Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION

TECHNICAL ARTICLE

Optimizing seeding density of fast-growing native trees for restoring the Brazilian Atlantic Forest

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Direct seeding is a promising method for reducing restoration costs, but methodological adjustments are still needed to reduce the uncertainties to achieve a desired seedling density in the field. Here, we investigated the technical approaches and outcomes of direct seeding of fast-growing native trees for cost-effective restoration of the Brazilian Atlantic Forest. Sixteen tree species were manually sown at three seeding densities in planting lines prepared with a subsoiler, in two experimental areas, which were weeded with hoes and had leaf-cutter ants controlled with insecticide baits. Seedling density was monitored for 30, 90, and 180 days after sowing. No substantial change in tree density was observed 30 days after sowing, thus allowing fast corrective actions to adjust tree density. Only a minor proportion of the sown viable seeds resulted in established seedlings at 180 days (4–12% for the community; approximately 25% for the species with the best performance). However, tree density was high (6,000 on average; approximately 1,400–13,000 trees/ha) and allowed an effective canopy development. Overall, seedling density was linearly and positively associated with seeding density, was highly influenced by the species used, and was higher in the soil with higher sum of bases. Buying seeds would be, for most species, less costly than buying nursery-grown seedlings for achieving the expected tree densities in the field. These results evidence the potential of direct seeding for reducing restoration costs, as well as the need to select species with better performance and adjust seeding densities to optimize the use of this method.

Key words: cost-effective restoration, direct seeding, direct sowing, restoration plantings, seedling establishment, tropical forests

Implications for Practice

- Direct seeding of fast-growing native trees is a cost-effective approach for a rapid recovery of a forest canopy in restoration sites.
- Direct seeding of fast-growing native trees shows better establishment in soils with higher sum of bases, so seeding densities can be lower.
- Plant functional traits as seed size and association with nitrogen-fixing bacteria may improve tree species establishment in direct seeding.
- Direct seeding of species with rapid germination allows anticipating corrective actions resulted from failures in seedling densities; hence, direct seeding can be used as a first try to recover native forest cover at low costs.

Introduction

Although recent initiatives have spawned voluntary commitments to implement large-scale restoration programs in many countries (Chazdon et al. 2016), there is no clear evidence so far about which restoration approaches shall be used in different circumstances, and recommendations emerging from bottom-up initiatives are needed (Holl 2017). Restoration needs to provide solutions to ecological problems, but these solutions should also (1) be cost-effective (Kimball et al. 2015), (2) provide perceived benefits to landowners, and (3) be aligned with local public policies and cultural features (Aronson et al. 2011; Melo et al. 2013). In fact, high costs of restoration have been a major barrier for upscaling this activity, despite the economic benefits of investing in it (De Groot et al. 2013).

Cost-benefits trade-offs may be offset through two alternative and complementary options. First, forest restoration can provide income to landowners, through payments for ecosystem services, agro-successional models, and exploitation of timber and nontimber forest products from forests undergoing restoration (Palmer & Filoso 2009; Vieira et al. 2009; Brancalion et al. 2012). Second, restoration implementation and maintenance

Author contributions: II, PHSB, RRR conceived the experiment; II led the research in the field and data analysis; ECCI, PHSB, MB helped to collect and process data; PM, II, PHSB processed data and wrote the paper; all authors discussed ideas and improved all previous versions of this manuscript.

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doi: 10.1111/rec.12567
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.12567/suppinfo

costs can be reduced, by developing innovative techniques or improving existing ones (Brancalion & van Melis 2017). Direct seeding, in particular, has been a well-known promise to reduce the costs of restoring tropical forests (Engel & Parrotta 2001; Palma & Laurance 2015; Silva et al. 2015; Ceccon et al. 2016). However, it has not been widely used so far as have restoration plantations with nursery-grown seedlings. The higher levels of uncertainty of using direct seeding, as a consequence of the limited knowledge on forest seeds, seeding techniques, and influences of environmental factors in seedling establishment, can particularly limit the use of this method, especially in restoration projects motivated by legal compliance (Brancalion et al. 2016). Methodological adjustments are then crucial for increasing the reliability of direct seeding to enable restoration practitioners to obtain the best benefits from this method for reducing the costs of their projects. For instance, direct seeding of tropical forests and savanna woodlands has been implemented at large scales in Central Brazil using adapted crop sowing machines (Campos-Filho et al. 2013; Durigan et al. 2013). Despite the widespread use, information is still limited about the differential performance of species and functional groups, optimal seedling densities, and technical procedures to allow sowing species with a wide range of seed sizes.

Seeding density is one of the most important issues in direct seeding: while low densities can result in a low and patchy occupation of degraded sites by trees, high densities may increase implementation costs and competition among trees (Burton et al. 2006; Campos-Filho et al. 2013). The risk of obtaining a not expected density of seedlings following direct seeding of native species is particularly high for pioneer trees, which predominantly produce small dormant seeds and provide an essential contribution for kick-starting restoration processes in degraded sites (Viani et al. 2015). Artificial dormancy breaking is not yet dominated for many tropical pioneer trees, and small seeds require fine control over seeding depth for successful seedling emergence. Thus, adjusting the technical procedures involved in the direct seeding of pioneer trees is key for supporting the use of this method in large-scale forest restoration programs. Here, we investigated the technical approaches and outcomes of direct seeding of fast-growing native trees for cost-effective restoration of the Brazilian Atlantic Forest. Our main goals were to (1) evaluate early establishment of 16 fast-growing native tree species sown at different density levels, assessing the influence of soil conditions and seed size on species establishment; (2) explore the patterns of species dominance and basal area development of the tree communities undergoing restoration by direct seeding; and (3) compare the costs of planting stock acquisition to restore native forests through direct seeding and seedling plantations.

Methods

Study Site

We conducted this study in Araras Municipality, São Paulo, Southeast Brazil (Fig. 1A). The climate is classified as Cwa, typically mesothermic with dry winter. Mean temperature varies from 18°C during the coolest month to 22°C during the hottest one, and mean annual precipitation is approximately 1,300 mm, being low during the winter. The municipality was covered by the Atlantic Forest and Cerrado biomes, but only approximately 5% natural vegetation cover remains. The experiments further described were established over areas previously covered by the seasonal semi-deciduous forest. This study is part of a large-scale restoration program coordinated by a sugarcane mill to comply with the Brazilian Forest Code, focused on the restoration of areas of permanent preservation (mostly, riparian buffers of different widths depending on the type and width of watercourses; see Rodrigues et al. 2011).

Species and Seed Densities

We selected 16 fast-growing, wide-canopy native tree species with different seed mass, commonly used in restoration plantations in the region (Rodrigues et al. 2009; Table 1). Traditional planting density in Atlantic Forest restoration is 1,666 seedlings/ha (3×2 m spacing); thus an equitable distribution of 1,666 seedlings among 12 species would result in the target of $\approx$139 seedlings per species/ha. The number of seeds needed to achieve this target density in the field was estimated by combining the germination percentage of each seed lot (evaluated in laboratory; Table S1), and the expectancy of seedling establishment for species grouped in different seed size classes, based on the premise that bigger seeds have more efficient establishment than small seeds (Doust et al. 2006; Tunjai & Elliott 2012). Seeding densities were then determined to represent three levels of expectancy of the number of viable seeds, determined according to germination tests, required to obtain one seedling established in the field 180 days after sowing (Fig. 1C).

Experimental Design, Seeding, and Maintenance

Direct seeding was implemented in two areas (Fig. 1B; Table S2). Area 1 was previously used as a rubble waste deposit from nearby road and a dam construction, received soil translocated from other areas to bury rubble mounts, and was further used for crop production (clay soil, sum of basis of 33 $mmol_c/dm^3$). Area 2 was composed of a nitisol (very clay soil, sum of basis of 58.7 $mmol_c/dm^3$), and was previously occupied by sugarcane plantations. Both areas were initially subjected to mechanized plowing, followed by two applications of glyphosate (5 L/ha) on regenerating ruderal plants. We randomly placed in Area 1 thirteen 10×20 m (200 m^2; 2×2 m spacing) plots for each seed density level, totaling 39 plots (0.78 ha; Fig. 1B). In Area 2, due to topographic variation, we used a randomized block design to distribute ten 10×30 m (300 m^2; 3×2 m spacing) plots for each density level, totaling 30 plots (0.90 ha) (Fig. 1B). As result of differential seed availability during the implementation, 12 species were used in each area, from a total of 16 species used in both experiments (Table S1). Direct seeding took place 10 days after subsoiling, at the mid of the rainy season; in February 2007 in Area 1 and in January 2008 in Area 2. Seeding lines were prepared with a subsoiler at 60 cm depth to remove eventual

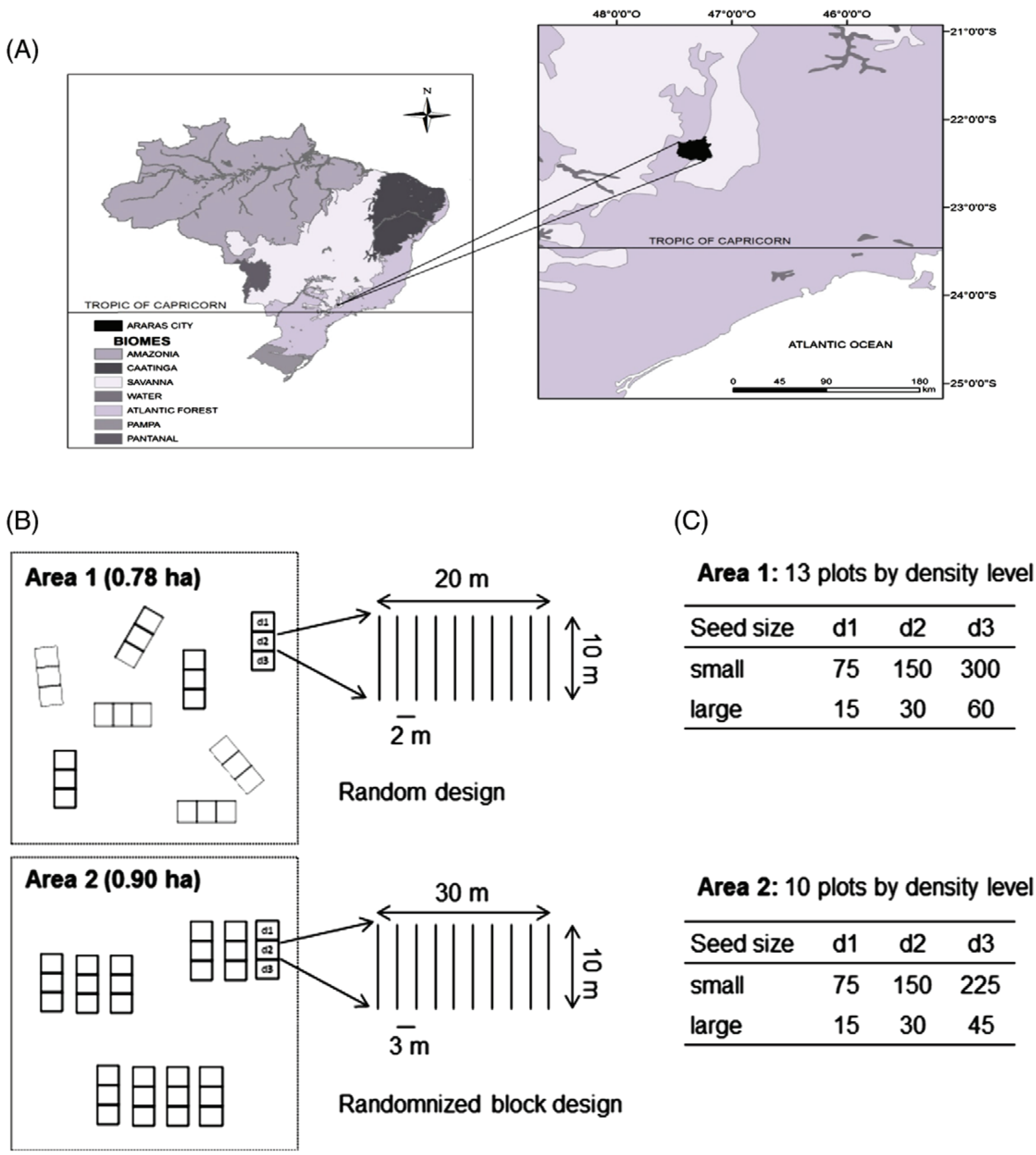

Figure 1. Direct seeding evaluation in two experimental restoration areas in the Atlantic Forest of Brazil. (A) Geographic location. (B) Experimental areas and plots design. Plot numbers and locations are only illustrative. (C) Seeding densities (d1, d2, and d3, representing the *n*-fold times the number of viable seeds estimated to obtain a seedling in field). See text for details.

compaction layers and, thus, to improve the conditions for water infiltration and root system development. Direct seeding was implemented in seeding lines in order to reduce the exposure of the soil seed bank of ruderal plants, as it would happen if the whole area was plowed for broadcast seeding, and to ease the operationalization of seed distribution at the appropriate densities in experimental plots (Fig. 1C). We first distributed big seeds, and covered them with a layer of approximately 2–3 cm of local soil. After, we distributed the small seeds mixed with sand over the planting lines and did not cover them with local soil. Invasive weeds were controlled around tree seedlings and in the planting rows with hoes, while leaf-cutter ants were controlled by the distribution of insecticide baits over the experimental sites; no irrigation was done.

Monitoring Seedling Establishment and Development

Seedling densities were monitored 30, 90, and 180 days after sowing. By combining seeding and seedling density data, we estimated the percentage of viable seeds required to obtain one seedling in the field (i.e. seedling establishment), considering average community means for the three seeding densities tested, and individual species performance, independently of seeding density. We further assessed the diameter at breast height of trees

Table 1. Seed lot characteristics of the 16 fast-growing native tree species tested in direct seeding experiments to restore the Atlantic Forest of Brazil. When required, dormancy breaking was done with acid scarification in concentrated (96%) sulfuric acid, with immersion periods recommended in the literature. Germination range (%) was estimated based on germination tests performed with the seed lots used in the experiments.

Species	*Family*	*Seed Dormancy Pretreatment*	*Seed Mass (mg/seed)*	*Germination Range (%)*
Alchornea triplinervia	Euphorbiaceae	None	40	40
Ceiba speciosa	Malvaceae	None	140	60–70
Colubrina glandulosa	Rhamnaceae	Acid, 120–50 min	20	40–60
Croton floribundus	Euphorbiaceae	None	40	40–60
Croton urucurana	Euphorbiaceae	None	4	20
Cytharexylum myrianthum	Verbenaceae	None	50	60
Enterolobium contortisiliquum	Fabaceae	Acid, 60 min	250	95
Guazuma ulmifolia	Malvaceae	Acid, 50 min	4	25–50
Heliocarpus popayanensis	Malvaceae	None	3	60
Luehea divaricata	Malvaceae	None	4	49
Peltophorum dubium	Fabaceae	Acid, 15 min	50	49
Senegalia polyphylla	Fabaceae	None	50	70–95
Senna macranthera	Fabaceae	Acid, 50 min	40	40–80
Senna multijuga	Fabaceae	None	13	40
Solanum lycocarpum	Solanaceae	None	25	40
Trema micrantha	Cannabaceae	Acid, 60 min	3	35

in the eight planting lines of the interior of the plots (effective plot area) and discounted the planting lines of the borders. These inventories were accomplished five and four years after sowing in Area 1 and Area 2, respectively, and were used to calculate basal area by hectare. We finally compared the costs of planting stock acquisition to restore native forests through direct seeding and seedling plantations. The cost of nursery-grown seedling acquisition was based on the market price of individual seedlings in commercial forest nurseries of the region, which do not apply differential prices to species (i.e. all species have the same price). The cost of seed acquisition was based on the number of seeds required to obtain one established seedling in the field at 180 days after sowing.

Results

Only a minor percentage of the viable seeds sown in the field resulted in established seedlings at 180 days after sowing (8.2 ± 3.7%); seedling establishment was higher in Area 2 (11.5 ± 0.7%) compared to Area 1 (4.8 ± 0.1%). Despite it, high tree densities were obtained for all seeding treatments: 1,408, 2,792, and 5,358 individuals/ha for the three sowing densities tested in Area 1, and 4,863, 8,947, and 13,006 individuals/ha for the three sowing densities employed in Area 2. No substantial change in tree density was observed 30 days after sowing. Seedling density (Fig. 2A), but not seedling establishment (i.e. percentage of the viable seeds sown that resulted in seedlings in the field; Fig. 2B), was linearly and positively associated with seeding density.

In both areas, *Enterolobium contortisiliquum*—a large-seeded legume tree—was the species showing the highest establishment (Fig. 3). Meanwhile, establishment of five species (*Croton urucurana*, *Cytharexylum myrianthum*, *Guazuma ulmifolia*, *Luehea divaricata*, *Senna macranthera*, and *Senna multijuga*) was less than 1% in both areas. These marked differences of seedling establishment among species resulted in the predominance of few species in the tree community; overall, only three species accounted for 60–70% of tree individuals in both areas (Fig. 4). The group of dominant species was composed in both areas by *Solanum lycocarpum* (Solanaceae) and two legume trees with medium to large seeds (*E. contortisiliquum* in both areas, accompanied by *Senegalia polyphylla* in Area 1 and *Peltophorum dubium* in Area 2). Basal area ranged from 20 to 42 m^2/ha at 4–5 years after sowing and showed higher values in Area 2, which had higher soil sum of bases and tree density (4,100–10,800 individuals/ha). Basal area increased linearly with tree density in Area 1, but not in Area 2 (Fig. 5).

Despite the low establishment values observed in the field, the estimated costs of planting stock acquisition would be lower, for most species, in direct seeding, compared to buying nursery-grown seedlings in forest nurseries for establishing tree plantations (Fig. 6). The exceptions were two species (*G. ulmifolia* and *C. urucurana*) with the lowest seed mass and very low establishment values. For species presenting a reasonable field establishment (>20%), the average cost of seed acquisition was low (<US$0.08 per established seedling).

Discussion

Most species showed low establishment values in the field, concurring data obtained in recent reviews about direct seeding for restoration (Palma & Laurance 2015; Ceccon et al. 2016). Nevertheless, tree densities obtained by direct seeding of fast-growing native trees was similar or higher than those obtained by traditional restoration plantings in the Atlantic Forest, evidencing that direct seeding can be a viable restoration method for promoting a fast and effective canopy development

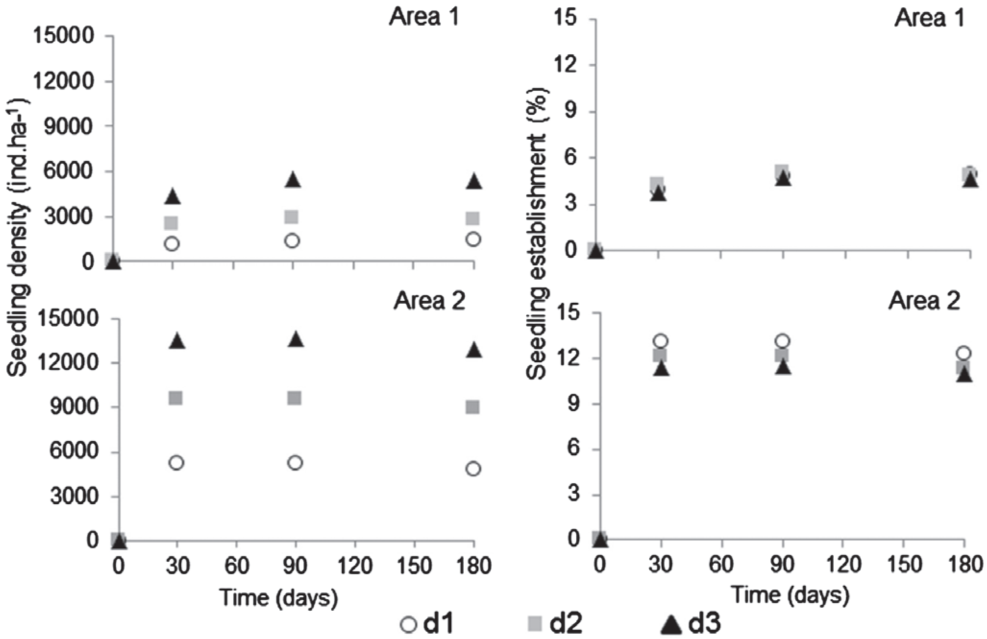

Figure 2. Total values (not cumulative) of seedling densities (A) and establishment (B) of 12 fast-growing tree species sown at three seeding densities (symbols in the figure) in two experimental restoration areas in the Atlantic Forest of Brazil. See Table 1 and Figure 1 for details on density levels used in each area and seed mass.

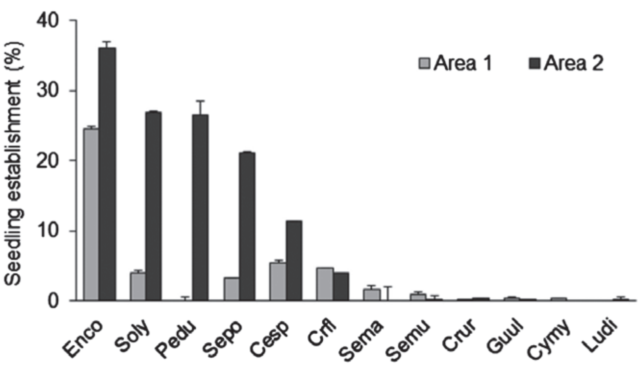

Figure 3. Establishment (180 days; mean + SE) of 12 fast-growing native tree species introduced by direct seeding in two experimental areas in the Atlantic Forest of southeastern Brazil. Species are shown in decreasing order according to their seed mass. Enco, *Enterolobium contortisiliquum*; Soly, *Solanum lycocarpum*; Pebu, *Peltophorum dubium*; Sepo, *Senegalia polyphylla*; Cesp, *Ceiba speciosa*; Crfl, *Croton floribundus*; Sema, *Senna macranthera*; Semu, *Senna multijuga*; Crur, *Croton urucurana*; Guul, *Guazuma ulmifolia*; Cymi, *Citharexylum myrianthum*; Ludi, *Luehea divaricata*.

of native trees in degraded sites. We initially expected that the use of pioneer species—some of them with dormant seeds—in direct seeding for restoration would yield a slow and irregular seedling emergence in the field, which would be a serious disadvantage for the use of this method. However, only 30 days after sowing, no substantial change in tree density was observed. The fast definition of the potential final seedling density is a favorable outcome for decision-making. One month seems to be enough for assessing the success of direct seeding and also for deciding if additional tree plantings are needed to achieve a target seedling density. Hence, it would be fairly viable to first try the cheaper option (direct seeding) to restore a tropical forest than going straight to expensive plantations of nursery-grown seedlings. If direct seeding is not successful, a complementary direct seeding or seedling plantation can then be adopted to occupy patches with reduced seedling densities. Once a forest canopy is developed and competition with invasive grasses reduces, enrichment plantings using either seedlings (Cole et al. 2011) or seeds (Bertacchi et al. 2016) can reintroduce targeted late-successional species and ecological groups that have not recolonized restoration sites spontaneously.

Species establishment varied greatly in direct seeding. Overall, large-seeded species tended to show higher values than small ones, and medium- to large-seeded legume species appeared to be good candidates for direct seeding. Some of these functional traits can be used to guide species selection in restoration projects to enhance the performance of direct seeding in obtaining a desirable seedling density in the field. In fact, seed size has been the major trait associated to successful seedling establishment in restoration projects implemented through direct seeding (Doust et al. 2006; Tunjai & Elliott 2012). A higher amount of stored reserves allows seedlings to emerge even if buried deeper, as well as developing even under restrictive conditions of soil fertility or water availability. Our results also evidence that nitrogen-fixing legume trees are good candidates for direct seeding. Nitrogen fixation is expected to greatly benefit seedling establishment in degraded soil conditions, as well as under competition with aggressive invasive grasses. These marked differences in seedling establishment resulted in the predominance of few species in the tree community, with only three species

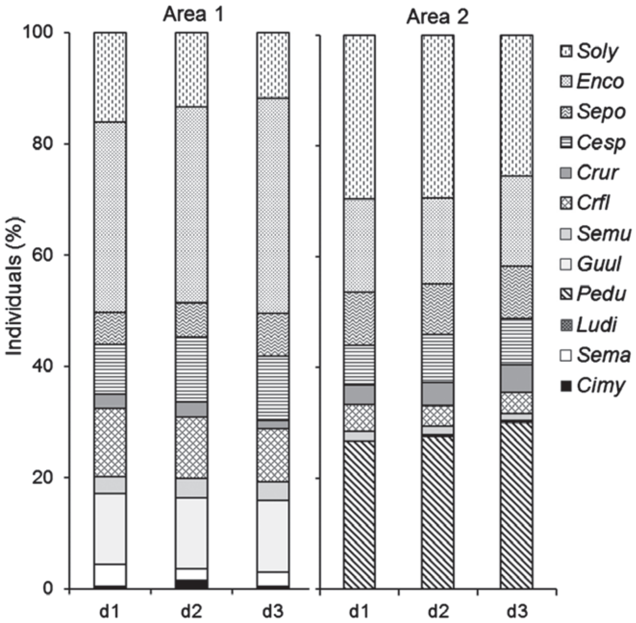

Figure 4. Established seedlings of 12 fast-growing native tree species, 180 days after direct seeding in two experimental areas in the Atlantic Forest of southeastern Brazil. See text, Figure 1, and Table 1 for details on density levels used in each area. Soly, *Solanum lycocarpum*; Enco, *Enterolobium contortisiliquum*; Sepo, *Senegalia polyphylla*; Cesp, *Ceiba speciosa*; Crur, *Croton urucurana*; Crfl, *Croton floribundus*; Semu, *Senna multijuga*; Guul, *Guazuma ulmifolia*; Pedu, *Peltophorum dubium*; Ludi, *Luehea divaricata*; Sema, *Senna macranthera*; Cimy, *Citharexylum myrianthum*.

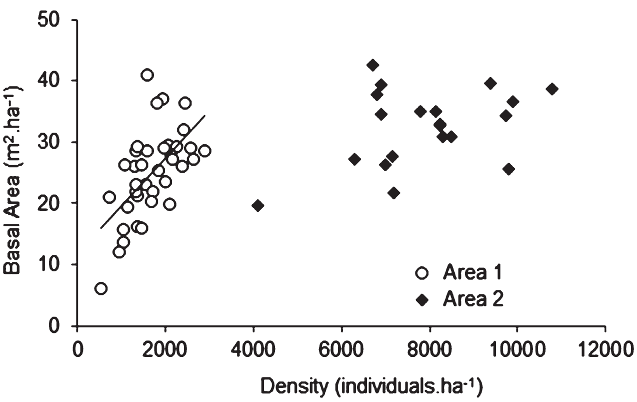

Figure 5. Basal area of forests established by three density levels of direct seeding of 12 native tree species 5 (Area 1) and 4 (Area 2) years after sowing in the Atlantic Forest of southeastern Brazil. Line represent linear function ($r^2 = 0.63$, $p < 0.001$).

accounting for 60–70% of established trees in both areas. Interestingly, this trend in species dominance is also found in regenerating forest gaps in tropical forests (Arroyo-Rodríguez et al. 2017), although the dominant species and functional groups may greatly differ between direct-seeded sites and regeneration gaps. Small-seeded species, which showed the worst establishment in our experiments, predominate in regeneration gaps,

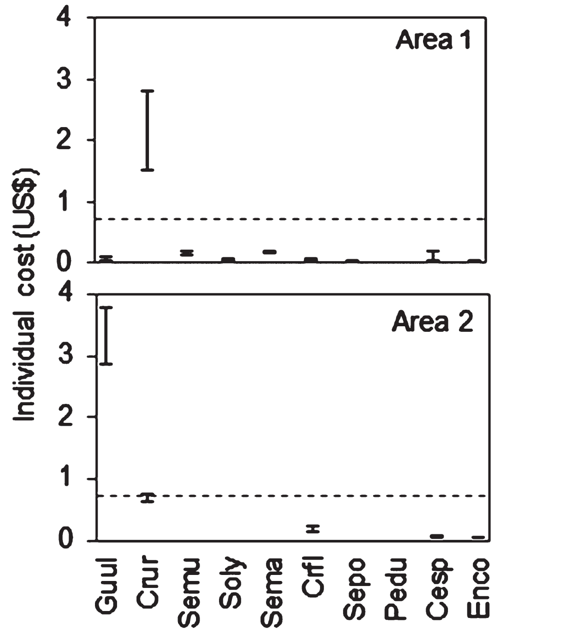

Figure 6. Costs range of seed acquisition to obtain a single established seedling in the field through direct seeding for 10 fast-growing native tree species in two experimental areas in the Atlantic Forest of southeastern Brazil. Species are shown in decreasing order according to the cost of seeds. The dashed line shows the individual cost of a nursery-grown seedling in a local forest nursery (US$0.72). Guul, *Guazuma ulmifolia*; Crur, *Croton urucurana*; Semu, *Senna multijuga*; Soly, *Solanum lycocarpum*; Sema, *Senna macranthera*; Crfl, *Croton floribundus*; Sepo, *Senegalia polyphylla*; Pedu, *Peltophorum dubium*; Cesp, *Ceiba speciosa*; Enco, *Enterolobium contortisiliquum*.

while medium-seeded, thick-coated legumes are more common in intermediate stages of succession. As it is not yet possible to predict which set of fast-growing species will perform better in each restoration condition, sowing reasonable amounts of seeds of a dozen of fast-growing tree species with good establishment in direct seeding can be a good strategy to achieve the optimal community composition and structure for dealing with unpredictable environmental filtering processes operating at the site level.

As expected, seedling density was positively and linearly associated to seeding density, while seedling establishment (i.e. percentage of the viable seeds sown that resulted in seedlings in the field) was not associated to seeding density, evidencing no density-dependence effect on the early development stages of direct seeding (Bonilla-Moheno & Holl 2010). Soil nutrient content could be a key factor explaining the markedly differences in direct seeding outcomes between Area 1 (approximately 4.8%) and Area 2 (approximately 11.5% of establishment). A recent review on direct seeding had already suggested that seeding density need to be tied to soil quality (Ceccon et al. 2016), and similar patterns of higher seedling establishment in more fertile soils have been found in studies on natural dispersed seeds (Rother et al. 2015). Increasing seeding density was an effective strategy to increase basal area of the forest undergoing restoration in the area with reduced soil sum of bases, but was ineffective in the other area, where very high tree densities may have prevented individual tree growth by intra- and interspecific competition. Thus, the early benefits of increased tree density for biomass accumulation are expected to stabilize after approximately 3,000 individuals/ha; from this density forward, competition for resources may increase mortality and reduce individual growth, thus keeping biomass values at the limits established by local site conditions.

Despite the low establishment values, buying seeds would be less costly than buying seedlings for achieving similar tree densities in restoration sites, evidencing the potential of direct seeding in reducing the costs of restoration, as well as the need to select species with better performance in direct seeding to optimize costs reduction. Traditional tree densities used in seedling plantations are constrained by the costs of seedling acquisition. Consequently, the density of trees planted in restoration sites is lower than that regenerating in forest gaps, as a strategy to reduce implementation costs (Meli & Dirzo 2013). However, lower tree densities favor the regeneration niche of ruderal weeds and, consequently, may increase the maintenance costs. Since direct seeding allows achieving higher densities of trees at lower costs, it may reduce the need for further intensive care to control invasive grasses. However, weed control in the first months after seeding can be problematic (Pereira et al. 2013), given the random or dense distribution of tree seedlings in the area, and should be considered when assessing the pros and cons of direct seeding for reducing maintenance costs. An additional strategy to suppress invasive grasses in sites restored by direct seeding is intercropping native trees with green manure species or agricultural crops at the early stages of reforestation (Campos-Filho et al. 2013; Silva et al. 2015). These plants can occupy the ecological niche of ruderal plants and further reduce the number and intensity of weed management actions (Balandier et al. 2009; Willoughby & Jinks 2009).

Establishing a tree community through direct seeding is expected to be much cheaper than that through seedling plantation. The cost reduction for the acquisition of seeds instead of seedlings for the species used in the experiments would be of the order of 40–90% for the area with higher sum of bases, and of 15–80% for the other area. Even better outcomes can be obtained if this method is supported by further research and technology development for selecting species with greater performance, for producing high-quality seed lots of native species, for enhancing pregermination treatments and sowing approaches, and for designing restoration models that integrate green manure species for effective suppression of invasive grasses. A clear innovation challenge for upscaling direct seeding for restoration is how to operationalize mechanized sowing of species with seeds of different shapes and sizes (Durigan et al. 2013). Potential negative impacts of large-scale seed collection should also be explored. Direct seeding may not be the best method for introducing most of the species currently used in tropical forest restoration, which may show a better performance if nursery-grown seedlings are used. However, dominating the technology of direct seeding of some few fast-growing trees seems to be an effective strategy for a rapid and low-cost recovery of a native forest physiognomy in degraded sites. Seedling plantation will also have an important role in this model of restoration, like for enrichment plantings with commercially valuable species or species with high conservation value. However, we expect there will no longer exist economic or ecological justification in the future for continued use of nursery-grown seedlings for introducing pioneer trees in restoration sites.

Acknowledgments

We thank staff from Usina São João (Araras, SP), Bioflora, and Sementes Piraí for fieldwork support and seed provision. We also thank Seed Technology Laboratory—ESALQ for providing the opportunity for the germination tests, and the staff of Laboratory of Forest Ecology and Restoration for their support. We acknowledge FAPESP for a doctoral grant to I.I. (FAPESP—DR 07/50465-9) and a postdoctoral grant to P.M. (2016/00052-9). P.H.S.B. thanks the National Council for Scientific and Technological Development of Brazil (CNPq) for a productivity grant (#304817/2015-5).

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Seed number used and total seed weight.
Table S2. Edaphic characteristics of the 0–20 cm soil layer in two experimental restoration areas in the Atlantic Forest in Brazil.

Coordinating Editor: Stephen Murphy

Received: 9 March, 2017; First decision: 10 April, 2017; Revised: 5 June, 2017; Accepted: 16 June, 2017