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Facilitation by Tree Species in Variable Retention Harvesting for the Restoration of Monoculture Plantations in Southern China

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Abstract

Facilitation can drive the successional dynamics and change the restoration trajectory of degraded forests. However, the relative importance of facilitation by tree species after variable retention harvesting is unclear. We used a field experiment to evaluate the effect of two facilitator species, *Castanopsis fissa (C. fissa)* and *Manglietia glauca (M. glauca)*, managed with variable retention harvesting, on the development of two target species, *Castanopsis hystrix (C. hystrix)* and *Erythrophloeum fordii (E. fordii)*, in a Masson pine (*Pinus massoniana*) monoculture. The following variables were measured for all of the four interplanted tree species: structural growth, regeneration, aboveground biomass accumulation, leaf area index, and soil conditions. The results indicate that the abundance, growth, and aboveground biomass were relatively greater in plots planted with *C. fissa* compared with *M. glauca* and that the target species performed best with 50% retention harvesting of *C. fissa*, with an improved establishment of both target species indicating a positive interaction. In addition, the regeneration, leaf area index and soil conditions differed between the two facilitators in the variable retention harvesting treatments because of the different intrinsic characteristic of the facilitators. In summary, our results imply that managers have considerable flexibility to employ various types of facilitation schemes coupled with different harvesting systems for successful short-term restoration within a monoculture.

Keywords

facilitation, variable retention harvesting, early successional species, ecological restoration

Introduction

Facilitation that directly influences forest structure and dynamics has emerged as a key paradigm for restoring degraded forests (Gómez-Aparicio et al., 2004). In recent decades, the determinant role of facilitation has been recognized as a positive interaction in which certain plants affect the establishment or the growth of other plants and of favorable microhabitats for seed germination or seedling recruitment in degraded forest (Brooker et al., 2008). For these reasons, it is important to consider the effects of facilitation to gain a better understanding of ecological restoration processes.

An example of the facilitation effect is the positive influence of plants on the germination and establishment of seedlings or individuals under their canopy; this effect occurs because of the amelioration of extreme environmental conditions (Gómez-Aparicio et al., 2004; Gómez-Ruiz, Lindig-Cisneros, & Vargas-Ríos, 2013; Padilla & Pugnaire, 2006). The myriad effects of

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facilitation on the organization and dynamics of many plant communities have been demonstrated (Callaway, 2007; Pugnaire, 2010). The facilitation effect may result from many factors, including growth dynamic, crown architecture, biomass increment, increased soil moisture, improved nutrition, and the enhancement of beneficial soil organisms (Callaway, 2007). The function of certain early successional forest tree species as facilitators has favorable implications in the context of ecological restoration and provides attractive prospects for the short-term application of these species (Avendaño-Yáñez, Sánchez-Velásqueza, Meaveb, & Pineda-Lópeza, 2014).

The use as facilitators of certain species with the capacity to modify and improve the environment may promote early succession in degraded areas within a restoration process and increase the probability of achieving the rehabilitation and restoration goals (Castro, Zamora, Hódar, & Gómez, 2002; Padilla & Pugnaire, 2006). The increasing recognition of facilitation as a primary process regulating the composition of communities has brought a change in the practice of restoration that is based on a better awareness of the benefits inherent in conserving neighboring vegetation (Gómez-Aparicio, 2009). Moreover, the effective strategy of facilitation has been used as a force that drives succession in many degraded habitats (Brooker et al., 2008), including Mediterranean mountains; hilly, sloping lands; secondary tropical dry forest; high Andean forest; tropical montane forest; tropical subhumid forest; and tropical coastal forest (Arroyo, Cavieres, Penaloza, & Arroyo-Kalin, 2003; Avendaño-Yáñez et al., 2014; Bertness & Yeh, 1994; Callaway, Delucia, Moore, Nowak, & Schlesinger, 1996; Castro et al., 2002; Gómez-Ruiz et al., 2013; Liu, Lu, Xue, & Zhang, 2014; Yang et al., 2009).

Subtropical monoculture plantations have been widely planted in South China using a number of fast-growing and commercially attractive timber tree species (Stone, 2009). The practice of using selective logging to encourage the introduction of native tree species into these plantation monocultures was introduced in the 1990s because of growing interest in the forms of reforestation and stand management that provide a wider variety of ecosystem services in addition to timber production. However, the type of successional development that occurs following selective logging depends not only on the density of the retained plantation trees but also on the composition of other species that have already colonized the plantation. Some of these species may facilitate further successional development, whereas others may inhibit such development or lead to the introduction of invasive alien species (e.g., *Ageratina adenophora*). Little is known concerning these successional patterns, and there is little experimental evidence for the performance of facilitation in monocultural plantations in southern China.

It is important to evaluate how the growth of certain target species planted within the residual plantation understory is affected by the presence of different potential facilitator species. Hence, the main objectives of this study were (a) to compare *Castanopsis fissa* and *M. glauca* act as facilitators of the two target species, (b) to examine if potential differences can be explained by retention harvesting practices produce differential effects on the development of the target species, and (c) to propose the implications of these findings for the restoration of monoculture plantations.

Methods

Study Site

The study site was located within the Fubo plantation station forests (21°57′–22°19′N, 106°39′–106°59′E) of the Experimental Center of Tropical Forestry of the Chinese Academy of Forestry, Pingxiang City, Guangxi Zhuang Autonomous Region, China (Figure 1). The annual rainfall in this subtropical region is between 1,200 and 1,500 mm, the temperature varies between 20.5°C and 21.7°C, and the relative humidity is 80% to 84% (Jiang et al., 2015). The plots are located at an elevation of 430 to 680 m above the sea level. The local soil is classified as soils with little or no profile differentiation (IUSS Working Group WRB, 2015), derive from granite and are classified as red soil in the Chinese soil classification, with a pH value of 4.8 and 5.5 (Jiang et al., 2015). The study site was originally occupied by a subtropical evergreen forest that was cleared and planted with Masson pine (*Pinus massoniana*) in 1950. Several rotations were grown, and then the land was allowed to lie fallow.

The site was reforested by *P. massoniana* in 1993 at a density of 2,500 stems per hectare. This density has declined over time because of self-thinning, herbivory, and damage that was sustained during a snowstorm. However, the canopy continued to be dominated by *P. massoniana*, with certain herbs, such as *Maesa japonica*, *Clerodendrum cyrtophyllum,* and *Psychotria rubra*, present as minor components. Before the treatments, the density of the monoculture stands averaged 1,787 stems ha^{-1} ($SD = 26.7$), the mean diameter of all the trees was 13.4 cm, their mean height was 12.7 m, and their basal area was 15.3 m^2 ha^{-1} ($SD = 8.6$).

Two facilitator species were used. *Castanopsis fissa (C. fissa)*, a member of the Fagaceae, is a rapidly growing, native tree species that is tolerant of shade and nutrient-poor environments. This species is a common pioneer in this region that fixes nitrogen and forms a heavy litter layer (Tang, Jeewon, & Hyde, 2005).

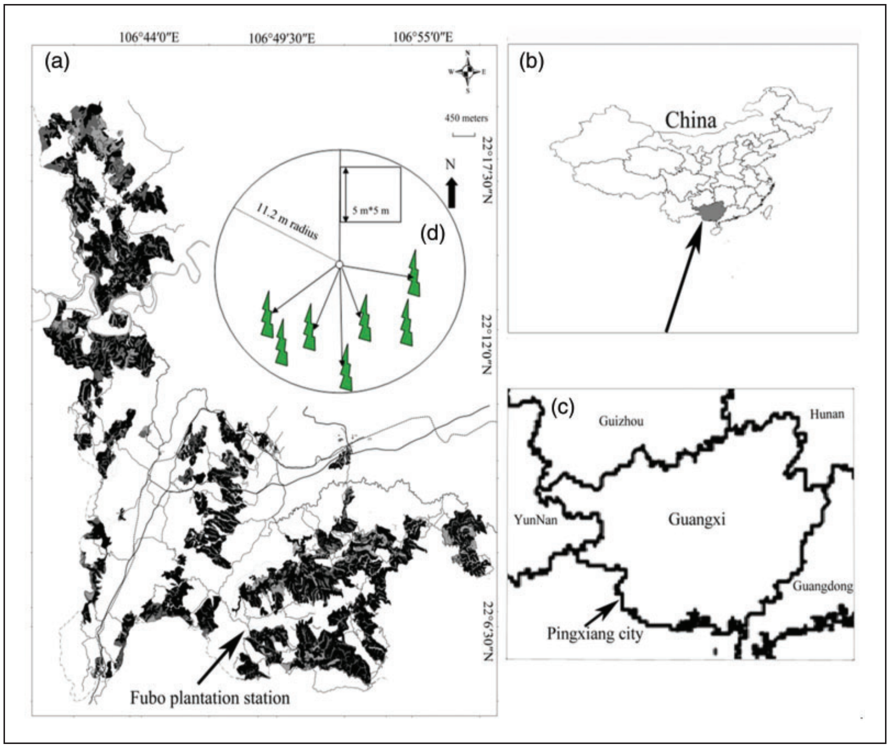

Figure 1. (a) to (c) Location of study sites in the subtropical monoculture plantation region, near Pingxiang City, Guangxi Zhuang Autonomous Region, China. (d) Experimental plot design: circular permanent plots of 400 m^2 with 11.2 m radius, and 5 m $\times$ 5 m square subplots.

Manglietia glauca, a member of the *Magnoliaceae*, is an exotic species introduced from Vietnam (Wang & Cai, 2008). This species is also fast-growing, drought resistant, and tolerates acidic soils. These two pioneer species are often planted in urban areas and used to reforest hillsides across the region (Pan & You, 1994). The two target species used are representative of a number of native species that might be established at these sites and are typical of reforestation trees in South China. *Castanopsis hystrix (C. hystrix)* is a long-lived, native species that can tolerate some shade and high moisture but not drought or low temperatures; this species grows best in acidic red soil, yellow soil, and brick-red soil developed from granite and sandstone and produces many seeds of high viability and rapid germination (Zhou, 2007). *Erythrophloeum fordii (E. fordii)* is a long-lived species, which prefers light and acidic soil and is capable of reaching a height of 37 to 45 m and a diameter of 200 to 250 cm, produces high-quality timber, and has important economic and ecological value (Sein & Mitlöhner, 2011).

Experimental Design

In the summer of 2007, four harvesting treatments that included unmanaged monoculture stands as controls (CT remaining after harvest density 1,500 tree·hm^{-2}) and the following three levels of canopy retention were applied in the monoculture plantation: 20 (R20 remaining after harvest density 300 tree·hm^{-2}), 50% (R50 remaining after harvest 750 tree·hm^{-2}) and 75% retention (R75 density 1,150 tree·hm^{-2}), respectively. The harvested trees were selected without regard for species or size, but as all compartments were monocultures (>85% *P. massoniana*) we assume that there is no systematic bias that could significantly affect the comparison between harvest retention levels. The canopy retention was calculated by the number of live trees present in the compartment before harvesting. The harvesting treatments were applied to 20 ha harvest units, which were each subdivided into four compartments. A thinning procedure was performed by poison girdling all of the nontimber tree species having a diameter at breast height (DBH) of 20 to 30 cm, which was measured 1.30 m above the ground, and systematically removing the postlogging competition. The harvesting equipment was restricted to the machine corridors but reached into the residual strips to remove the trees; thus, there was a minimal disturbance of the forest floor and soils in the retained strips.

The four harvesting treatments were assigned to a total of 64 permanent, circular plots located within stands of the monoculture, with each treatment applied in 16 of the plots (Table 1). The plots each covered 400 m^2 (11.2 m radius) and were traced systematically

Table 1. Experimental Treatment and Number of Plots for Each Retention Level and Combination of Facilitator and Target Plant Species and for the CT.

Planting treatment	Facilitated species	Target species	Retention level (%)	*P. massoniana* (%)	No. of plots
1. CaFi-CaHy	*C. fissa*	*C. hystrix*	25	86	4
2. CaFi-CaHy	*C. fissa*	*C. hystrix*	50	85	4
3. CaFi-CaHy	*C. fissa*	*C. hystrix*	75	89	4
4. CaFi-ErFo	*C. fissa*	*E. fordii*	25	94	4
5. CaFi-ErFo	*C. fissa*	*E. fordii*	50	85	4
6. CaFi-ErFo	*C. fissa*	*E. fordii*	75	92	4
7. MaGl-CaHy	*M. glauca*	*C. hystrix*	25	89	4
8. MaGl-CaHy	*M. glauca*	*C. hystrix*	50	87	4
9. MaGl-CaHy	*M. glauca*	*C. hystrix*	75	90	4
10. MaGl-ErFo	*M. glauca*	*E. fordii*	25	88	4
11. MaGl-ErFo	*M. glauca*	*E. fordii*	50	91	4
12. MaGl-ErFo	*M. glauca*	*E. fordii*	75	93	4
CT	Unmanaged forest			97	16
Total					64

Note. CT = control; *C. fissa* = *Castanopsis fissa*; *C. hystrix* = *Castanopsis hystrix*; *E. fordii* = *Erythrophloeum fordii*; *M. glauca* = *Manglietia glauca*.

(Figure 1(d)). The location of the plots within the area was selected according to the homogeneity and accessibility of the plots, which were randomly separated from one another. We initiated the experiment to examine the effects of planting additional species on the processes of succession and restoration within monoculture plantations.

In the spring of 2008, we planted saplings of the four tree species (*C. hystrix*, *E. fordii*, *C. fissa*, and *M. glauca*) across the entire treatment unit for the three retention harvesting treatments (Table 1). One- to 2-year-old seedlings of the facilitator species were planted at the same distance (3 m $\times$ 3 m) between individuals in all the plots, providing a density of approximately 1,200 seedlings ha^{-1} in the treatments. The plots were divided into subplots, and a combination of each facilitator species (*C. fissa* or *M. glauca*) with each target species (*C. hystrix* or *E. fordii*) was planted in each subplot. The spacing between the planted trees was 3 m $\times$ 3 m. We alternated the identity of the species by planting row. The native target seedlings were watered and fertilized when transplanted and were then permitted to grow naturally. Sixty-four 5 m $\times$ 5 m subplots were thus established on the monoculture plantation for the four harvesting treatments (including the CT; Table 1). Forty-eight 5 m $\times$ 5 m subplots that received plantings and 16 unmanaged control subplots of similar dimensions that did not receive plantings composed the four harvesting treatments. The planted subplots were divided into four planting treatments (T1, *C. fissa* and *C. hystrix*; T2, *C. fissa* and *E. fordii*; T3, *M. glauca* and *C. hystrix*; and T4, *M. glauca* and *E. fordii*) according to the relations of the facilitator and target species, and there were four subplots of each planting treatment. In 2016, we again measured the facilitator and target species in all of the treatments.

Forest Surveys

The population structure of the monoculture plantation was studied from August to September 2007 in the Experimental Center of Tropical Forestry. The first survey was installed prior to harvest in September 2007. We surveyed once again before the harvest during the summer of 2007 and during the summers of 2008, 2012, and 2016. Within an 11.2 m radius from the center of each plot, all of the trees (DBH >5 cm) were botanically identified, individually marked, and counted, and their diameters were measured. The tree density was quantified in this way to account more precisely for the density of the retained trees at a specific location, given the inherent variability in the preharvest tree densities since the last harvest. The DBH, measured 1.3 m above the ground, was noted, and the tree height was measured using an optical height meter (PM-5/1520 P, Suunto, Vantaa, Finland). The mean height and diameter increments were calculated by dividing the height and diameter by the tree age. For each 5 m $\times$ 5 m subplot, we determined the number of the planted specimens and their leaf area index (LAI), DBH, height and live aboveground biomass (AGB) as well as the composition and the number of any naturally generated trees and shrubs. We assessed the AGB variation of the four transplanted species in the four planting treatments along with the variable retention harvesting of the tropical monoculture plantation. The DBH and the height of the planted individuals were measured in every permanent plot. Then, the two parameters were used to calculate the aboveground biomass using the following four biomass equations from the literature:

C. hystrix: $W = 0.0641(D^2H)^{0.8699} + 0.01050(D^2H)^{0.8246}$ (He et al., 2012)

E. fordii: $W = 0.1957D^{2.0341} + 0.0431D^{1.9442}$ (Ming et al., 2014)

C. fissa: $W = 0.044(D^2H)^{0.9169}$ (H. K. Li & Lei, 2010)

M. glauca: $W = 0.022(D^2H)^{1.023}$ (J. Z. Li et al., 2011), where W is the individual aboveground biomass (kg), D is the DBH (cm), and H is the tree height (m).

Resource Measurements

To evaluate the effects of the experimental treatments on resource availability, we measured the light and nutrient availability at each of our sample points. The LAI is defined as the hemisurface area of green leaves (needles) per unit of horizontal ground surface area (Chen & Black, 1992). Thus, it is a measure of the amount of photosynthetically active tissue in a forest stand. We measured the light availability during 2008, 2012, and 2016. Photographs were captured in late August below the canopy in every plot at 1.5 m above the ground using a digital camera (Nikon) equipped with a fisheye lens. The measurements were made on cloudy days or early in the morning to obtain more contrast between the leaves and the gaps between them (sky or clouds) as well as to avoid direct sunlight. The photographs were exposed automatically because under- or overexposure did not improve the analysis. The LAI was obtained from the photographs by a canopy analysis system (Hemiview 2.1, Delta-T Devices Ltd., Cambridge, UK).

The soil sampling and measurements in 2008 were performed on 400 m^2 circular plots. For the nutrient analyses, the soil samples from the different retention harvesting levels were collected in the middle of each plot to evaluate the role of the facilitation species on the soil condition. Three punch-tube samples of the upper 15 cm of sandy soil were collected and mixed together for every plot. These bulk samples were then analyzed for total N by micro-Kjeldahl analysis, for soil acidity using the pH of water at a 1:2.5 soil to water ratio, and total organic matter by a modified Walkley–Black procedure (Holmgren et al.,1993).

Data Analysis

The cumulative volume growth was calculated for each year using the basal area multiplied by the corresponding tree height and a common form factor of 0.6 (Cannell, 1984), as shown in the following equation: $V_t = \pi \times (\frac{DBH_t}{2})^2 \times h_t \times f$, where V_t is the volume at age t, DBH_t is the diameter at age t, h_t is the tree height at age t, and f is the form factor (the ratio of tree volume to the volume of a cylinder with the same basal diameter and height). The Shannon–Wiener index (H) was used to estimate the diversity among the observed individuals (Magurran, 1988). We compared the structural traits of the trees within the plots by means of one-way analysis of variance (ANOVA), with the retention harvesting level as a factor. The data were checked for normality and heterogeneity of variance before analysis and found to be acceptable for analysis without transformation. The four planting treatment levels were then compared using a Tukey's test based on the overall effect. The measurements taken once were analyzed using ANOVA, and individual comparisons were based on a Tukey's test. Indicator species analyses (ISAs, duleg function in the labdsv package; Roberts, 2007) were used to identify the tree species that were significantly associated with one stand origin category or another. Species with values > 0.3 were interpreted as species highly associated with the corresponding category. This test compares the relative frequency of occurrence and abundance of species in different treatments and identifies the tree species that vary more between treatments than would be expected by chance (Legendre & Legendre, 1998). The statistical significance of each indicator value was determined by a Monte Carlo test using 999 permutations. Finally, the variation of the soil elements in the different planting levels was analyzed and compared using a one-way ANOVA and a Tukey's test. All of the statistical analyses were performed with R statistical software.

Results

Forest Structure

The variable retention harvesting significantly changed most of the studied variables. Several forest attributes differed among the retention levels (R20, R50, and R75; Table 2). The number of trees and effective LAI decreased incrementally with declining retention, whereas the mean height displayed the opposite response, increasing with decreasing retention. These patterns were mostly attributable to the reduced cover and density of trees. There were also significant differences in the mean diameter and basal area. The mean diameter increased to 26.3 cm in R50 because of the selection of larger trees for retention. The basal area significantly increased in R50 compared with the other treatments. A lower basal area was observed in R20 because of the presence of larger gaps. Finally, the total volume was also higher in R50 than in the other treatments.

Planted Species Among Harvesting Scenarios

There was a significant influence of the retention level on the composition of the planted saplings in all of the analyses (Table 3). The number of trees per hectare declined with the retention level, but all of the contrasts were significant (Table 3, $p < .05$ based on Turkey's test.). Although the number of individual trees increased

Table 2. Forest Structure Results (Mean ± *SE*) for Different Retention Harvesting Types (R20, R50, and R75) and Primary Unmanaged Forests That Consider the Number of Trees (N) (n hm^{-1}), MD (cm), BA (m^2 hm^{-1}), MH (m), TV (m^3 hm^{-1}), and Effective LAI.

Harvesting treatment	N	MD	BA	MH	TV	LAI
R20	318.4 ± 118.7a	19.3 ± 1.1a	30.2 ± 1.8a	18.2 ± 2.2a	187.36 ± 10.11a	1.04 ± 0.11a
R50	732.2 ± 84.3b	19.4 ± 3.2b	41.2 ± 0.8b	16.7 ± 1.9b	238.62 ± 8.54b	1.38 ± 0.18b
R75	1083.1 ± 127.9c	18.7 ± 2.2c	36.3 ± 0.9b	15.5 ± 1.7b	211.63 ± 7.19c	1.77 ± 0.21c
CT	1592.7 ± 103.2c	15.8 ± 4.3d	38.7 ± 2.1b	15.8 ± 2.3b	225.77 ± 12.12c	1.89 ± 0.11c

Note. Different letters denote significant differences at $p < .05$ by Tukey's test. MD = mean diameter; BA = basal area; MH = mean height; TV = total volume; LAI = leaf area index; CT = control.

Table 3. Characteristics After a 5-Year Period for Four Planted Species at Three Different Harvesting Retention Levels and for an Unmanaged CT That Included the Number of Live Trees Per Hectare (stems hm^{-2}) (N), the MN_d (stems hm^{-2}), and, Except for the Control, the Results of an ISA for the Tree Species.

		N			MN_d			ISA	
Planting species	R20	R50	R75	R20	R50	R75	R20	R50	R75
C. hystrix	877 ± 89a	827 ± 104a	783 ± 59a	314 ± 73d	321 ± 38d	394 ± 101c	0.354	0.413	0.116
E. fordii	819 ± 74c	803 ± 116c	732 ± 131c	368 ± 65a	332 ± 48c	414 ± 85a	0.291	0.420	0.122
C. fissa	815 ± 110d	811 ± 124d	701 ± 103d	342 ± 63b	351 ± 56b	382 ± 79d	0.058	0.146	0.003
M. glauca	868 ± 69b	808 ± 113b	727 ± 91b	347 ± 123b	356 ± 89a	408 ± 96b	0.008	0.287	0.024
CT	214 ± 68d	272 ± 57d	293 ± 86e	109 ± 66c	174 ± 47e	138 ± 51e	–	–	–

Note. Within rows, means followed by different letters are significantly different ($p < .05$) based on Tukey's test. ISA values > 0.3 are interpreted as species highly associated with the corresponding category. MN_d = mean number of dead plants; ISA = indicator species analysis; CT = control; *C. fissa* = *Castanopsis fissa*; *C. hystrix* = *Castanopsis hystrix*; *E. fordii* = *Erythrophloeum fordii; M. glauca* = *Manglietia glauca*.

over time in all harvest plots (Table 2, with Turkey's test $p < .05$.), the number of individuals of the four planted species declined with increasing harvest retention level (Table 3, with Turkey's test $p < .05$.). In addition, the number of all of the planted species was higher in the R20 treatment than in the other two retention treatments. For all of the treatments, the plots planted with *C. hystrix* showed significantly more individuals (877 stems hm^{-2}) than the other plots (Table 3, with Turkey's test $p < .05$.). The mean number of dead plants was quite variable among the retention levels, and all of the contrasts were significant (Table 3, with Turkey's test $p < .05$.). The mortality of the four species of saplings was significantly higher for the R75 treatment than for the other two retention levels. For the R75 treatment, *E. fordii* showed the largest number of dead trees (414 stems hm^{-2}), followed by *M. glauca* (408 stems hm^{-2}), *C. hystrix* (394 stems hm^{-2}), and finally *C. fissa* (382 stems hm^{-2}), with the smallest number. In addition, the planted species with different preferences responded differently to the retention levels after harvesting. The ISA indicates that the planted tree species were associated with particular retention levels (Table 3, with Turkey's test $p < .05$.). *C. hystrix* was significantly associated with R20 and R50 (with values of 0.354 and 0.413, respectively), whereas *E. fordii* showed a positive relation with R50 (0.420).

Facilitator Species Performance

C. fissa and *M. glauca* both performed as facilitators where the planted trees were present. For the total DBH and the sapling height of the four planting treatments, the saplings grew taller and greater in diameter when the treatments included *C. fissa* (T1 and T2) in the retention harvesting regimen (Figure 2). Most of the saplings had their greatest DBH in the treatments that included *C. fissa*, except for T3 with R20 (Figure 2). The height of the saplings was also greater in the company of the planted species, especially *C. fissa* (Figure 2). The maximum sapling height was 3.8 m, achieved in T1 with R50, whereas the maximum height for the *M. glauca* treatments was 3.2 m, lower than that for the *C. fissa* treatments and achieved in T3 with R20.

The mean annual DBH growth of the tree species differed significantly among the four planting treatments in the variable retention harvesting regimens (Table 4, with Turkey's test $p < .05$.). *C. hystrix* showed the greatest annual DBH growth in the treatment combination of T1 (CaFi-CaHy; Table 4) with R50 (0.74 cm $year^{-1}$), followed by *E. fordii* in the combination of T2 (CaFi-ErFo) with R20 (0.71 cm $year^{-1}$). A similar but even stronger trend was evident for the mean growth in height of *C. hystrix* and *E. fordii* in the presence of *C. fissa*, with both *C. hystrix* and *E. fordii* showing the

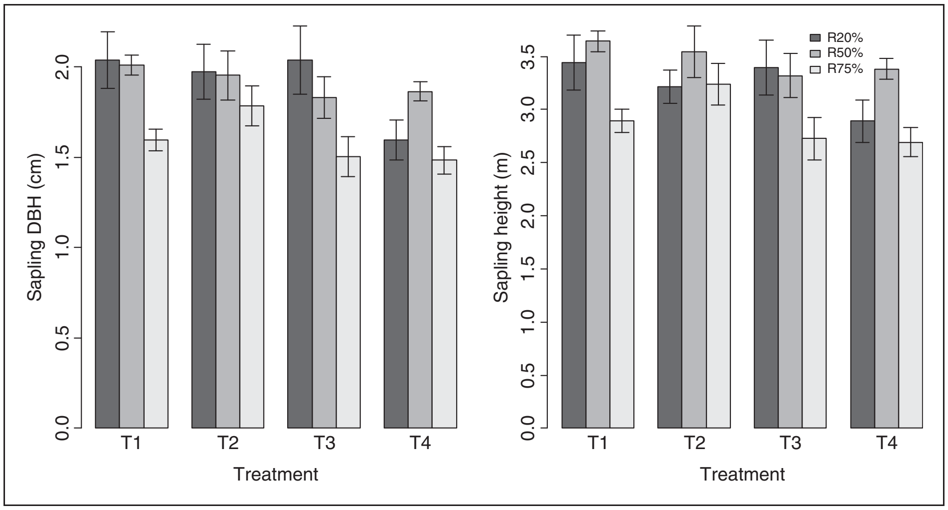

Figure 2. Sapling DBH and sapling height of four planting treatments (T1.CaFi-CaHy= C. *fissa* + *C. hystrix*; T2.CaFi-ErFo = *C. fissa* + *E. fordii*; T3.MaGl-CaHy= *M. glauca* + *C. hystrix*; T4. MaGl-ErFo= *M. glauca* + *E. fordii*) in three variable retention harvesting (R20%, R50% and R75%) in 2012. Bars represent one standard error. DBH = diameter at breast height.

Table 4. Results of Analyses Examining the Influence on the Target Species Saplings (*C. hystrix* and *E. fordii*) of the Species Planting and Retention Harvesting Treatments. The Variables Examined in the Target Species Included the MDG (cm year^{-1}), MHG (m year^{-1}), and Total AGB (t hm^{-2}).

Planting Treatment	Target species	MDG			MHG			AGB		
		R20	R50	R75	R20	R50	R75	R20	R50	R75
T1	*C. hystrix*	0.68±0.01b	0.74±0.02a	0.58±0.01a	0.34±0.01a	0.38±0.03a	0.27±0.01b	118.6±11.2a	129.2±12.1a	99.8±8.2b
T2	*E. fordii*	0.71±0.01a	0.67±0.01c	0.51±0.03d	0.31±0.02b	0.35±0.03b	0.28±0.03b	110.9±10.1c	122.1±10.9b	98.3±11.2a
T3	*C. hystrix*	0.67±0.02b	0.69±0.03b	0.57±0.01b	0.29±0.02c	0.25±0.01c	0.31±0.02a	117.04±12.2b	118.7±10.7c	97.0±14.4c
T4	*E. fordii*	0.66±0.01c	0.63±0.01d	0.56±0.01c	0.26±0.01c	0.27±0.02c	0.24±0.01c	99.73±9.2d	116.6±13.7c	94.3±13.2c

Note. T1, CaFi-CaHy = *C. fissa* + *C. hystrix*; T2, CaFi-ErFo = *C. fissa* + *E. fordii*; T3, MaGl-CaHy = *M. glauca* + *C. hystrix*; and T4, MaGl-ErFo = *M. glauca* + *E. fordii*. Different letters indicate differences that are statistically significant at $p < .05$ by Tukey's test. MDG = Mean DBH Growth; DBH = diameter at breast height; MHG = mean height growth; AGB = aboveground biomass; *E. fordii* = *Erythrophloeum fordii; M. glauca* = *Manglietia glauca*; *C. fissa* = *Castanopsis fissa*; *C. hystrix* = *Castanopsis hystrix*.

greatest growth in the plots with 50% retention harvesting (0.38 m year^{-1} and 0.35 m year^{-1}, respectively). This result clearly demonstrated the facilitator effect of the two plant species, with positive effects on the growth of the two target species.

The results also indicated significant differences among the planting treatments in the aboveground biomass (Figure 3), with the highest biomass produced by the treatment combination of R50 with T1, followed by T2. Both T3 and T4 exhibited lower aboveground biomasses than those of T1 and T2 at similar retention harvesting levels, except for T2 at R75. The aboveground biomass of the planted species differed significantly among the three retention levels and four planting treatments. For the retention levels, the R50 harvesting treatment presented a higher biomass (T1 and T2 were 129.2 t hm^{-2} and 122.1 t hm^{-2}, respectively) than those of the other two levels (Table 4). The aboveground biomass was higher in the *C. fissa* than in the *M. glauca* treatments (Table 4) and, on average, was highest in the plots with *C. fissa* combined with R50 (129.2 t hm^{-2}). The biomass in T4 was lowest (94.3 t hm^{-2}) at the R75 level because *E. fordii* grows very slowly. For the planting treatments, *C. fissa* performed better than *C. hystrix* as a facilitator at all of the retention levels (Table 4).

The abundance and the diversity of the naturally regenerated saplings differed significantly among the four planting treatments managed with variable retention harvesting (Table 5). Furthermore, the average abundance (649 N hm^{-2}) and diversity (*H*: 1.3) in T1 were significantly higher for R50 than for the other treatments. At the same retention harvesting levels, the abundance and diversity were higher in the plots planted with

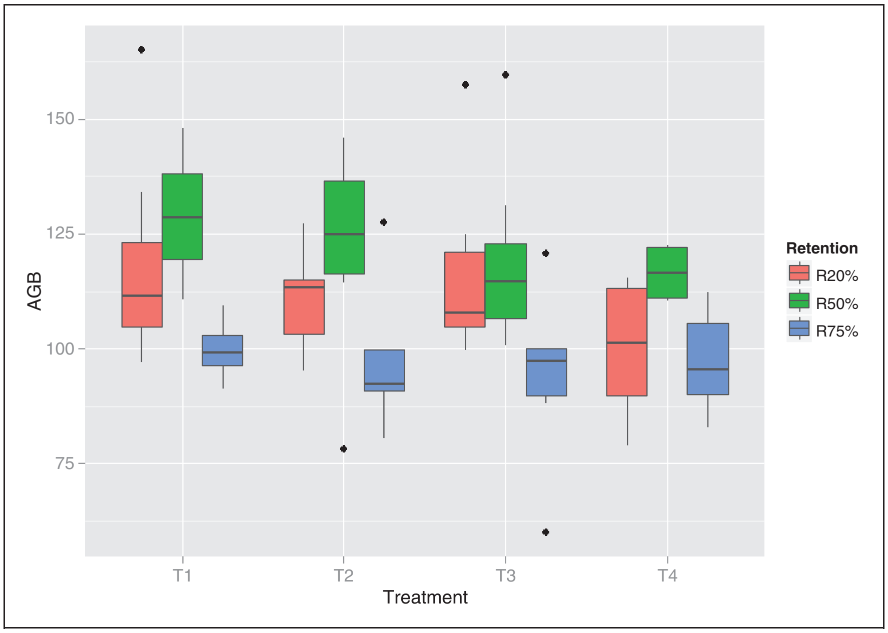

Figure 3. Box plots showing AGB (t hm^{-2}) of planted species for four planted treatments in three variable retention harvests. The horizontal line in each box is the median. Boxes enclose the 75th and 25th percentiles, and error bars enclose the 90th and 10th percentiles. Significant differences ($p < .05$) between treatments are indicated by different letters above the boxes. AGB = aboveground biomass.

Table 5. The N_R (stems hm^{-2}), Shannon–Wiener Index (*H*), and LAI of Naturally Regenerated Saplings for Each Treatment Over a 5-Year Period (Mean ± *SE*).

Planting treatment	N_R			*H*			LAI		
	R20	R50	R75	R20	R50	R75	R20	R50	R75
T1	527±17b	649±41a	567±38b	0.83±0.11a	1.30±0.11a	1.09±0.33b	1.17±0.44b	1.37±0.14a	1.38±0.10b
T2	513±22b	611±53a	575±22a	0.79±0.31a	1.01±0.21b	1.11±0.28a	1.01±0.37c	1.36±0.11a	1.37±0.14c
T3	564±26a	588±77b	568±16b	0.64±0.17c	0.97±0.19b	0.93±0.14c	1.21±0.24a	1.32±0.25b	1.44±0.10a
T4	498±37c	546±19c	543±15c	0.71±0.24b	0.89±0.16c	0.90±0.18d	1.11±0.29b	1.31±0.10b	1.33±0.10b

Note. T1, CaFi-CaHy = *C. fissa* + *C. hystrix*; T2, CaFi-ErFo = *C. fissa* + *E. fordii*; T3, MaGl-CaHy = *M. glauca* + *C. hystrix*; and T4, MaGl-ErFo = *M. glauca* + *E. fordii*. Different letters indicate differences that are significant at $p < .05$ by Tukey's test. N_R = number per hectare; LAI = leaf area index. *E. fordii* = *Erythrophloeum fordii; M. glauca* = *Manglietia glauca*; *C. fissa* = *Castanopsis fissa*; *C. hystrix* = *Castanopsis hystrix*.

C. fissa than in those planted with *M. glauca*. The plots planted with *C. fissa* also showed a higher recruitment of species than those planted with *M. glauca*. The abundance (498 N hm^{-2}) and the diversity (*H*: 0.64) were lowest for the plots containing the T4 with R20 and the T3 with R20 treatment combinations, respectively. The LAIs differed significantly among the four planting treatments with Turkey's test ($p < .05$). Overall, the LAI decreased because of thinning. The average LAI (1.44) was significantly higher in the T3 with R75 plots planted with *M. glauca* than in the other planting treatment plots (Table 5). T1 with R75 showed the second highest LAI (1.38), but the differences between *C. hystrix* and *E. fordii* were not significant when the data were pooled by species within R75 (e.g., T1, T2 and T3, T4). Finally, the mean LAI for the R75 treatments was larger than the means for the other two retention levels. Across the tree retention treatments, the plots with less tree retention showed higher light availability.

Many soil properties in the monoculture were altered by the different planting treatments 5 years postharvest (Table 6). The different treatments affected the soil properties (N, pH, and organic matter) very differently (Table 6). The average N totals of T1, which was planted with *C. fissa*, were significantly higher than those of the other planting treatments. The total N increased

Table 6. Soil Total N, pH, and Organic Matter (Mean ± *SE*) in Four Treatments.

Planting treatment	Total N ($g\ kg^{-1}$)			pH			Organic matter ($g\ kg^{-1}$)		
	2008	2012	Difference	2008	2012	Difference	2008	2012	Difference
T1	0.59 ± 0.13	1.08 ± 0.18	0.49a	4.2 ± 0.21	4.3 ± 0.072	0.1a	18.76 ± 4.21	23.33 ± 3.6	4.57c
T2	0.69 ± 0.20	1.01 ± 0.15	0.32b	4.1 ± 0.14	4.3 ± 0.201	0.1a	17.91 ± 1.35	21.59 ± 2.22	3.68a
T3	0.64 ± 0.11	0.91 ± 0.20	0.27c	4.2 ± 0.16	4.4 ± 0.08	0.2b	18.84 ± 5.6	20.67 ± 2.88	1.83b
T4	0.67 ± 0.18	0.76 ± 0.11	0.09d	4.3 ± 0.11	4.5 ± 0.43	0.2b	19.04 ± 7.1	20.65 ± 4.52	1.61c
CT	0.63 ± 0.29	0.68 ± 0.21	0.05e	4.1 ± 0.12	4.2 ± 0.07	0.1a	18.68 ± 6.9	18.57 ± 5.3	−0.11d

Note. Different letters indicate significant differences at $p < .05$ based on ANOVA. ANOVA = analysis of variance; CT = control.

significantly over the study period for the *C. fissa* planting treatments (T1 and T2), whose values were clearly higher than those of the other treatments. The total N in the CT plots changed the least (0.05 $g\ kg^{-1}$). The differences in soil pH among the treatments were found to be just statistically significantly. The average soil pH (4.5) in T4, which was planted with *M. glauca*, was higher than those in the other treatments, with T3 having the second highest value. The change in soil pH for the *C. fissa* treatments (T1 and T2) was significantly lower than that for the *M. glauca* treatments (T3 and T4) during the 5-year period. The average soil organic matter differed significantly among the four treatments ($p < .05$). The T1 plots had the highest soil organic matter (23.33 $g\ kg^{-1}$) when compared with the T2, T3, and T4 plots. The soil organic matter in the plots planted with *C. fissa* was higher than that in the plots planted with *M. glauca*. The soil organic matter was lowest, on average, for T4, but increased significantly beneath *C. fissa* in T1 and T2 ($p < .05$) and decreased by 0.11 $g\ kg^{-1}$ in the CT plots.

Discussion

There is significant interest in silvicultural systems that can emulate natural disturbance and change the structural complexity, biological diversity, and microenvironment in managed forests (Franklin et al., 2002). Variable retention harvesting has emerged as one strategy to achieve such goals (Gustafsson et al., 2012; Lindenmayer et al., 2012). Forest managers use variable retention harvesting to change the structure and the condition of communities and thereby accelerate alternative succession processes.

Our results confirmed that retention harvesting can produce significant changes in the structure of managed forests and that the resulting composition of naturally regenerated saplings are quite different from those found in unmanaged areas, suggesting that active management may achieve the desired conditions more rapidly than passive approaches. Moreover, compared with unmanaged forests, harvesting modifies the microclimate through alterations in the overstory canopy, increasing temperature, radiation, and soil moisture modifications in the crown canopy (e.g., gaps) and changes the microclimate and available resources at the understory level (e.g., soil, light and nutrient cycling). These findings suggest that variable retention harvesting may be a strategy to hasten the structural development of more complex conditions in currently unmanaged forests.

We found that 50% retention harvesting was the most effective of the three tested levels at generating live-tree structural characteristics and growth. This finding indicates that 50% retention harvesting may have generated faster recovery than the lower retention levels and be more likely to foster earlier succession species. It can thus be concluded that regeneration rates are a direct function of the harvesting impact on the overstory canopy. However, an effective management strategy for restoring monoculture plantations cannot depend only on retention harvesting because monocultures are sometimes also degraded by logging. Combining variable retention harvesting with the planting of facilitator species provided a way to reestablish an initial assemblage of species and initiate the desired successional trajectory.

An applications for community restoration facilitation between plants is the nurse plant effect because of the amelioration of extreme environmental conditions (Gómez-Ruiz et al., 2013).The results of our research offer evidence that the effect of the plant–plant interaction between the facilitator species and the two target species was positive, with both *M. glauca* and especially *C. fissa* acting as facilitator plants, favoring the development of the target tree species. Our study shows that the interaction between facilitators and target species can improve such communities over a 5-year period. Moreover, our study demonstrated a positive interaction between the planted species, with the influences of *C. fissa* and *M. glauca* facilitating increased abundance, diversity, and improved soil conditions that can contribute to habitat restoration. Our results thus support the hypothesis that the initial assemblage of a plant community is crucial in determining the composition of a plant community (Bezemer, Harvey, Kowalchuk, Korpershoek, & Van Der Putten, 2006) and the hypothesis that the functional characteristics of an initial plant assemblage within communities are important in driving plant community composition, influencing the community assemblage (Gleason, 1917).

Overall, the DBH and height growth rates were greater in the *C. fissa* treatments than in the *M. glauca* treatments. This result may reflect intrinsic differences between the growth rates of these two species or may be an artifact of each species' response to the transplantation and retention harvesting methodology. Additional evidence for the positive facilitative effects of *C. fissa* on the planted tree species is provided by the fact that the AGB was greater in the *C. fissa* than in the majority of the *M. glauca* planting treatments, indicating the existence of facilitation. The target species most likely had a greater capacity to accumulate biomass because the resource utilization by *C. fissa* and *C. hystrix* was less competitive, raising their total aboveground biomass accumulation when planted together. The results obtained in this study indicate that facilitator treatment with *C. fissa* could lead to more rapid biomass accumulation than treatment with *M. glauca*, a fact that should be taken into account when designing ecological restoration strategies. This relatively rapid recovery may have been caused in part by the facilitator species when the original retention harvesting was performed because the biological interaction also depends on the intrinsic characteristics of the species.

As fast-growing broadleaf species, *C. fissa* and *M. glauca* raise the stand LAI and produce a denser canopy with greater shading. However, for natural regeneration, the variable retention harvesting removed certain individuals that can impact the heterogeneous overstory canopy structures. It appears that a facilitator is able to take advantage of the increased solar radiation created by canopy removal, provided enough residual trees are present to buffer the effects of increased exposure. *C. hystrix* and *E. fordii* require gaps for successful germination and establishment, and the unplanted natural facilitator treatment had a lower biomass than the planted facilitator treatments. We suggest that an altered cover canopy provides changes that are related to plasticity in the growth of intermediate- and late-stage species along light gradients. *C. hystrix* was observed to behave as a heliophilous species, with rapid growth under favorable conditions, enhanced by the presence of *C. fissa*. By contrast, *E. fordii* is a much slower growing species that because it is a late pioneer and requires more stable medium conditions for better development (Sein & Mitlöhner, 2011; Zhao, Lin, Guo, & Zeng, 2014). The advantage of using heliophilous species with rapid growth as facilitators is that they remain within the ecosystem for a definite period of time, assisting the establishment of pioneer species, and subsequently creating appropriate environmental conditions for later species (Lamb, Erskine, & Parrotta, 2005). By the time the monoculture conditions change, the beneficiary species have already adapted to the medium because of the improved conditions produced by the facilitator, and it is thereby possible to naturally reactivate a successional dynamic to which other species of interest can be added, either in the form of propagules or individuals.

Other factors provided by facilitators can also improve the growth of the understory species. Total soil nitrogen was higher under the *C. fissa* treatments than under the *M. glauca* treatments. As was the case with nitrogen, the soil organic matter increased more with *C. fissa* than with *M. glauca*. Increased soil organic matter should benefit the shade-tolerant understory plants. Our results demonstrate that both facilitator species, but mainly *C. fissa*, assisted the establishment of *C. hystrix* and *E. fordii* at the study site and confirmed that the latter two species presented greater growth and natural regeneration in the 50% retention harvesting plots containing *C. fissa*. This facilitation most likely occurred because *C. fissa* have the strong potential to increase soil nutrition through nitrogen fixation by their root nodules.

We found that *C. fissa* was the species that performed best in the facilitator role, as demonstrated by the greater development of both target species when grown alongside *C. fissa*. Gómez-Aparicio (2009) argues that plants are the life form with the greatest potential to act as facilitators in the context of restoration activities because their resource distribution and architecture imply that they do not compete strongly at the soil level. Our research supports his claim. It is known that the facilitator effect of *C. fissa* through nitrogen fixation and the improvement of certain abiotic conditions, such as soil organic matter, is due to the heavy litters (Choong, 1996).

In certain cases, it may be necessary to restore site fertility using an exotic drought-resistant species before using any native species in plantations (Lamb & Gilmour, 2003). *M. glauca* is an exotic species that was introduced from Vietnam (Wang & Cai, 2008) and shows a broad vegetal coverage, resistance to drought, tolerance to some shade and acidic soil, and the capacity to help prevent the erosion of bare soils. In China, timber plantations are often established as monocultures using this exotic species, which grows rapidly and is well established in the marketplace. This knowledge can be used to decide how to choose combinations of species with different species traits and growth strategies that can favor successional progress in the desired direction. Nevertheless, compared with *C. fissa*, *M. glauca* would not be a good facilitator because these plants are slower in accumulating biomass or more sensitive to light. Still, this exotic tree species may be a useful addition to monocultures at severely degraded sites when this is the only species able to tolerate the existing site conditions.

The use of a facilitator in the early successional stage of a restoration program that includes variable retention harvesting can be an effective strategy for accelerating the progress of succession (Gómez-Aparicio, 2009). This strategy for restoring monoculture plantations not only changed the microenvironment conditions (such as soil and light availability, among others) but also established an initial plant assemblage that matched the expected target forest. These results highlight the conclusion that facilitation can play a critical role in determining growth and regeneration within monoculture plantations. In this regard, the study of restoration as well as the selection of facilitator plants must be considered in the planning and the execution of management and restoration activities because the capacity to drive the successional dynamics and guide the desired initial assemblage of plants in a degraded forest ecosystem constitutes an instrument of great value.

Implications for Conservation

Here, we present evidence that the planting of facilitator species during early successional stages has great potential for use as a practical restoration strategy for monoculture plantations. The result showed that *C. fissa* and *M. glauca* act as facilitators of the two target species, the results demonstrated that both species, but mainly *C. fissa*, acted as nurse plants for the native species that were assisted in their establishment at the study site. The results also supported that different retention harvesting treatments produce a differential effect on the development of target species. The growth of both native species was greater when they were planted with *C. fissa*, which demonstrated a better capacity than *M. glauca* to improve the environmental conditions that favor the native species. Finally, facilitation can be used to structure plant communities that can drive the process, and variable retention harvesting should be used in strategies planned to restore damaged and altered stand conditions. Facilitation by native species in variable retention harvesting can shape the establishment of plant communities and ameliorate the microenvironment conditions to favor the development of target species.

For monoculture plantations, it is urgent to develop different restoration and conservation strategies for the establishment and the growth of early regeneration, which varies with the species and stage of seedling development. Although tradeoffs must be found among the functional integrity of the forest ecosystem, timber yield, and biodiversity, managers have considerable flexibility to employ various types of facilitation patterns coupled with the planting of facilitators on monoculture plantations, at least at the levels of retention studied here.

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