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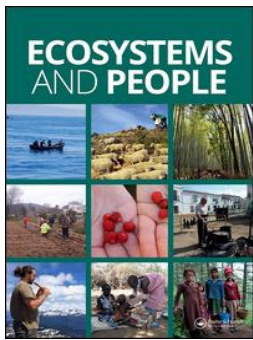Holl, Karen D
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Enrichment planting to restore degraded tropical forest fragments in Brazil

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ABSTRACT

In tropical areas with high levels of fragmentation due to agricultural use, forest fragments play an important role for biodiversity conservation at the landscape scale. But these fragments are subject to recurrent disturbances, which lead to arrested succession and loss of functional groups. In such cases, active restoration, such as enrichment planting, could facilitate recovery. We studied enrichment planting methods to restore tropical forest fragments in the Brazilian Atlantic Forest, and we evaluated the costs to implement them in the field. We planted four later successional tree species as seeds, small seedlings, and large seedlings in three remnants embedded in a landscape dominated by sugarcane plantations. Overall, survival of seedlings was low using all methods due to a severe drought during the study period, and there were no differences in seedling survival or growth across the three study sites. Direct seeding was the least expensive technique but was successful only for one large-seeded species, *Hymenaea courbaril*. Large seedlings survived better than did small seedlings, for all four species, suggesting that the additional cost of growing large seedlings is warranted to enhance success. Our results highlight that a combination of planting methods at species level is likely to increase restoration success.

1. Introduction

The majority of tropical forests are now secondary forests, in some stage of recovery from past human disturbance (FAO 2012). Although the biodiversity conservation value of large tracts of pristine forests is irreplaceable (Gibson et al. 2011), secondary forest fragments play an important role in supporting ecosystem services, especially their value for carbon mitigation (Bongers et al. 2015), biodiversity conservation (Chazdon et al. 2009), and increasing landscape forest connectivity in highly deforested landscapes (Arroyo-Rodríguez et al. 2009).

Nonetheless, secondary forest fragments are commonly subjected to several disturbances, including selective logging, recurrent fires, edge effects and hyper-abundance of vines, which limits their potential for conserving species and supplying ecosystem services (Melo et al. 2013; Viani et al. 2015). These disturbances shift plant community composition in forest remnants, as they commonly favor the proliferation of pioneer species and vines, and have deleterious effects on large seeded and late successional species (Melo et al. 2007; Liebsch et al. 2008; Arroyo-Rodríguez et al. 2015). In landscapes with less than 30% of forest cover, such as our study region, forest fragments can persist in an alternative state of arrested succession, due to lack of nearby sources of propagules (Arroyo-Rodríguez et al. 2015).

Traditionally, the 'natural forest management' concept refers to low or reduced impact logging of tropical forests (Bawa and Seidler 1998) and is usually related to economic goals (Putz et al. 2001). However, in tropical agricultural landscapes with low forest cover, such as the Brazilian Atlantic Forest, forest management should focus on strategies to increase the role of forest fragments in biodiversity conservation through reintroducing or increasing populations that are rare and at risk of extinction or functional groups that are missing, such as later successional species (Brancalion et al. 2013; Viani et al. 2015; Vidal et al. 2016). Reintroducing such species to existing forest fragments through enrichment plantings can help to provide stepping stone populations and increase functional connectivity and persistence of species in the landscape (Rodrigues et al. 2011; Banks-Leite et al. 2014).

Although many authors have suggested enrichment planting in forest fragments as a conservation strategy (Gardner et al. 2009; Brancalion et al. 2013; Melo et al. 2013), few studies have tested specific techniques. Thus far, research has focused on testing methods to recover open and highly degraded areas (Viani et al. 2015). Among forest management studies, forest enrichment has been tested for enhancing the biodiversity of restoration plantings (Bertacchi et al. 2015) or to increase the economic value of secondary forests, by introducing valuable species

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(Montagnini et al. 1997). To date, most studies have focused on planting seedlings (Palma and Laurance 2015). Past studies have shown that seedling survival and growth rates are greatly influenced by local microclimate, mainly light availability (Montagnini et al. 1997; Keefe et al. 2009), but have focused less on rainfall.

In this study, we tested direct seeding and planting of small and large seedlings of four later successional tree species. We assessed the most suitable method to enrich degraded forest fragments to improve their biodiversity conservation value in highly deforested landscapes. We hypothesized higher survival with small or large seedlings than direct seeding (Palma and Laurance 2015). We anticipated higher mortality for seeds and small seedlings in areas with high light levels, due to competition with light-demanding vines and grasses, and in areas with high litter fall, as a result of thick litter inhibiting germination and growth (Facelli and Pickett 1991; Schnitzer and Carson 2010). We also compared the costs of the three enrichment methods to recommend the most economically effective strategy for enrichment planting.

2. Methods

2.1. Study sites

The experiment was implemented in three secondary fragments of tropical semideciduous forest (hereafter, sites), which are located in the Corumbataí River Basin of Piracicaba and Charqueada municipalities, São Paulo State, Brazil (See Supplementary Material – Figure S1). This catchment is located between the latitudes 22° 04′ 46” S and 22° 41′ 28” S, and longitudes 47° 26′ 23” W and 47° 56′ 15” W and covers an area of approximately 1,700 km^2 (Cassiano et al. 2013). Over the past 30 years, mean annual rainfall was 1,331 mm, but in 2014, it experienced a severe drought, during which it rained 904 mm, the fifth driest year from the past century (Biosystems Engineer Department, São Paulo University). During the rainy season of 2014 (January to May), it rained only 348 mm, which is ~48% of mean rainfall during this period. During the dry season (June to October), it rained a total of 143 mm, 52% of the historical average rainfall for this period. In November and December 2014, and during the second year of the study, rainfall was close to average.

We selected three sites that have Lithic Entisols (Rossi 2017) and similar chemical and physical soil characteristics (Supplementary Material – Table S1); all sites have loamy soils that are highly fertile and rich in organic matter and are separated by at least 10 km. The oldest site is the most degraded remnant in the landscape (57 ha); one site is a secondary forest with ≥18 years of regeneration (70 ha); and one is an abandoned

Eucalyptus plantation with an understory of natural regeneration (113 ha). The *Eucalyptus* plantation was abandoned about 40 years ago, and is dominated by native tree species with sparse *Eucalyptus* individuals in the canopy (supplementary information about the vegetative structure of the three sites is presented in Table S2).

Land cover in this region has been strongly influenced by humans for more than 200 years, with substantial changes in forest cover and in the agricultural matrix over the past 50 years. The landscape is dominated by sugarcane fields, but native vegetation cover has increased from 8 to 15% in recent years, due to new areas of natural regeneration that occur mostly around previously existing old growth forest patches (Ferraz et al. 2014). Therefore, forest fragments are highly heterogeneous, which is reflected in the three sites where the experiment was conducted; hence, we used a randomized complete block design, as described in Section 2.3.

2.2. Species selection

We selected four later successional tree species (a group that includes long-lived shade-tolerant species that can remain in the understory or above the canopy as emergent trees – Gandolfi 2000) that were available in nurseries: *Myroxylon peruiferum* L.f., *Cariniana estrellensis* (Raddi) Kuntze, *Copaifera langsdorffii* Desf., and *Hymenaea courbaril* L. Previous floristic assessments showed that these species are present in the landscape, as regenerating and adult individuals, but in very low densities (Mangueira et al., unpublished data). All four species have high commercial value for furniture and construction industry (Lorenzi 2002), so they have been heavily harvested in the past in these forest fragments.

Each species was introduced using three planting methods: direct seeding (DS), small seedlings (SS – 2 months of growth in plant nursery, average height among all species 8.3 cm ± 0.2 SE), and large seedlings (LS – 9 months in plant nursery; average height among all species: 26.7 cm ± 0.2 SE). Seeds and seedlings were all obtained from the same plant nursery, located in Piracicaba (São Paulo state), which guarantees genetic diversity and performs germination tests to assure seed quality. All seedlings were grown in polyethylene tubes (290 cm^3) and were planted with the nursery soil. The four species have different seed germination characteristic, including dormancy through a seed coat impervious to water, orthodox seeds that tolerate dehydration, and non-dormant seeds that germinate soon after sowing (Table 1). *H. courbaril* and *C. langsdorffii* seeds have dormancy, but we applied no pre-treatment before sowing.

Table 1. Enrichment planting species characteristics.

Species Name	Family	Number of seeds/kg[a]	Ecological characteristics
Myroxylon peruiferum L.f.	Fabaceae	2250	Late Secondary Canopy, Anemochory, orthodox non-dormant seeds
Cariniana estrellensis (Raddi) Kuntze	Lecythidaceae	11,100	Late Secondary Canopy, Anemochory, orthodox non-dormant seeds
Copaifera langsdorffii Desf.	Fabaceae	2128	Late Secondary Canopy, Zoochory, orthodox dormant seeds
Hymenaea courbaril L.	Fabaceae	197	Late Secondary Canopy, Zoochory, orthodox dormant seeds, with impervious seed coat

[a]Nogueira & Brancalion, 2016

2.3. Experimental design

The study was set up in a randomized-block design; three blocks were established in each site (nine blocks in total). The blocks were at least 36 × 160 m and were set up a minimum of 3 m from forest edges and 50 m distant from each other. We avoided planting under large canopy gaps and areas infested by hyper-abundant climbers. Each block included 12 plots of 10 × 40 m; in each plot, 30 individuals of a single species and propagule type (DS, SS, or LS) were planted. Individuals were planted in a 3 × 4 m grid. Therefore, 360 individuals were planted in each block; 3240 individuals in total. One large or small seedling was planted at each planting location; for direct seeding, three seeds of each species were sown (but counted as one individual), totaling 90 seeds per plot. Seeds were planted in a hole approximately as deep as their size and covered with litter, so that they were not buried deeply nor were left exposed. For DS, we considered survival as the number of individuals that emerged and survived until the last field evaluation. If any of the three seeds germinated or survived this was considered as surviving, and if more than one seed germinated (only for *H. courbaril*) then the heights of all individuals at the location were averaged and counted as one surviving individual.

We initiated the experiment in March 2014, during the rainy season. All individuals were irrigated immediately after planting, but not thereafter. We controlled leaf-cutting ants using granulated ant baits to reduce herbivory. Survival was recorded four times over 22 months, during the peak of each dry and rainy season. Seedling height was measured immediately following planting and after 22 months by measuring the distance between the soil surface and the shoot apical meristem. In order to analyze the mechanical pressure of litter fall on the survival of seeds and seedlings, we measured litter depth to the nearest millimeter at three points in each plot. We also estimated canopy openness per plot by taking hemispheric photographs using a FUJI FinePix S5000 camera with a fish-eye lens (Opteka, 0.22X, AF). Rainfall data were obtained from the Biosystems Engineer Department, São Paulo University (ESALQ/USP).

2.4. Cost comparison

We used prices for seeds and seedlings based on their purchase costs from a local nursery and estimated the costs of planting 835 seedlings/ha, which is about half that used in restoration plantings where there are no trees (1666/ha, Rodrigues et al. 2009) and the density that we planted in this experiment. We did not include labor costs for planting since they were similar across treatments For seeds, since some of them are quite small, we calculated the cost to implement the 270 individuals directed seeded in the experiment by using the cost of kg of seeds and the amount of seeds per kg of each species; we then multiplied that number by 3.1 to scale up to 835 individuals/ha. For large and small seedlings, we use the nursery price for each individual and multiplied those by 835. We averaged values for individual species to calculate the overall cost of a given method. We also adjusted the cost/ha of each species and methods for their survival rates to calculate what it would cost to end up with the same density of seedlings.

2.5. Data analyses

We analyzed height increase and survival rate after 22 months using a randomized-block analysis of variance (ANOVA). Our model included planting method, species, and their interaction, as well as site and block within site factor to reduce the effects of within and among site heterogeneity. Survival rates were calculated as percentage of individuals surviving per plot for each species and planting method, and analyzed using arcsine square-root transformed percent data to meet assumptions of normality and homogeneity of variance. Height increase (height at 22 mo – height at time of planting) of all surviving individuals within a plot were averaged, and the mean was square-root transformed. For both response variables, if there was a significant model effect for planting method or species ($p < 0.05$), then they were compared using Tukey's tests. To synthesize the relative establishment success of each species and planting method, we included a 'Performance Index' (unitless, adapted from De Steven 1991), which is a product of the survival rate and height increase after 22 months.

We tested for correlations between survival and height increase with the litter depth and canopy openness using Spearman rank correlation or Pearson correlation coefficients, according to whether data met normality and homogeneity of variance assumptions.

Analyses were conducted using JMP 13.0 for SAS 9.3 (SAS Institute Inc., Cary, NC, USA). Hemispheric photographs were analyzed using Hemisfer 1.41 (Schleppi et al. 2007).

3. Results

The most severe drought of the last 30 years greatly reduced the survival of all species and propagules types. Across all combinations of species and planting methods only 9.2% of individuals survived after 22 months. Survival differed as a function of species ($F_{3, 88} = 20.7$; $p < 0.0001$), planting method ($F_{2, 88} = 19.7$; $p < 0.0001$), and their interaction ($F_{6, 88} = 27.8$; $p < 0.0001$), but there was no site effect ($F_{2, 88} = 0.4$; $p = 0.6939$). Direct seeding had the highest survival rate (13.3%), but all individuals were from one species; 11.7% of large seedlings and only 2.9% of small seedlings survived.

H. courbaril had the highest survival rate across all treatments (20.4%) and was the only species that survived when direct seeded (91% germinated and 78% survived, Figure 1(a)). Interestingly, all *H. courbaril* seeds germinated a year after planting

and 44 individuals (15%) emerged only in the last field evaluation. *M. peruiferum* had the highest survival for large seedlings (32%) and was the only species for which >5% of small seedlings survived. *C. langsdorfii* and *C. estrellensis* had <10% survival across the three propagules types and performed best when large seedlings were planted (Figure 1(a)).

Across all treatments, height increase was quite low during the study (Figure 1(b)), and height increase differed significantly by species ($F_{3,88} = 40.9$, $p < 0.0001$), planting method ($F_{2,88} = 15.8$, $p < 0.0001$), and their interaction ($F_{6,88} = 29.2$, $p < 0.0001$), but did not vary by site ($F_{2,88} = 1.02$, $p = 0.3647$). For large seedlings, individuals from all species grew an average 3 ± 7 cm, and *C. langsdorfii* grew more than the other species (4 cm ± 10 cm). Direct-seeded individuals of *H. courbaril* were the tallest of all species and planting method at the end of the study (32 ± 6 cm) (Figure 1(b)). As a result of both higher growth and survival rate, direct-seeded *H. courbaril* had the highest Performance Index (Table 2).

Litter depth ranged from 2 to 13 cm and canopy cover from 80 to 100%. These environmental
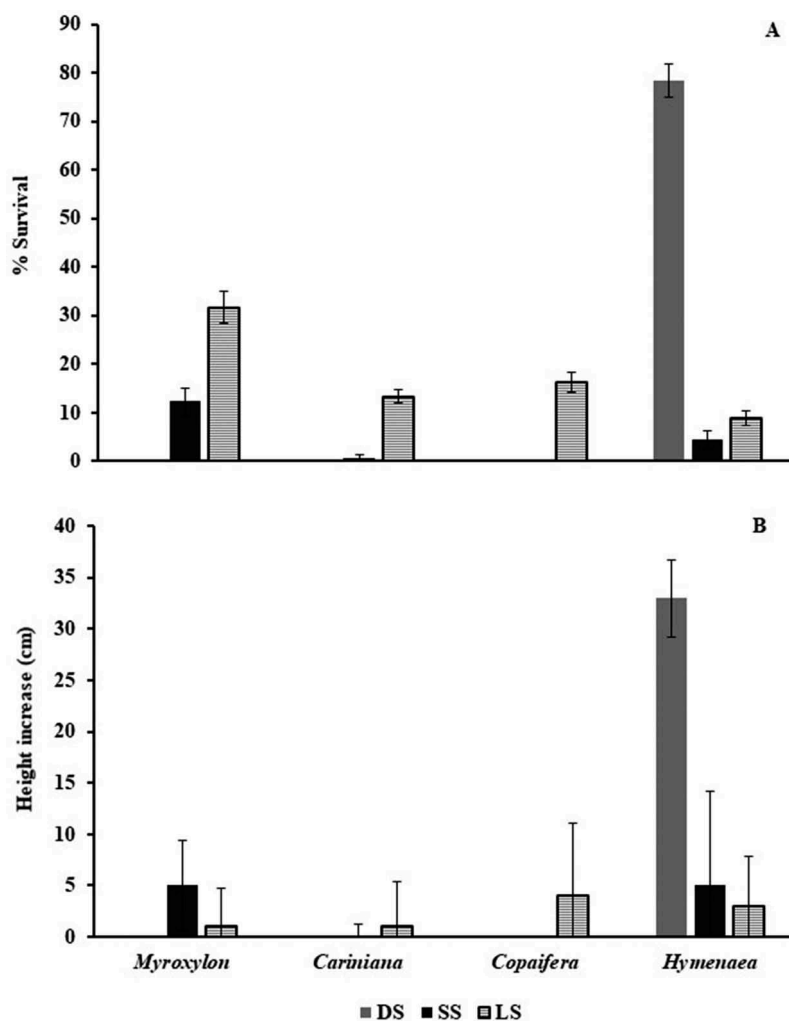

Figure 1. (a) Percent survival and (b) average height increase (cm) of *Myroxylon peruiferum, Cariniana estrellensis, Copaifera langsdorfii*, and *Hymenaea courbaril* planted in three forest remnants through Small Seedlings (SS), Large seedlings (LS) and Direct Seeding (DS), 22 months after planting. Error bars represent the 5% confidence intervals.

Table 2. Species Performance Index (PI) listed in decreasing order, for each planting method after 22 months of enrichment experiment in degraded forest fragments in Brazil. S = Mean survival rate (%); H = Mean height increase (cm; the difference between height immediately after planting and after 22 months); Performance Index (survival x height increase). Adapted from De Steven (1991).

Species	Propagule Type	Performance Index		
		S	H	PI
H. courbaril	DS	15.7	32.7	511.6
C. langsdorfii	LS	3.2	4.0	12.9
M. peruiferum	SS	2.4	4.5	11.0
M. peruiferum	LS	6.3	1.3	8.3
H. courbaril	LS	1.8	3.2	5.7
H. courbaril	SS	0.9	4.7	4.2
C. estrellensis	LS	2.7	1.5	3.9
C. estrellensis	SS	0.1	0.2	0.0
M. peruiferum	DS	0.0	0.0	0.0
C. langsdorfii	SS	0.0	0.0	0.0
C. langsdorfii	DS	0.0	0.0	0.0
C. estrellensis	SS	0.0	0.0	0.0

parameters were not significantly correlated with survival or height increase (r < 0.55 and p > 0.08 in all cases).

3.1. Cost comparison

Planting large seedlings is almost 10 times more expensive per hectare than direct seeding (Table 3). Considering survival rates, however, direct seeding is cheaper only for *H. courbaril*, since the other species had 100% mortality. Small seedlings cost 34–42% of large seedlings of the same species, but considering survival rates, it is twice as expensive.

4. Discussion

Previous studies have shown that the efficacy of specific restoration methods is highly contingent on weather conditions, particularly the amount of rainfall, in a given year (e.g. Bakker et al. 2003). The exceptional water stress of the year negatively affected the survival and growth of propagules in our study. Other enrichment studies in Brazilian Atlantic forest remnants conducted during average rainfall periods reported higher survival and growth (Rozza et al. 2006; Jordão 2009).

Due to the annual variations in weather conditions, restoration efforts should be allocated over multiple years to increase the chance of encountering favorable conditions (Wilson 2015), and also consider differential species response to water stress (Engelbrecht et al. 2005).

We expected that direct seeding would increase the likelihood of establishment in low rainfall conditions, since seeds may not germinate if conditions are not favorable. This happened with *H. courbaril*; since we did not break seed dormancy, seeds survived during the first low rainfall year and showed high germination in the second year after planting, when there was sufficient rainfall. This result suggests that species with thick seed coats may be particularly well suited to direct seeding in variable rainfall conditions, as previously reported in the literature (reviewed by Moles and Westoby 2004). Past studies also concur with our results that large-seeded species, such as *H. courbaril*, have a higher probability of early establishment and increased success probability when compared to small-seeded species (Bonilla-Moheno and Holl 2010; Ceccon et al. 2016), and are therefore well suited for direct seeding in restoration.

On the other hand, the other three species had low germination and survival rates, consistent with previous direct seeding studies (Engel and Parrotta 2001; Doust et al. 2006; Clark et al. 2007; Rother et al. 2013; Ceccon et al. 2016). Low survival during both the germination and seedling phase are common in restoration projects and seed addition experiments; values of less than 20% probability of germination and survival until seedling phase are typical for tropical species (Holl 2002; Clark et al. 2007; Rother et al. 2013; Ceccon et al. 2016; César et al. 2016). Therefore, the choice of species with higher chances of survival when direct seeded is a key to restoration success (Souza and Engel 2018). We did not measure seed predation, which can also be a major cause of failure in direct seeding plantings (Rother et al. 2013) —especially in forest environments—and potentially could explain high mortality of seeds in our experiment.

Table 3. Cost comparisons between planting seeds, small and large seedlings of four later successional species used in enrichment experiment of degraded forest fragments. The costs were calculated for planting 835 seedlings/ha. NA = no individuals survived, so the cost was considered incalculable.

	Seeds			Small seedling			Large seedling		
	US$[a] – seeds[b]	US $/ha	U$/ha considering survival rates	US $/seedling	US $/ha	US$/ha considering survival rates	US $/seedling	US $/ha	US$/ha considering survival rates
Myroxylon peruiferum	10	31	NA	0.17	142	1183	0.5	418	1305
Cariniana estrellensis	4	12	NA	0.17	142	14,195	0.5	418	3212
Copaifera langsdorfii	12	38	NA	0.17	142	NA	0.5	418	2609
Hymenaea courbaril	21	65	83	0.17	142	3549	0.4	316	3509
Cost per method[c]	12	37	NA		142	6309		392	2659

[a]US dollar = 2.3 BRL (2014 quotation)
[b]For each species, we multiplied the price of kg of seeds by 270 (number of individuals directed seeded in the experiment) and then divided by the amount of seeds per kg of each species.
[c]The cost per method is the average cost of planting the four species so would be equivalent to a mixed-species planting of the four species.

Our results are consistent with a recent meta-analysis (Ceccon et al. 2016) showing that a mix of direct seeding and planting larger seedlings show promise for enrichment planting, depending on the site conditions and species. Planting seedlings is the most successful method for most species, but it is also the most expensive (Engel and Parrotta 2001; Sampaio et al. 2007). In an attempt to reduce costs, we also tested planting small seedlings, which is roughly a third of the cost of large seedlings individuals. Larger seedlings survived better than smaller ones did, which was consistent with the literature (reviewed by Palma and Laurance 2015). Because of the high mortality rate of small seedlings, however, the costs are too high, and we do not recommend this technique for enrichment projects. Our and past research suggest that direct seeding is considerably cheaper than planting large seedlings (Engel and Parrotta 2001; Cava et al. 2016), even when the differential survival rates are considered. It is also easier to implement on uneven terrain and in dense vegetation typical of forest environment, but it only works for certain species.

In conclusion, our results demonstrate the importance of using a combination of planting methods rather than the common restoration practice of using the same methods at the community level. Species that share functional traits, such as thick coat seeds or large seeds, may be successful when introduced by the same methods, but further research is necessary to increase success in enrichment plantings. Past and current research show that large-seeded species perform better when directed seeded, but different strategies should be tested on a small scale to determine the most cost-effective approach for reintroducing target species. The high amount of degraded forest fragments in arrested succession calls for an urgent need of low-cost restoration techniques, focusing on conservation purposes, to facilitate their recovery from the steady state of degradation (Viani et al. 2015). In highly deforested landscapes, secondary forests are the last refuges of biodiversity and therefore should be targeted for conservation and restoration projects (Beca et al. 2017; Farah et al. 2017).

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Disclosure statement

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