

Cluster planting facilitates survival but not growth in early development of restored tropical forest



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Abstract

Interspecific interactions are considered to be important structuring forces in early successional vegetation. Whereas competition seems to prevail in less severe environments, facilitation tends to increase in importance in harsh environments. Hence, facilitation is expected to play an important role in degraded tropical areas with high irradiance, heat loads, and evapotranspiration, where conditions are far from optimum for most forest species. We planned a restoration project on the southeastern Brazilian coastal plain to compare growth and survival of tree seedlings planted at two densities (isolated or aggregated) in a factorial experiment with nutrient addition. We monitored survival, height, ground level diameter, and crown projection of 4132 saplings from 19 species that ranged along a successional gradient, over an 18-month period. We used mixed-effect models to analyze the relationship between species performance and treatments, and Akaike's information criterion (AIC) to select the models. The best model showed higher survival in aggregated plantations (indicating facilitation) for non-pioneer (slower growing) species. In contrast, we found lower diameter growth in aggregated plantation (indicating competition). Fertilizer addition did not affect survival in clusters, but, surprisingly, it had a negative effect on isolated plants of both pioneer and non-pioneer species. Fertilizer addition had a positive effect on diameter and crown projection growth in aggregated plantations (reducing competition), especially for pioneer species. Thus, whether facilitation or competition was the predominant interaction depended on the effect analyzed. As establishment of non-pioneer species in disturbed sites can be challenging, restoration designs could take advantage of higher survival rates in clusters and use resource addition to ameliorate growth and decrease competition for limited resources.

Zusammenfassung

Interspezifische Interaktionen werden als wichtige strukturierende Kräfte für die frühe Sukzessionsvegetation angesehen. Während Konkurrenz bei weniger strengen Umweltbedingungen vorzuherrschen scheint, tendiert 'facilitation' bei harschen Umweltbedingungen an Bedeutung zuzunehmen. Deshalb wird erwartet, dass 'facilitation' eine wichtige Rolle in degradierten tropischen Gebieten mit hoher Einstrahlung, Wärmebelastung und Evapotranspiration spielt, wo die Bedingungen weit vom Optimum für die meisten Waldarten entfernt sind. Wir planten ein Renaturierungsprojekt in der Küstenebene Südost-Brasiliens, um Wachstum und Überleben von Baumsetzlingen zu vergleichen, die in zwei Dichten (isoliert und aggregiert) in einem faktoriellen

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Experiment mit Nährstoffzugabe gepflanzt wurden. Wir erfassten über 18 Monate hinweg Überlebensrate, Höhe, basalen Stammdurchmesser und Kronenprojektionsfläche von 4132 Setzlingen aus 19 Arten in einem Sukzessionsgradienten. Wir benutzten gemischte Modelle, um die Beziehung zwischen der Performanz der Arten und den Behandlungen zu analysieren, und wählten die Modelle mit Hilfe des Akaike-Informationskriteriums (AIC) aus. Das beste Modell zeigte höhere Überlebensraten bei aggregierter Pflanzung (Indiz für 'facilitation') für langsam wachsende Nicht-Pionier-Arten. Dagegen fanden wir geringeres Dickenwachstum bei aggregierter Pflanzung (Indiz für Konkurrenz). Düngung beeinflusste die Überlebensrate bei aggregierter Pflanzung nicht, sie hatte aber überraschenderweise einen negativen Effekt auf isolierte Pflanzen von sowohl Pionier-Arten als auch Nicht-Pionier-Arten. Düngung hatte besonders bei Pionierpflanzen einen positiven Effekt auf Dicken- Kronenwachstum bei aggregierter Pflanzung (Indiz für reduzierte Konkurrenz). Ob 'facilitation' oder Konkurrenz die vorherrschende Interaktion war, hing damit vom betrachteten Effekt ab. Da die Etablierung von Nicht-Pionier- Arten auf gestörten Flächen sehr schwierig sein kann, könnten Renaturierungsplanungen sich die höheren Überlebensraten bei aggregierter Pflanzung zunutze machen und Düngung einsetzen, um das Wachstum zu verbessern und die Konkurrenz um begrenzte Ressourcen zu vermindern.
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Introduction

Interspecific interactions play an important role in the establishment of new plant communities. Competition (Dybzinski & Tilman 2007; Weigelt et al. 2007) and facilitation (Bruno, Stachowicz, & Bertness 2003; Brooker et al. 2008) can act simultaneously and interact in complex ways in structuring communities, and both mechanisms have been reported to explain species coexistence (Cavieres & Badano 2009; Wright 2002). Whereas competition has been proposed to be a major structuring force in less severe environments, facilitation tends to increase in importance in harsh environments (Bertness & Callaway 1994; Callaway et al. 2002; Maestre, Callaway, Valladares, & Lortie 2009), where nurse plants (Padilla & Pugnaire 2006) improve environmental conditions for target plants through shading, ameliorating temperature extremes, changing soil properties, and increasing resource availability (Callaway 1995).

Therefore, facilitation could well play an important role in degraded tropical areas with high irradiance, heat loads, and evapotranspiration, conditions that are far from the optimum for most forest species (Gómez-Aparicio 2009). Some remnant trees and small patches of trees have been shown to facilitate plant establishment in tropical degraded areas (Schlawin & Zahawi 2008; Corbin & Holl 2012; Zwiener, Cardoso, Padiál, & Marques, 2014). Moreover, in active restoration pioneer trees can also act as nurse plants (Gómez-Aparicio 2009; Prévosto, Monnier, Ripert, & Fernandez 2012) because they are more tolerant to harsh microclimatic conditions, grow quickly, and ameliorate conditions for non-pioneer species (Connell & Slatyer 1977).

Organisms in close proximity can also compete, and resource competition theory predicts that when species compete for a single resource, those able to cope with the lowest resource levels are likely to win (Dybzinski & Tilman 2007). Moreover, rapidly colonizing, fast-growing species (pioneers) are typically weaker competitors for nutrients (Wedin & Tilman 1993). Therefore, responses to biotic interaction

and resource addition may differ according to the successional status, and it would be expected that pioneer species are most likely to benefit from nutrient enrichment (Lawrence 2003; Siddique et al. 2010), because of subsequent reductions in competition.

In this context, we planned a restoration project in the coastal plain of Brazil to experimentally test how plant proximity and changes in resource availability impact the survival and growth of species from different successional groups. We compared the performance of individuals in multi-species clusters (aggregated plantings) with that of individuals from the same species in less dense (isolated) plantings to determine whether they performed better when planted more densely, which we interpreted as facilitation, or in isolated conditions, indicating competition. We also evaluated the effect of adding resources (fertilizer) on interspecific interactions. Following the framework presented above, we predicted that (1) fast growing plants (pioneers) would provide shade for slow growing species (non-pioneers) and facilitate their survival and growth in degraded areas (Yang, Ren, Liu, & Wang 2010); thus non-pioneers would respond more positively in the aggregated planting; and (2) pioneers should be in competitive disadvantage for nutrients and hence would benefit more from nutrient enrichment. Such manipulative experiments in restoration projects represent excellent opportunities to test and refine ecological theories, which in turn may contribute to new insights in developing restoration models (Young, Petersen, & Clary 2005). Despite the theory and empirical bases for those predictions, they have never been tested in a multi-species restoration context in the tropics.

Materials and methods

Study area

We conducted this study adjacent to the Camburu River on the coastal plain, in Caraguatatuba, São Paulo state, south-eastern Brazil (23°39'27"S, 45°30'03"W). The climate is

warm (mean annual temperature is 24.5 °C, with mean minimum 18.2 °C, and mean maximum 34.5 °C), characterized by rainy summers and less rainy winters, but there is no well-defined dry season. Mean annual precipitation from 1943 to 2004 was 1784 mm (Santos & Galvani 2012). The site is ~7 m a.s.l., and the topography is almost flat with some areas subject to periodic flooding due to heavy rains or upwelling of groundwater. The soil is a mix between original sandy soil and clay soil originating from a landslide in 1967 (Ferreira 2013). The area was dominated by invasive grasses and was used for grazing prior to the start of this study. The landscape is comprised of a pasture matrix, with a few small fragments of secondary forest on the coastal plains surrounded by a dense tropical forest in the mountain range ca. 1.5 km away.

Experimental design

The experimental design consists of two main factors: planting system and fertilization set up in an orthogonal fashion with four factorial treatment combinations: isolated plantation fertilized (I-F), isolated non-fertilized (I-NF), aggregated plantation fertilized (A-F), and aggregated non-fertilized (A-NF). There were eight replicate blocks which included ~20 m × 50 m plots of each treatment and were

separated by an un-manipulated area (Fig. 1A). We selected six pioneer and 13 non-pioneer native tree species to plant using the categorizations of Swaine and Whitmore (1988). Saplings from those species were planted in two planting system: isolated (I) on a 2Ym × 2Ym-grid with alternating lines of pioneer and non-pioneer species (Fig. 1B); and aggregated (A), where mixed-species clusters of 13 saplings were planted with 5-m separation (Fig. 1C). Within each cluster, saplings were separated by 30 cm. Each cluster was composed of five species previously classified as pioneers and eight as non-pioneers species (Fig. 1D). We used two different cluster compositions with a total of 19 species monitored in both the aggregated and isolated plantings.

The soil was prepared by adding lime to the entire study area at a rate of 1500 kg/ha. The planting holes were dug mechanically to 30 cm × 30 cm × 30 cm. Prior to planting, 5 g of hydrogel diluted in 1 L of water were added in each planting hole in order to reduce initial mortality due to water stress. Seedlings were planted manually. Seedlings varied between 6 and 18 months age at the time of planting, but most seedlings of the same species were the same age.

The fertilization treatment comprised two additions of 100 g of slow release NPK 20:0:20 per plant separated by 9 months; each addition divided into three equal portions and applied once monthly for three months. We followed soil

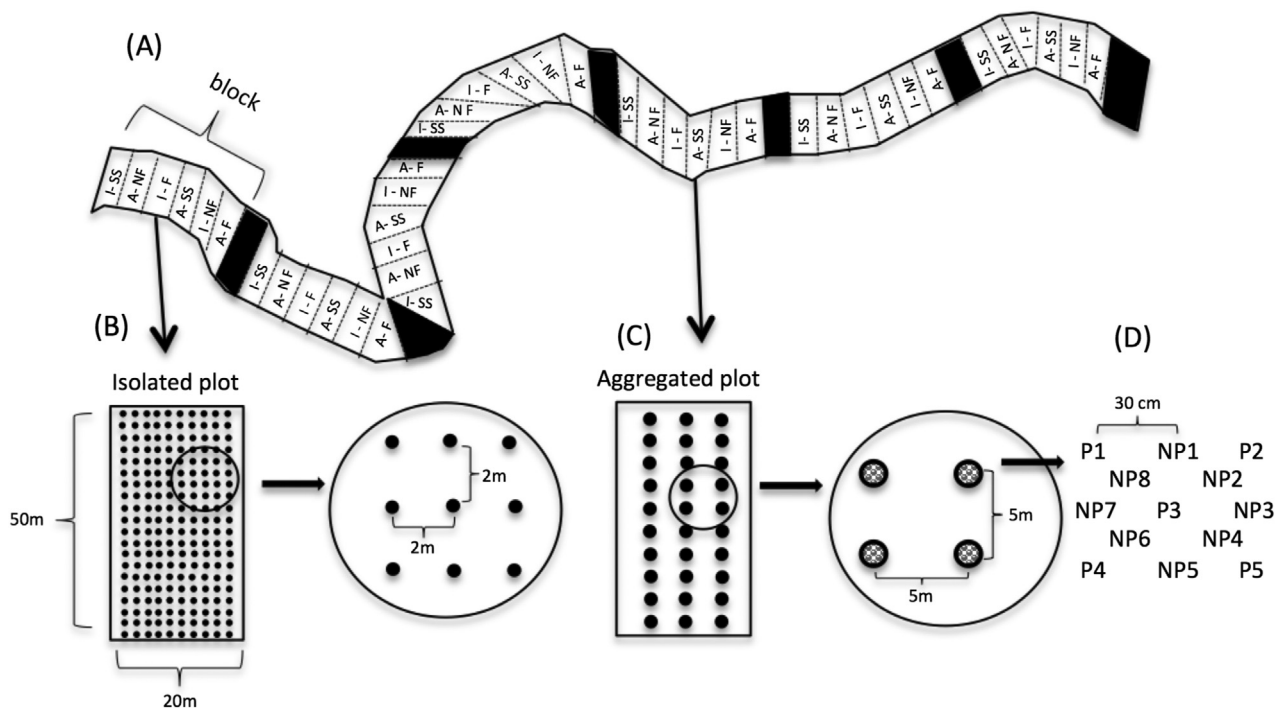


Fig. 1. (A) Experimental design. Each block was composed of six 20 m × 50 m plots and was separated by an empty plot (filled in black). I-SS: Isolated plot with standardized soil (2 liters of humus per plant) used to determine the proxy for successional index (data not used in this experiment); A-NF: Aggregated plot non fertilized; I-F: Isolated plot fertilized; A-SS: Aggregated plot with standardized soil (data not used in this experiment); I-NF: Isolated plot non fertilized; A-F: Aggregated plot fertilized. (B) In isolated plots seedlings were planted equidistant (2 m) throughout the plot; (C) In aggregated plots cluster centers were separated by 5 m from each other; (D) In each cluster seedlings were planted 30 cm apart from each other inside clusters, with five different pioneer species (P) in the center and on the edge of each plot and 8 different non-pioneer species (NP) around the pioneers.

Table 1. Selected models ($\Delta AIC < 2$) for the effect of treatments on the survival and growth of 16 species over 18-months. Survival models were binomial generalized mixed models (GLMM) with survival probabilities as response variable, and growth models used Gaussian distribution and had relative growth rate (RGR) as response variable. Successional index (continuous variable), fertilizer (fertilized or non-fertilized), and planting system (aggregate or isolated), and all possible interactions were considered as fixed effects. Every model included block as a random effect. SI: Successional index; F: Fertilizer; PS: Planting system.

Parameters							Survival	Growth rate	
PS × F × SI	PS × SI	SI × F	PS × F	SI	PS	F		Diameter	Crown
							ΔAIC	ΔAIC	ΔAIC
	×		×	×	×	×	0	–	–
	×	×	×	×	×	×	1.7	–	–
	×	×		×	×	×	–	1.2	–
	×	×	×	×	×	×	–	0	–
				×			–	–	0

analysis recommendations for the amount and proportion of nutrients to add, consistent with typical restoration practices in this area. The contrast was a non-fertilized treatment with no nutrient addition. In addition to the treatments described above there was another pair of aggregated and isolated planting plots per block (not presented in our main results) with standardized soil conditions, where 2 L of humus per plant were incorporated at the time of the outplanting. We used the isolated-planting, standardized-soil plots to establish a proxy for successional index based on plant height growth (see next section).

In each plot, we monitored a minimum of six randomly-selected individuals from each species totaling 4132 saplings from 19 species. At the time of outplanting, saplings varied in initial size from 2 cm (mostly the palms, since we measured from apical bud) to 140 cm. Although variation among species was high, variation among individuals of the same species was quite low, since they were all from the same cohort. After three months we replanted all dead individuals to eliminate mortality due to outplanting stress, and 30 days after replanting we took initial measurements.

Data collection and analysis

We measured survival, height of tallest stem, ground level diameter, and crown projection of saplings. Crown projection was quantified using the ellipse area calculated from two perpendicular measures. We calculated the Relative Growth Rate (RGR – *sensu* Hoffmann & Poorter 2002) for each growth variable from initial census to the 18-month census for all surviving saplings. We excluded from our analysis species for which all individuals died in one or more factorial treatments, which resulted in 16 species for data analysis.

Because classification of successional characteristics can be subjective and is certainly better represented as a continuum rather than dichotomous groups (i.e., pioneers and non-pioneers) (Alvarez-Buylla & Martinez-Ramos 1992; Lieberman, Lieberman, Peralta, & Hartshorn 1995; Souza & Válio 2003), we decided to establish a continuum proxy for successional classification instead of using the binary pioneer

vs. non-pioneer classification. Assuming that pioneer species have higher growth rates than non-pioneers under high light conditions (Baker, Swaine & Burslem 2003), we used the median height RGR of each species from the 18-month period in the isolated system of the standardized soil plots as a proxy. However, in order to assess whether the proxy used for successional index strongly affected the results, we also performed all analyses using the dichotomous groups according to literature (i.e. pioneer and non-pioneer species) and the results were qualitatively similar (see Appendix A).

We used mixed-effects models to analyze the relationship between species performance and treatments, because they allow for differences in mean responses across blocks of a field experiment (Crawley 2013). The response variables were (1) proportion surviving, (2) ground level diameter RGR, and (3) crown projection RGR. We considered successional index (SI), fertilizer (F), planting system (PS) and all possible interactions as fixed effects, and blocks as a random effect.

We used generalized linear mixed effect models (GLMM) to model proportion of surviving seedlings as a linear response, assuming binomial error distribution. For diameter and crown RGR we used linear mixed effect models (LMM). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. To estimate model coefficients we used Maximum Likelihood Estimation using packages lme4 and bbmle in the R programming environment (Bates, Maechler, Bolker, & Walker 2015). We contrast the most parsimonious model (null model) with all biologically meaningful combinations of fixed variables (Table 1). The overall fit of all models was compared using Akaike's Information Criterion (AIC). We considered every model with $\Delta AIC < 2.0$ to be equally plausible.

Results

Our results showed that height RGRs are continuous for species in the isolated system with standardized soil (Fig. 2), since there was no break point, and 10–90% quantiles of data clearly overlap among species. Species previously

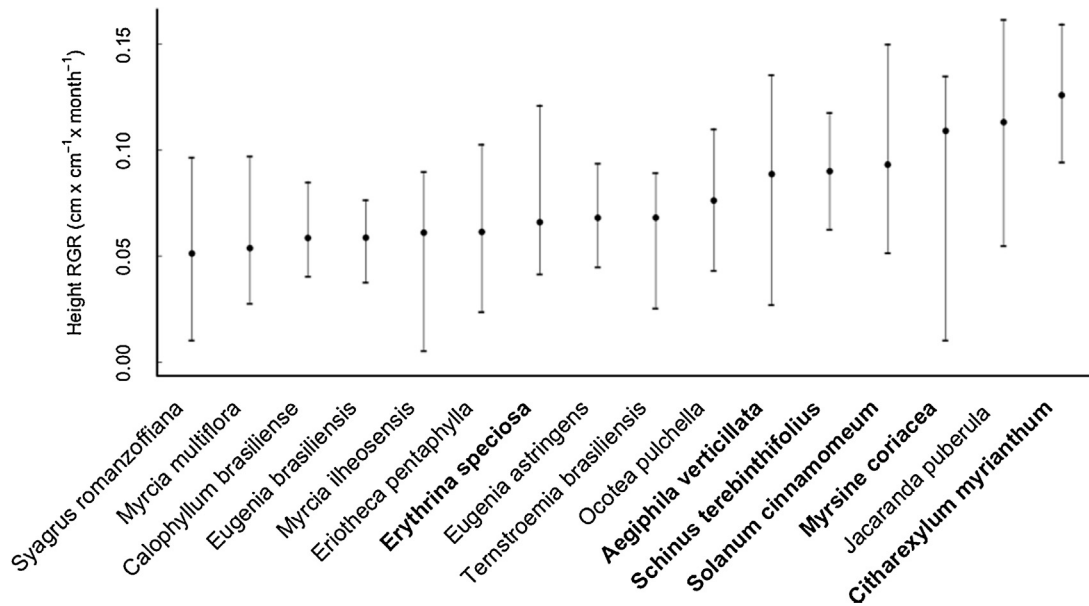


Fig. 2. Median values of height relative growth rate (RGR) over 18-months for 16 species monitored in the isolated, standardized soil treatment. Error bars represent data from quantiles 10–90%. Species previously classified as pioneer are marked in bold.

categorized as pioneers had the highest RGR for height with two exceptions, *Jacaranda puberula* Cham., which was previously considered as a non-pioneer showed fast growth rates, and the pioneer *Erythrina speciosa* Andr. which grew slowly.

Two models were equally plausible in explaining survival data (Table 1). The estimated coefficients shared between those models are similar and the additional term retained in the second model (SI:F) is weak. The best fit selected model included F, PS, SI, and the PS:SI and PS:F interactions. Survival was higher for pioneer species in isolated systems; fertilizer had a negative effect on plants in isolated systems, but no effect in aggregated systems; and the aggregated system had a stronger positive effect on non-pioneers as compared to pioneers (Fig. 3).

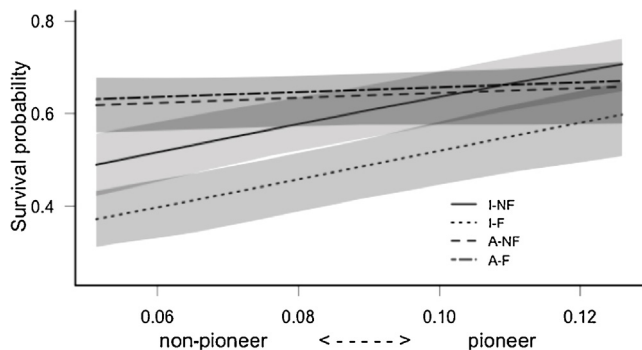


Fig. 3. Values predicted by model selection using the Akaike Information Criterion for the relationship between survival probability and successional index of species in different factorial treatments for the best fit selected model. A = aggregated, I = isolated, F = fertilized, NF = non-fertilized. Shading represents the 95% confidence interval from 1000 simulations of the predicted values (the confidence interval for A-F is not showed since it overlapped A-NF).

Two different models for ground level diameter RGR were equally plausible (Table 1). The model selected with the lowest AIC included all terms except the triple interaction and all the confidence intervals did not overlap zero (Table 1). Diameter growth was higher in isolated compared to aggregated systems, particularly for non-pioneers, but the pioneer species showed even higher diameter growth in clusters when fertilized (Fig. 4). Fertilizer addition increased growth in the aggregated system, especially for pioneers, and slightly increased growth of pioneers in isolated planting systems.

The model selected for crown projection RGR only included successional index (Table 1). As expected crown projection RGR was greater for pioneers.

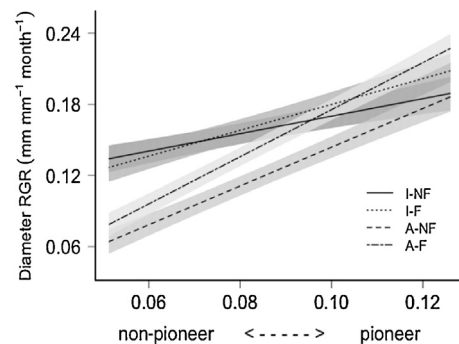


Fig. 4. Values predicted by the best fit model using the Akaike Information Criterion for the relationship between relative diameter growth rate and successional classification of species in different factorial treatments. A = aggregated, I = isolated, F = fertilized, NF = non-fertilized. Shading represents the 95% confidence interval from 1000 simulations of the predicted values.

Discussion

Although competition and facilitation can occur together, the balance between them will result in net positive or negative interaction. Our results show that this balance varies within the same system (Callaway 1995), depending on the effect analyzed (Hastwell & Facelli 2008; Gómez-Aparicio 2009; Prévosto et al. 2012). In our study, whereas growth was reduced, survival was enhanced in aggregated systems, especially for non-pioneers, which is consistent with previous studies showing more positive responses of shade-tolerant non-pioneer species to nurse plants (Gómez-Aparicio et al. 2004; Padilla & Pugnaire 2006; Yang et al. 2010).

The results suggest that high irradiance stress and temperature may be major factors limiting seedling survival in open tropical degraded areas. Accordingly, Castanho and Prado (2014) found that shade, either artificial or from an adult plant, was the mechanism responsible for facilitating seedling survival (although not growth) in this system. Since high irradiance and temperatures can lead to photoinhibition (Loik & Holl 1999; Ehleringer & Sandquist 2006), pioneer species able to cope with higher light conditions may act as nurse plants (Padilla & Pugnaire 2006) by reducing irradiance and temperature, improving conditions for more non-pioneer species. In this sense, Pereira (2014), studying in the same area, reported seedlings showing signs of photoinhibition, but with lower levels of photosynthetic stress, soil and foliar temperature in an aggregated system.

On the other hand, surviving seedlings in clusters appeared to compete for nutrients since diameter growth was lower in the aggregated system, and this reduction was counteracted by fertilizer addition, especially for pioneer species. Other studies have reported facilitation for survival but not for growth, in the Brazilian coastal plain (Castanho & Prado 2014), as well as a wide range of ecosystems around the world (Gómez-Aparicio 2009 and references therein). Therefore, ideal environmental conditions for seedling survival are different than for seedling growth (Gómez-Aparicio 2009). Interestingly, however, growth in crown projection was not affected by competition in the aggregated system, which may change over time, as space becomes a limited resource.

Surprisingly, seedling survival was lower in fertilized plots in the isolated system. One possible explanation for this result is that excess of fertilizer might have damaged seedlings in isolated systems. Species can lose water through their roots due to high osmotic potential resulting from high fertilizer levels (Jacobs & Timmer 2005). In aggregated systems reduction of irradiance intensity may have diminished plant transpiration and some species able to uptake a larger amount of fertilizer may have ameliorated conditions for others. Another possibility is that nutrient addition has been shown to increase herbivory (Andersen, Corre, Turner, & Dalling 2010; Santiago et al. 2012). Although we did not measure herbivory, we saw no obvious patterns of differential herbivore damage.

In aggregated systems, fertilizer addition seemed to reduce the competition effect for pioneer species much more strongly than non-pioneers. The same patterns have been reported for grass interactions (Wedin & Tilman 1993) and for adult trees in regeneration plots in Amazon (Siddique et al. 2010), where pioneer species were favored by nutrient addition. According to Burslem, Pinard and Hartely (2005), pioneers could outcompete non-pioneers over the short term, as they monopolize and pre-empt resources, yet non-pioneers would prevail in the long term due to competitive success related to low resource requirements. In this study, however, the higher growth rate of pioneers could be leading to individual level asymmetric competition (Freckleton & Watkinson 2001), as competition for seedling establishment can have a stronger biomass effect on early developmental stages (Weigelt, Steinlein, & Beyschlag 2002). During later developmental stages it is likely that pioneer species will stop growing and asymmetric competition may diminish.

Over time, the pioneer species will likely die earlier than non-pioneers, freeing up space and resources for non-pioneers to thrive after the juvenile stage, which is critical to survival. It is likely, however, that the pioneers will release seeds in the soil before they die, since several pioneer species have already fruited in the restoration area. These seeds in turn, may show a relatively longer ecological longevity in the soil seed bank (Vázquez-Yanes & Orozco-Segovia 1993) and can germinate when there are natural clearings or in areas that remains open due to the mortality of planted seedlings.

Despite competing for height growth with non-pioneer species in early restoration phase, pioneer species had higher initial survival rates, which makes them suitable for restoration projects (Elliott et al. 2003). However, these species usually have short life cycles and many restoration projects in Brazil have failed after they died (Barbosa et al. 2003; Souza & Batista 2004; Rodrigues, Brancalion, & Isernhagen 2009), highlighting the importance of introducing non-pioneer, long-lived species at some point in the restoration process (Rodrigues, Lima, Gandolfi, & Nave 2009). Since establishment of non-pioneer species in degraded areas can be challenging (Gómez-Aparicio 2009), restoration designs could take advantage of higher survival rates of slow growing species in cluster (i.e. they should be outplanted close to pioneer trees). Furthermore, outplanting clusters may enhance spatial heterogeneity in the system (Holl, Stout, Reid, & Zahawi 2013), which may promote an increase in diversity in late successional stages.

Understanding structuring forces in tropical plant communities is important to develop efficient restoration model based on scientific results, since theoretical basis of restoration ecology derives from basic concepts of community ecology (Young et al. 2005). Evaluating performance of tropical trees requires a longer time to observe consistent patterns, and results presented here may show just the first step of the undergoing processes. However, our study shows that cluster planting facilitates survival of non-pioneers species at the beginning of restoration when abiotic conditions are harsh. At

the same time, the non-pioneer species are subject to greater competition for diameter growth at this stage, possibly due to competitive asymmetry. The observed shifts in the balance of facilitation and competition as well as the interaction with successional species index can be used to adjust the management regime for restoration projects. Besides practical implications, the results from experimental restoration projects may improve our ecological knowledge of the successional dynamic and community structuring in these systems.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2016.04.006>.

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