seedlings (trees, shrubs, and lianas) with dbh < 1 cm in these plots were tagged, identified to species, and their heights were measured.

ENVIRONMENTAL FACTORS.—At the center of each plot, hemispherical canopy photographs were taken at 1 m above the ground level using a fish-eye lens (HMV1v8; Delta-T Devices Ltd, Cambridge, U.K.) mounted on a tripod. Canopy cover was measured from each photograph as the percentage of closed-canopy pixels using the Gap Light Analyzer software (Burnaby, British Columbia, Canada, http://www.rem.sfu.ca/forestry/publications/downloads/ gap\_light\_analyzer.htm). This provided an approximate measure of the percentage of transmitted diffuse and direct radiation in the understory. Canopy openness (CO, %) = 1 – canopy cover.

We collected two soil samples at a depth of 0-20 cm from the center of each plot during the dry season (in April) over the course of 3 d to measure soil characteristics. There had been no rainfall for more than 3 wks prior to sampling. One fresh soil sample was weighed immediately after extraction, dried at 105°C to a constant weight and weighed again to determine SWC (%). The other soil sample was used for nutrient analysis and was dried at ambient temperature in the lab to prevent the volatilization of nitrogen compounds that can occur when samples are dried at high temperatures. The measurements included soil pH, soil organic matter content (SOM, g/kg), total nitrogen content (TN, g/kg), total phosphorus content (TP, g/kg), total potassium content (TK, g/kg), available nitrogen content (AN, mg/kg), available phosphorus content (AP, mg/kg), and available potassium content (AK, mg/kg). Soil pH was measured in a standard solution made of one volume of soil diluted in three volumes of water (Anderson & Ingram 1989). SOM was determined using the K<sub>2</sub>Cr<sub>2</sub>O<sub>7</sub>-H<sub>2</sub>SO<sub>4</sub> oxidation method. Soil TN, TP, and TK were measured by the Kjeldahl method, the molybdenum-antimony colorimetric method, and the sodium hydroxide meltdown method, respectively. Soil AN, AP, and AK were measured by the alkali hydrolyzation, NaHCO3 and NH4OAc and blaze photometer methods, respectively (Anderson & Ingram 1989).

BIOTIC FACTORS.—To quantify the effect of adult trees on seedling diversity, we calculated tree species richness, abundance, and the basal area of all adult stems (dbh  $\geq 1$  cm) as biotic factors in each tree plot from the same chronosequence of forests.

DATA ANALYSIS.—For each plot, we calculated the total number of seedling and tree individuals (abundance) and the rarefied species richness. The rarefied species richness was calculated using the 'rarefy' function in the 'vegan' library in R (R Development Core

Team 2014). To test the spatial autocorrelation between the plots at the same successional stage, we performed a Mantel test using the 'mantel.test' function in the 'ade4' library (Dray & Dufour 2007) in R. We set seedling species richness and abundance as the response variables in the spatial correlation analysis. The number of permutations was set at 999. Based on the results of Mantel test, we can reject the null hypothesis that there was spatial autocorrelation among the plots. The test (all the P > 0.05) suggests that the sampled sites were spatially independent (Table 1). Thus, spatial autocorrelation is not a problem in our further analyses.

To assess whether seedling species richness and abundance were significantly different among the four successional stages, we used one-way analysis of variance (ANOVA). In addition, we classified the species in the studied forest into three regeneration groups based on observations and flora references regarding the tree crown light environments of both tree and seedling species (Bongers et al. 2009). Early successional species are generally exposed to high light levels, notably so as seedlings. Non-pioneer light-demanding species tend to be shaded as seedlings and illuminated when mature, and both seedlings and trees of shadetolerant species can tolerate shaded environments. We then calculated the seedling species richness and abundance of the three regeneration groups at the different successional stages. We also calculated the relative abundance of the seedlings of the major species at the different successional stages. We then calculated the relative dominance of the seedlings of the major species as follows: relative dominance = seedling species height/seedling total height × 100 percent (Fei & Steiner 2009).

Differences in abiotic and biotic factors among the four successional stages were assessed using one-way ANOVA. If the variation was significant ( $P \leq 0.05$ ), we further performed Tukey honest significant difference multiple comparison tests to determine which stages were significantly different. A principal components analysis (PCA) of abiotic and biotic factors was conducted to examine their coordinated variation with succession. All data were log transformed to improve normality and the equality of variances. To assess the collinearity among predictor variables, we used the 'corvif' function in R supplied by Zuur *et al.* (2009). The variance inflation factors (VIFs) values were used to detect

TABLE 1. The results of the Mantel test among the seedling sample plots.

	Species rich	ness	Abundan	Abundance		
Forest age	Observation	Р	Observation	Р		
18-year-old second growth forest	0.09	0.06	0.047	0.15		
30-year-old second growth forest	0.01	0.45	-0.004	0.52		
60-year-old second growth forest	-0.02	0.66	-0.08	0.98		
Old growth forest	0.01	0.42	0.05	0.18		

collinearity. There is no collinearity in these variables when all VIF values  $\leq 3$ .

To determine the relative importance of different abiotic and biotic factors in shaping species richness and abundance, multiple regression was performed using the model selection procedure in the Spatial Analysis in Macroecology (SAM) 4.0 software (Rangel et al. 2010). The response variables were seedling species richness and abundance, and the explanatory variables were the following measured environmental and biotic factors: CO, SWC, soil organic mass, TN, TP, TK, AN, AP, AK, rarefied tree richness, tree abundance, and tree basal area. The model selection process in SAM calculates all possible combinations of the explanatory variables and ranks these models from best to worst according to their Akaike information criterion (AIC) values. We considered all models with a delta AIC < 4 as equally informative and determined the importance of the explanatory variables for each response variable. In view of the fact that landscape factors can affect seedling regeneration (Schreeg Laura et al. 2005), we considered the proportion of the surrounding landscapes covered by old growth forest and land-use history to be two important factors. The proportion of the surrounding landscapes within a 1 km buffer of the study plots that were covered by old growth forest was calculated in ArcGIS 8.3 (ESRI, Redlands, CA, USA). The land-use history could be classified into the following two types: shifting cultivation that is now covered by regenerating second growth forest and land with very little anthropogenic disturbance that is now covered by old growth forest. We added the proportion of the landscape covered in old growth forest as a continuous covariate and the land-use history as a categorical covariate in the SAM model selection procedure.

We performed a non-metric multidimensional scaling (NMS) analysis based on Chao (Chao *et al.* 2005) dissimilarity values for each successional stage using the 'metaMDS' function in the 'vegan' library of R (R Development Core Team 2014). NMS is commonly regarded as the most robust unconstrained ordination method in community ecology (Minchin 1987). The function metaMDS in R attempts to find a stable solution using several random starts. In addition, it standardizes the scaling of the result so that the configurations are easier to interpret and adds species scores to the site ordination. We used analysis of similarities (ANOSIM) to test whether species composition differed among the four successional stages using the 'anosim' function in the 'vegan' package in R.

#### RESULTS

SEEDLING SPECIES RICHNESS AND ABUNDANCE.—The general trend in the change in diversity (species richness and abundance) with succession revealed a bimodal pattern, with peak values in the 60-year-old second growth forest. The rarefied species richness of the 30-year-old second growth forests was lower than that of the 18-year-old second growth forest, and species richness was highest in the 60-year-old second growth forest. The species richness of younger forests (18 and 30 yr) was significantly lower than that of older forests (60 yr and old growth, which were not significantly different) (Fig. 1A). The pattern of variation in seedling abundance was similar to that of species richness. The abundance was highest in the 60-year-old second growth forest, although the abundances in the earlier three successional stages were not significantly different (Fig. 1B). Compared with the 18and 60-year-old second growth forests, the seedling abundance in the old growth forest was significantly lower.

SEEDLING COMPOSITION.—The species diversity of the different regeneration groups reached a peak during different stages of succession (Table 2). Species richness (59.3%) and abundance (47.3%) of the early successional species showed high peaks in the 18-year-old second growth forests. Non-pioneer light-demanding species showed a high peak in the 30- and the 60-year-old second growth forests. Shade-tolerant species were most abundant in the old growth forest, where the percentages of shade-tolerant species in terms of richness and abundance were 59.0 percent and 74.8 percent, respectively.

The dominants in the seedling and canopy layers were different in the 60-year-old second growth forest (Ding 2006, Bu et al. 2014), while they were similar at other stages of succession. The dominant seedling species differed across successional stages (Table S1). In general, some light-demanding pioneer species, such as Cratoxylum cochinchinense and Aporosa dioica, were dominant in both the seedling and tree layers in the 18- and the 30-year-old second growth forests. Shadetolerant species, such as Vatica mangachapoi and Cyclobalanopsis patelliformis, were dominant in both the seedling and tree layers in the old growth forest. Some non-pioneer light-demanding species, such as Engelhardtia roxburghiana and Schima superba, were important in the seedling layer in the 60-year-old second growth forest. Meanwhile, Castanopsis carlesii and Symplocos poilanei were dominant in the tree layer in the 60-year-old second growth forest.

As expected, CO decreased during succession (Fig. 2A). The 60year-old second growth forest and the old growth forest had low CO, whereas the 18-year-old second growth forest had the highest CO values. The 18- and 30-year-old second growth forests had lower SWC, and the forests at later successional stages (the 60-year-old second growth and old growth forests) had higher values. Soil pH was higher in the 30- and 60-year-old second growth forests and lower in the 18-year-old second growth forest and the old growth forest. Both SOM and phosphorus content showed a decreasing pattern of variation across the four successional stages. TN had a higher value in the 30-year-old second growth forest and a lower value in the old growth forest. The forests at later successional stages (the 60-year-old second growth forest and old growth forest) had lower TK. AN was the lowest in the 60-year-old second growth forest. The 30-year-old second growth forest had the highest AK, while the old-growth forest had the lowest AK (Fig. 2). Tree species richness reached the lowest value in the 60-year-old second growth forest. Tree abundance decreased during succession. In contrast, tree basal area showed an increasing trend during succession.

All VIF values of the collinearity analysis were <3, indicating there is no collinearity in these variables (Table S2). We kept all variables in the analysis. The first axis of the PCA of the abiotic and biotic factors accounted for 37.5 percent of total variation (Fig. 3). This axis was strongly related to CO, SOM, nitrogen and potassium content, and tree species richness and basal area. The second axis accounted for 12.5 percent of the total variation and was mainly related to soil pH, AN content, and tree abundance.

ABIOTIC AND BIOTIC DRIVERS OF SEEDLING DIVERSITY/ COMPOSITION.—Abiotic and biotic factors generally played different roles in determining seedling species richness and abundance,





TABLE 2.	The number of species and all	oundance of seedlings in the three	ee regeneration groups in the	sites at different success	ional stages. Percenta	pes are indicated in parentheses.
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	Early successional species		Non-pioneer light-demanding species		Shade-tolerant species	
Forest age	Number of species	Abundance	Number of species	Abundance	Number of species	Abundance
18-year-old second growth	54 (59.3)	1399 (47.3)	21 (23.1)	1384 (46.7)	16 (17.6)	177 (5.9)
30-year-old second growth	26 (23.9)	1192 (47.7)	63 (57.8)	1127 (45.1)	20 (18.3)	181 (7.2)
60-year-old second growth	12 (9.5)	353 (11.6)	70 (55.56)	1692 (55.6)	44 (34.9)	997 (32.8)
Old growth forest	6 (4.1)	15 (0.7)	54 (36.9)	516 (24.5)	86 (59.0)	1576 (74.8)



FIGURE 2. Dynamics of environmental factors during succession. The data with different letters are significantly different at  $P \le 0.05$ . The abbreviations are as follows: 18, the 18-year-old second growth forest; 30, the 30-year-old second growth forest; 60, the 60-year-old second growth forest; OG, the old growth forest; CO, canopy openness; SWC, soil water content; SOM, soil organic mass; TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, available nitrogen; AP, available phosphorus; AK, available potassium; Rarefied Tree.R, rarefied tree species richness; Tree.A, tree abundance; and Tree.BA, tree basal area. The different letter (a, b, c, d) indicates significant differences (P < 0.05).

at the four successional stages (Table 3). The species richness of seedlings was positively correlated with SWC, soil pH, soil organic mass, and tree species richness in the 18-year-old second

growth forest. Seedling abundance was positively correlated with SWC, tree species richness and abundance, while it was negatively correlated with AN in the 18-year-old second growth forest.

SOM, tree abundance, and tree basal area were negatively correlated with seedling species richness, which was positively correlated with TN in the 30-year-old second growth forest. Seedling abundance was negatively correlated with soil pH and AK and was positively correlated with tree species richness and abundance in the 30-year-old second growth forest. The species richness of seedlings was positively correlated with CO and tree abundance but was negatively correlated with soil organic mass and AP in the 60-year-old second growth forest. Seedling abundance was positively correlated with CO, TN, and tree abundance, but was negatively correlated with TN in the 60-year-old second growth forest. In the old growth forest, the species richness of seedlings



FIGURE 3. Principal components analysis (PCA) of the abiotic and biotic factors at the four successional stages. The abbreviations are given in Figure 2.

was positively correlated with pH and TP but was negatively correlated with CO and TK. The abundance of seedlings was positively correlated with pH and TK but was negatively correlated with CO and AK at this successional stage.

In the 18-year-old and 30-year-old second growth forests, the coefficient of the proportion of old growth forest coverage on seedling diversity was greater than that of land-use history. In the 60-year-old second growth forest and the old growth forest, the coefficient of land-use history on seedling diversity was greater than that of the proportion of old growth forest coverage (Table 3).

We observed significant differences in species composition at the four successional stages (ANOSIM test, P = 0.001). There were strong associations between species composition and some abiotic and biotic factors during succession (Fig. 4). SWC, SOM, AK, and tree species richness and abundance were the most important factors affecting species composition in the 18-year-old second growth forest. Seedling species composition in the 30year-old second growth forest was influenced by SWC, pH, AK, tree species richness and tree abundance. In the 60-year-old second growth forest, CO, TN, TK, AP and tree abundance were the most important factors affecting the seedling community composition. Meanwhile, CO, TK, and AP were correlated with species composition in the old growth forest.

#### DISCUSSION

RECOVERY OF SPECIES COMPOSITION AND DIVERSITY.—Secondary succession in tropical forests is characterized by shifts in

TABLE 3. The relative importance of different environmental factors in influencing the seedling species richness and abundance in sites at the four successional stages (results of the multiple regression models, all listed factors were significant at P < 0.05). The abbreviations are given in Figure 2.

	Species richness				Abundance			
Forest age	Coeff. of covariate				Coeff. of covariate			
	Proportion of OG	Land-use history	Factors	Importance	Proportion of OG	Land-use history	Factor	Importance
18-year-old second	0.63	0.37	SWC (+)	0.47	0.58	0.31	SWC (+)	0.38
growth forest			pH (+)	0.51			AN (-)	0.60
			SOM (+)	0.53			Rarefied Tree.R (+)	0.42
			Rarefied Tree.R (+)	0.79			Tree.A (+)	0.41
30-year-old second	0.32	0.18	SOM (-)	0.36	0.38	0.11	рН (—)	0.54
growth forest			TN (+)	0.37			AK (-)	0.57
			Tree.A (-)	0.86			Tree.R (+)	0.42
			Tree.BA (-)	0.36			Tree.A (+)	0.99
60-year-old second	0.39	0.42	CO (+)	0.39	0.66	0.97	CO (+)	0.40
growth forest			SOM $(-)$	0.66			TN (+)	0.42
			AP (-)	0.33			AP (-)	0.82
			Tree.A (+)	0.42			Tree.A (+)	0.87
Old growth forest	0.20	0.58	CO (-)	0.46	0.13	0.37	CO (-)	0.50
			pH (+)	0.38			pH (+)	0.34
			TP (+)	0.30			TK (+)	0.70
			TK (-)	0.31			AK (-)	0.30



FIGURE 4. The non-metric multidimensional scaling (NMS) analysis on the relationships between seedling composition and abiotic/biotic factors at different successional stages. The abbreviations are given in Figure 2.

dominance from short-lived pioneers to longed-lived pioneers and, finally, to shade-tolerant species typical of mature forests (Finegan 1984). Our results demonstrated that seedling diversity differed significantly across stages of succession. The seedling communities of the 18- and 30-year-old second growth forests were characterized by the dominance of a few pioneer species. Some non-pioneer light-demanding species became dominant species in the seedling community of the 60-year-old second growth forest. The seedling community of the old growth forest was dominated by shade-tolerant species. Our results showed that the change in seedling diversity with succession generally revealed a bimodal pattern. Seedling diversity of early successional, nonpioneer light-demanding and shade-tolerant species reached their peaks in the 18- and 60-year-old second growth and the old growth forests, respectively. Seedling composition and diversity were significantly related to some key abiotic and biotic factors at each stage of succession. The observed patterns of seedling diversity across our study sites are generally in accordance with secondary successional patterns in tropical forests observed in many parts of the world (Lebrija-Trejos 2009, Chazdon 2014, Suganuma et al. 2014). In shifting cultivation fallows in Amazonian tropical forest, pioneer and early successional species were most abundant in the initial 3-5 yr after abandonment, and climax species dominated in the old growth forest (Uhl 1987). In terms of species composition, sites in early successional stages tend to differ considerably from sites in late successional stages (Whitfeld et al. 2014).

Our results showing a bimodal change in diversity with succession were consistent with the IDH described by Connell (1978), which suggests that species density first rises to a maximum level and then declines during the process of succession. In our study, with the recovery of the abandoned shifting cultivation lands, new species began to colonize and recruit, leading to a gradual accumulation of species over time. The number of

seedling species and individuals reached a peak in the 60-year-old second growth forest, where seedlings of both earlier and later successional stages could be found. Numerous studies have confirmed the IDH in different forests. Douglas (2001) applied a series of long-term permanent sample plot data spanning seven decades to this hypothesis and confirmed that the stem abundance peaked at the mid-successional stage. Kalacska et al. (2004) also found higher tree species richness at intermediate stages of succession. Changes in seedling diversity may vary with vegetation types and abiotic or anthropogenic conditions. Some studies have documented continuously increasing species diversity with stand age. Prach et al. (2014) found that the total number of species increased with successional age in a majority of series. Studies in tropical forests have found a progressive increase in tree species richness and diversity from early to late successional stages (Lebrija-Trejos et al. 2008, Madeira et al. 2009). Ruiz et al. (2005) found a similar pattern for a 56-yr chronosequence in dry tropical forest on the island of Providencia, Colombia; species richness increased steadily with increasing age since abandonment. However, Denslow and Guzman (2000) found that estimates and indices of seedling species richness did not vary with stand age across a 70-yr tropical moist forest chronosequence in Panama. It appears that there might be something unusual about the 30-yr second forest in our study, as many chronosequence studies indicate a steady increase in species richness over time (Guariguata & Ostertag 2001). Which factors have contributed to the low diversity of the 30-yr secondary forest, the edaphic conditions or the landscape configuration? Future research is needed to assess the underlying mechanisms of this unusual variation.

ABIOTIC AND BIOTIC FACTORS AFFECTING SEEDLING DIVERSITY/ COMPOSITION.—We found that different abiotic and biotic factors played different roles in determining seedling diversity during different stages of succession. Seedling diversity was correlated with SWC and soil nutrients in the 18-year-old second growth forest where light was ample but water was deficient. However, in later successional stages (the 60-year-old second growth forest and the old growth forest), where soil water was ample but light was deficient, seedling diversity was related to CO and soil nutrients. These results suggest that environmental filtering played an important role in the reassembly of tropical lowland rain forest following shifting cultivation.

Dramatic changes in environmental conditions and resource availability characterize different stages of tropical forest succession and impose strong filters on species establishment, growth, and recruitment (Chazdon 2014). Such an environmental variation is often characterized by the understory environment, particularly light conditions and root environments (Wright 2002). As observed in other systems, CO gradually decreased and light became less available as succession proceeded in our studied forest system. SWC in the two latter successional stages was higher than in the two previous stages. Soil nutrients generally decreased with succession. These results were consistent with previous studies (Schiffers et al. 2010, Lebrija-Trejos et al. 2011). Secondary succession involves a feedback mechanism between vegetation and the environment (Lebrija-Trejos et al. 2011). The environment can promote the coexistence of species with different resource requirements or reduce species richness when conditions beyond the tolerances of the species occur. Our results indicate that along a gradient of secondary succession following shifting cultivation, the general environmental conditions for the regenerating seedlings changed gradually from relatively dry and nutrientor light-rich in earlier successional stages to light- and nutrientpoor in later successional stages. Competition for soil water is more important than competition for light during earlier successional stages because species density and abundance were positively correlated with SWC but were not correlated with CO at this successional stage. The results of our study revealed that seedling diversity and composition were constrained by varied abiotic factors at different successional stages. Light seems to play an important role in species composition and diversity at later stages of succession, when it is more limiting to growth (Lohbeck et al. 2014, Sterck et al. 2014).

The species richness, abundance, and basal area of neighboring trees also had significant effects on seedling diversity during succession. The identity of the adult trees in a seedling neighborhood may affect seedling survival. Several studies have shown that intraspecific negative density dependence is important in slowing competitive exclusion and maintaining diversity in tropical forests (Harms et al. 2000, Webb et al. 2006). Our results showed that both tree species richness and abundance had significant effects on seedling diversity in the 18-year-old second growth forest. All of the biotic factors were important drivers of seedling diversity in the 30-year-old second growth forest. Tree abundance was the only biotic factor affecting seedling diversity in the 60year-old second forest. Confirming the results of previous studies, seedling diversity was affected by the adult trees in seedling neighborhoods (Lin et al. 2012, Paine et al. 2012). The adult trees may affect seedling survival via negative density dependence.

Density dependent survival is prevalent in tropical forests and is recognized as a driving mechanism for maintaining species diversity (Harms *et al.* 2000, Kobe & Vriesendorp 2011). Seedlings may experience strong asymmetric resource competition with adult trees.

In contrast to the second growth forest, biotic factors did not significantly affect seedling diversity in the old growth forest. Our findings suggest that the effect of adult trees on seedling diversity is less than has been previously suggested, at least in the old growth forest. This result stands in contrast with previous results, in which the basal area of adults and the density of seedlings both increased seedling mortality, thus reducing seedling diversity. This may be due to increased competition among all seedlings for abiotic resources at this stage. Most of the abiotic factors (except SWC) in our study showed a decreasing pattern at this stage. In the secondary forests, seedling diversity was constrained by both abiotic and biotic factors when environmental resources were ample. In the old growth forest, all of the seedlings contended for environmental resources, which were scarce. Therefore, seedling diversity was affected only by abiotic factors and not by the abundance or species richness of adult trees. The biotic factors appeared to affect seedling diversity more strongly and more pervasively than did abiotic factors in the old growth forest.

SUCCESSION AND LANDSCAPE CONTEXT.-The diversity of regenerating woody plants is constrained by a set of factors, which vary with climate, soil type, and landscape structure (Crouzeilles et al. 2016). Because the regeneration of tropical forest depends upon the intensity of land use and the distance to sources of colonizers (Pascarella et al. 2000), we assumed that land-use history and the proportion of neighboring old growth forest would determine the rate of forest recovery and the species diversity of secondary forests. Our findings show that the effect of the proportion of the surrounding landscape covered by old growth forest on seedling diversity is greater than that of land-use history at earlier successional stages, but the effect of land-use history is greater than that of the proportion of the surrounding landscape covered by old growth forest at later stages of succession. The proportion of the surrounding landscape covered by old growth forest showed a shift in our study plots from 0 to 20 percent at earlier successional stages to 40-80 percent at later successional stages. This pattern of change means that when the proportion of the surrounding landscape covered by old growth forest was low, it was the main landscape factor affecting seedling diversity. With an increase in the proportion, land-use history was the main landscape factor.

The dynamics of succession can be assessed at multiple spatial and temporal scales (do Nascimento *et al.* 2014). At the specific local level, the rates of forest recovery following natural and human disturbances are always slower than the rate of deforestation. However, at the landscape level, landscape context variables, such as the fragmentation pattern and shape index, were shown to be significant factors influencing species composition in shifting cultivation fallows (Lawrence 2004, Chazdon 2014). Land-use intensity and distance to old growth remnant forests across the landscape were shown to have great influences on the regeneration and composition of the abandoned shifting cultivation lands in our studied forests (Ding *et al.* 2012). Logged forests in the study by showed good recovery, with species richness being actually higher than in the forests that had recovered on abandoned lands after several cycles of shifting cultivation Ding *et al.* (2012). Human disturbance is a good predictor of changes in species composition and diversity. These results confirm the importance of land-use history for forest recovery (Lawrence 2004). The reproductive mode of different species (the relative proportions of sprouting and seeding) also has an influence on the regeneration of seedling or tree communities (Ding & Zang 2005).

In this study, all of the second growth forests were allowed to naturally recover after the last cycle of shifting cultivation. This recovery was due to several main reasons as follows: (1) most of the re-clearing shifting cultivation practices were non-profitable for the local farmers after several cycles of shifting cultivation; (2) the national Natural Forest Conservation Program (logging ban and shifting cultivation ban) was established on Hainan Island in 1994, which ceased most of the anthropogenic disturbances to the natural tropical forests on Hainan Island; and (3) the Bawangling National Nature Reserve was established in 1980, which allowed large areas of the shifting cultivated lands (approximately 70% of the lowland rain forest in this region) to be protected and undergo a natural recovery process. The reserve area expanded from 66.3 to 300 km<sup>2</sup> in 2003 when it became clear that the original reserve was too small for effective protection of the Hainan gibbon (Zang et al. 2010).

In this naturally recovering forest, a few small areas of old growth forest fragments and later successional species within them are scattered across the entire studied forest region. Seed dispersal is a major limiting factor for later successional species during succession, especially for large-sized seeds because many of their dispersal agents, such as mammals, have disappeared in the study area. Thus, seed size and the dispersal mode of trees in areas at different successional stages may be the important factors limiting seedling establishment. Our integrated dataset on seed size and dispersal mode, which was compiled from references and data bases (such as the Kew Gardens Seed Information Database [http://www.rbgkew.org.uk/data/sid/], the Wood Density Database [http://www.Worldagroforestrycentre.org/sea/Products/AFDbases/WD/Index.htm], and TRY [http://www.try-db.org]), showed that seeds of early successional species are generally small and dispersed by wind, while seeds of late successional species are large and dispersed over short distances. Kepfer-Rojas et al. (2014) examined the effects of the distance to seed sources on species density and species composition. Dispersal was a strong driver at the early stages of succession, and lack of effective land management was an obstacle to tree colonization after more than a century since abandonment. Therefore, planting later-successional species may be one of the most effective methods for improving forest regeneration during succession in this tropical lowland rain forest. In fact, we have now been doing this type of biodiversity enrichment

planting experiment in the 60-year-old second growth of the lowland rain forest in the studied area for the past 3 yrs (Runguo Zang, unpubl. data).

Simple pseudoreplication based on the evaluation of a single site for each successional stage is the most common form of pseudoreplication (Ramage et al. 2013). Simple pseudoreplication occurs when multiple samples from a single contiguous treatment unit are analyzed as if they were independent replicates and the results are then used to infer treatment effects (Hurlbert 1984). As is the reality of many studies, our study has the shortcoming of making generalizations about regional successional changes based on a limited dataset. Due to the limitations of our sampling efforts, we only selected two sites at each successional stage and investigated 25 seedling plots at each site. In future studies, more sites and randomly sampled seedling and tree plots are needed to make robust generalizations and predictions about the actual successional dynamics of tropical secondary forests on abandoned shifting cultivation lands at the landscape or regional scale.

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#### SUPPORTING INFORMATION

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

TABLE S1. The relative abundance and dominance of dominant seedling species in sites at the four successional stages.

TABLE S2. The VIF values for the abiotic and biotic factors for detecting collinearity.

# LITERATURE CITED

- ALVAREZ-BUYLLA, E. R., AND M. MARTÍNEZ-RAMOS. 1990. Seed bank versus seed rain in the regeneration of a tropical pioneer tree. Oecologia 84: 314–325.
- ANDERSON, S. E., AND J. S. I. INGRAM. 1989. Tropical soil biology and fertility: A handbook of methods. C.A.B. International, Aberystwyth, U.K.

- BENITEZ-MALVIDO, J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. Conserv. Biol. 12: 380–389.
- BONGERS, F., L. POORTER, W. D. HAWTHORNE, AND D. SHEIL. 2009. The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. Ecol. Lett. 12: 798– 805.
- van BREUGEL, M. 2007. Dynamics of secondary forests. PhD Dissertation. Wageningen University, Wageningen, the Netherlands.
- BU, W., R. ZANG, AND Y. DING. 2014. Functional diversity increases with species diversity along successional gradient in a secondary tropical lowland rainforest. Trop. Ecol. 55: 393–401.
- CAPERS, R. S., R. L. CHAZDON, A. R. BRENES, AND B. V. ALVARADO. 2005. Successional dynamics of woody seedling communities in wet tropical secondary forests. J. Ecol. 93: 1071–1084.
- CATOVSKY, S., AND F. A. BAZZAZ. 2002. Feedbacks between canopy composition and seedling regeneration in mixed conifer broad-leaved forests. Oikos 98: 403–420.
- CECCON, E., S. SÁNCHEZ, AND J. CAMPO. 2004. Tree seedling dynamics in two abandoned tropical dry forests of differing successional status in Yucatán, Mexico: A field experiment with N and P fertilization. Plant Ecol. 170: 277–285.
- CHAO, A., R. L. CHAZDON, R. K. COLWELL, AND T.-J. SHEN. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol. Lett. 8: 148–159.
- CHAZDON, R. L. 2003. Tropical forest recovery: Legacies of human impact and natural disturbances. Perspect. Plant Ecol. Evol. Syst. 6: 51–71.
- CHAZDON, R. L. 2008a. Beyond deforestation: Restoring forests and ecosystem services on degraded lands. Science 320: 1458–1460.
- CHAZDON, R. L. 2008b. Chance and determinism in tropical forest succession. *In* W. P. Carson, and S. A. Schnitzer (Eds.). Tropical forest community ecology, pp. 384–408. Wiley-Blackwell, Oxford, U.K.
- CHAZDON, R. L. 2014. Second growth: The promise of tropical forest regeneration in an age of deforestation. The University of Chicago Press, Chicago, IL and London, U.K.
- CHAZDON, R. L., AND M. R. GUARIGUATA. 2016. Natural regeneration as a tool for large-scale forest restoration in the tropics: Prospects and challenges. Biotropica 48: 844–855.
- COMITA, L. S., J. THOMPSON, M. URIARTE, I. JONCKHEERE, C. D. CANHAM, AND J. K. ZIMMERMAN. 2010. Interactive effects of land use history and natural disturbance on seedling dynamics in a subtropical forest. Ecol. Appl. 20: 1270–1284.
- COMITA, L. S., M. URIARTE, J. THOMPSON, I. JONCKHEERE, C. D. CANHAM, AND J. K. ZIMMERMAN. 2009. Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. J. Ecol. 97: 1346–1359.
- CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.
- CROUZEILLES, R., M. CURRAN, AND Y. CLOUGH. 2016. Which landscape size best predicts the influence of forest cover on restoration success? A global meta-analysis on the scale of effect. J. Appl. Ecol. 53: 440–448.
- DENSLOW, J. S., AND S. GUZMAN. 2000. Variation in stand structure, light, and seedling abundance across a tropical moist forest chronosequence, Panama. J. Veg. Sci. 11: 201–212.
- DHAKAL, B., M. A. PINARD, I. A. U. N. GUNATILLEKE, C. V. S. GUNATILLEKE, AND D. F. R. P. BURSLEM. 2015. Strategies for restoring tree seedling recruitment in high conservation value tropical montane forests underplanted with cardamom. Appl. Veg. Sci. 18: 121–133.
- DING, Y. 2006. Study on recovery ecology of the degraded tropical forest vegetation in hainan island, South China. PhD Dissertation. Chinese Academy of Forestry, Beijing, China.
- DING, Y., AND R. ZANG. 2005. Community characteristics of early recovery vegetation on abandoned lands of shifting cultivation in Bawangling of Hainan Island, South China. J. Integr. Plant Biol. 47: 530–538.
- DING, Y., R. G. ZANG, AND Y. X. JIANG. 2006. Effect of hillslope gradient on vegetation recovery on abandoned land of shifting cultivation in Hainan Island, south China. J. Integr. Plant Biol. 48: 642–653.

- DING, Y., R. ZANG, S. LIU, F. HE, AND S. G. LETCHER. 2012. Recovery of woody plant diversity in tropical rain forests in southern China after logging and shifting cultivation. Biol. Conserv. 145: 225– 233.
- DOUGLAS, S. 2001. Long-term observations of rain forest succession, tree diversity and responses to disturbance. Plant Ecol. 155: 183–199.
- DRAY, S., AND A.-B. DUFOUR. 2007. The ade4 package: Implementing the duality diagram for ecologists. J. Stat. Softw. 22: 1–20.
- FEI, S., AND K. C. STEINER. 2009. Rapid capture of growing space by red maple. Can. J. For. Res. 39: 1444–1452.
- FINEGAN, B. 1984. Forest succession. Nature 312: 109-114.
- GUARIGUATA, M. R., AND R. OSTERTAG. 2001. Neotropical secondary forest succession: Changes in structural and functional characteristics. Forest Ecol. Manag. 148: 185–206.
- HARMS, K. E., S. J. WRIGHT, O. CALDERON, A. HERNANDEZ, AND E. A. HERRE. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404: 493–495.
- HELSEN, K., M. HERMY, AND O. HONNAY. 2015. Changes in the species and functional trait composition of the seed bank during semi-natural grassland assembly: Seed bank disassembly or ecological palimpsest? J. Veg. Sci. 26: 58–67.
- HERNÁNDEZ-STEFANONI, J. L., AND J. M. DUPUY. 2008. Effects of landscape patterns on species density and abundance of trees in a tropical subdeciduous forest of the Yucatan Peninsula. Forest Ecol. Manag. 255: 3797–3805.
- HERNÁNDEZ-STEFANONI, J. L., J. DUPUY, F. TUN-DZUL, AND F. MAY-PAT. 2011. Influence of landscape structure and stand age on species density and biomass of a tropical dry forest across spatial scales. Landscape Ecol. 26: 355–370.
- Hu, Y. J., AND Y. X. LI. 1992. Tropical rain forest of Hainan Island. Guangdong Higher Education Press, Guangzhou, China.
- HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54: 187–211.
- JAKOVAC, C. C., M. PEÑA-CLAROS, T. W. KUYPER, AND F. BONGERS. 2015. Loss of secondary-forest resilience by land-use intensification in the Amazon. J. Ecol. 103: 67–77.
- JURINITZ, C. F., A. A. de OLIVEIRA, AND E. M. BRUNA. 2013. Abiotic and biotic influences on early-stage survival in two shade-tolerant tree species in Brazil's Atlantic forest. Biotropica 45: 728–736.
- KALACSKA, M., G. A. SANCHEZ-AZOFEIFA, J. C. CALVO-ALVARADO, M. QUESADA, B. RIVARD, AND D. H. JANZEN. 2004. Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest. Forest Ecol. Manag. 200: 227–247.
- KEPFER-ROJAS, S., I. K. SCHMIDT, J. RANSIJN, T. RIIS-NIELSEN, AND K. VER-HEYEN. 2014. Distance to seed sources and land-use history affect forest development over a long-term heathland to forest succession. J. Veg. Sci. 25: 1493–1503.
- KOBE, R. K., AND C. F. VRIESENDORP. 2011. Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. Ecol. Lett. 14: 503–510.
- LALIBERTÉ, E., G. ZEMUNIK, AND B. L. TURNER. 2014. Environmental filtering explains variation in plant diversity along resource gradients. Science 345: 1602–1605.
- LAUGHLIN, D. C., C. JOSHI, S. J. RICHARDSON, D. A. PELTZER, N. W. H. MASON, AND D. A. WARDLE. 2015. Quantifying multimodal trait distributions improves trait-based predictions of species abundances and functional diversity. J. Veg. Sci. 26: 46–57.
- LAWRENCE, D. 2004. Erosion of tree diversity during 200 years of shifting cultivation in Bornean rain forest. Ecol. Appl. 14: 1855–1869.
- LEBRIJA-TREJOS, E. 2009. Tropical dry forest recovery: processes and causes of change. PhD Dissertation. Wageningen University, Wageningen, the Netherlands.
- LEBRIJA-TREJOS, E., F. BONGERS, E. A. PÉREZ-GARCÍA, AND J. A. MEAVE. 2008. Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. Biotropica 40: 422–431.

- LEBRIJA-TREJOS, E., E. A. PÉREZ-GARCÍA, J. A. MEAVE, L. POORTER, AND F. BONGERS. 2011. Environmental changes during secondary succession in a tropical dry forest in Mexico. J. Trop. Ecol. 27: 477–489.
- LIN, L., L. S. COMITA, Z. ZHENG, AND M. CAO. 2012. Seasonal differentiation in density-dependent seedling survival in a tropical rain forest. J. Ecol. 100: 905–914.
- LOHBECK, M., L. POORTER, M. MARTÍNEZ-RAMOS, J. RODRIGUEZ-VELÁZQUEZ, M. van BREUGEL, AND F. BONGERS. 2014. Changing drivers of species dominance during tropical forest succession. Funct. Ecol. 28: 1052– 1058.
- LU, X., R. ZANG, Y. DING, S. G. LETCHER, W. LONG, AND Y. HUANG. 2014. Variations and trade-offs in functional traits of tree seedlings during secondary succession in a tropical lowland rain forest. Biotropica 46: 404–414.
- MADEIRA, B. G., M. M. ESPÍRITO-SANTO, S. D. Â. NETO, Y. R. F. NUNES, G. A. S. AZOFEIFA, G. W. FERNANDES, AND M. QUESADA. 2009. Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. Plant Ecol. 201: 291–304.
- MARTÍNEZ-RAMOS, M., A. PINGARRONI, J. RODRÍGUEZ-VELÁZQUEZ, L. TOLEDO CHELALA, I. ZERMEÑO-HERNÁNDEZ, AND F. BONGERS. 2016. Natural forest regeneration and ecological restoration in human modified tropical landscapes. Biotropica 48: 747–757.
- MINCHIN, P. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *In* I. C. Prentice, and E. van der Maarel (Eds.). Theory and models in vegetation science, pp. 89–107. Springer, Dordrecht, The Netherlands.
- MUSCARELLA, R., M. URIARTE, J. FORERO-MONTAÑA, L. S. COMITA, N. G. SWEN-SON, J. THOMPSON, C. J. NYTCH, I. JONCKHEERE, AND J. K. ZIMMERMAN. 2013. Life-history trade-offs during the seed-to-seedling transition in a subtropical wet forest community. J. Ecol. 101: 171–182.
- do NASCIMENTO, L., de SÁ BARRETTO SAMPAIO E., M. RODAL, AND A. LINS-E-SILVA. 2014. Secondary succession in a fragmented Atlantic Forest landscape: Evidence of structural and diversity convergence along a chronosequence. J. For. Res. 19: 501–513.
- PAINE, C. E. T., N. NORDEN, J. CHAVE, P.-M. FORGET, C. FORTUNEL, K. G. DEXTER, AND C. BARALOTO. 2012. Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. Ecol. Lett. 15: 34–41.
- PASCARELLA, J., T. AIDE, M. SERRANO, AND J. ZIMMERMAN. 2000. Land use history and forest regeneration in the Cayey Mountains, Puerto Rico. Ecosystems 3: 217–228.
- PÉREZ-RAMOS, I. M., T. MARAÑÓN, AND B. WILSON. 2012. Community-level seedling dynamics in Mediterranean forests: Uncoupling between the canopy and the seedling layers. J. Veg. Sci. 23: 526–540.
- POTTER, K. M., AND C. W. WOODALL. 2012. Trends over time in tree and seedling phylogenetic diversity indicate regional differences in forest biodiversity change. Ecol. Appl. 22: 517–531.
- PRACH, K., K. ŘEHOUNKOVÁ, K. LENCOVÁ, A. JÍROVÁ, P. KONVALINKOVÁ, O. MUDRÁK, V. ŠTUDENT, Z. VANĚČEK, L. TICHÝ, P. PETŘÍK, P. ŠMILAUER, AND P. PYŠEK. 2014. Vegetation succession in restoration of disturbed sites in Central Europe: The direction of succession and species richness across 19 seres. Appl. Veg. Sci. 17: 193–200.
- PURSCHKE, O., B. C. SCHMID, M. T. SYKES, P. POSCHLOD, S. G. MICHALSKI, W. DURKA, I. KÜHN, M. WINTER, AND H. C. PRENTICE. 2013. Contrasting changes in taxonomic, phylogenetic and functional diversity during a

long-term succession: Insights into assembly processes. J. Ecol. 101: 857-866.

- R Development Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- RAMAGE, B. S., D. SHEIL, H. M. W. SALIM, C. FLETCHER, N.-Z. A. MUSTAFA, J. C. LURUTHUSAMAY, R. D. HARRISON, E. BUTOD, A. D. DZULKIPLY, A. R. KASSIM, AND M. D. POTTS. 2013. Pseudoreplication in tropical forests and the resulting effects on biodiversity conservation. Conserv. Biol. 27: 364–372.
- RANGEL, T. F., J. A. F. DINIZ-FILHO, AND L. M. BINI. 2010. SAM: A comprehensive application for spatial analysis in macroecology. Ecography 33: 46–50.
- RUIZ, J., M. C. FANDIÑO, AND R. L. CHAZDON. 2005. Vegetation structure, composition, and species richness across a 56-year chronosequence of dry tropical forest on Providencia Island, Colombia. Biotropica 37: 520–530.
- SCHIFFERS, K., K. TIELBÖRGER, AND F. JELTSCH. 2010. Changing importance of environmental factors driving secondary succession on molehills. J. Veg. Sci. 21: 500–506.
- SCHREEG LAURA, A., K. KOBE RICHARD, AND B. WALTERS MICHAEL. 2005. Tree seedling growth, survival, and morphology in response to landscapelevel variation in soil resource availability in northern Michigan. Can. J. For. Res. 35: 263–273.
- SHUAI, F. Y. WANG, AND S. YU. 2014. Density dependence in forests is stronger in tropical and subtropical climates among closely related species. Ecography 37: 659–669.
- STERCK, F., L. MARKESTEIJN, M. TOLEDO, F. SCHIEVING, AND L. POORTER. 2014. Sapling performance along resource gradients drives tree species distributions within and across tropical forests. Ecology 95: 2514–2525.
- SUGANUMA, M. S., G. B. ASSIS, AND G. DURIGAN. 2014. Changes in plant species composition and functional traits along the successional trajectory of a restored patch of Atlantic Forest. Community Ecol. 15: 27–36.
- UHL, C. 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. J. Ecol. 75: 377–407.
- VANDECAR, K. L., D. LAWRENCE, T. WOOD, S. F. OBERBAUER, R. DAS, K. TULLY, AND L. SCHWENDENMANN. 2009. Biotic and abiotic controls on diurnal fluctuations in labile soil phosphorus of a wet tropical forest. Ecology 90: 2547–2555.
- WEBB, C. O., G. S. GILBERT, AND M. J. DONOGHUE. 2006. Phylodiversitydependent seedling mortality, size structure, and disease in a Bornean rain forest. Ecology 87: S123–S131.
- WHITFELD, T. J. S., J. R. LASKY, K. DAMAS, G. SOSANIKA, K. MOLEM, AND R. A. MONTGOMERY. 2014. Species richness, forest structure, and functional diversity during succession in the New Guinea lowlands. Biotropica 46: 538–548.
- WRIGHT, J. 2002. Plant diversity in tropical forests: A review of mechanisms of species coexistence. Oecologia 130: 1–14.
- ZANG, R.-G., Y. DING, Z.-D. ZHANG, F.-Y. DENG, AND P.-L. MAO. 2010. Ecological base of conservation and restoration for the major functional groups in tropical natural forests on Hainan Island. Science Press, Beijing, China.
- ZUUR, A. F., E. N. IENO, N. J. WALKER, A. A. SAVELIEV, AND G. M. SMITH. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York.