

Dams consequences to the woody regeneration layer of dry forests

Consequências de represas na regeneração de plantas arbóreas em matas secas

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Abstract Local changes caused by dams have drastic consequences on ecosystems, however, studies assessing temporal changes on the regeneration layer after these disturbances are rare. Thus, the consequences of the water line closeness to the regeneration layer of two seasonal dry forests, a deciduous dry forest and a semideciduous dry forest, on southeastern Brazil were evaluated. These forests have a severe dry season on winter and many plant species are deciduousness and disperse their seeds by wind, two mechanisms used to reduce the negative effects of the dry season. However, with the waterline closeness, the dry season can be smoothed and species with other traits should colonize this environment in detriment of the typical dry forest species. Then, one points out the hypothesis that several changes may have occurred in the regeneration layer just three years after damming, such as an increase in richness and the establishment of evergreen and zoochoric species, because the damming increased the water supply to the community. Thus, 40 plots of 5 x 5 m were distributed close to the dam margin and all plants with circumference below 15 cm were cataloged before and three years after damming. Two plant traits were also evaluated: (i) the deciduousness and (ii) dispersion syndrome of all species. The results show an expressive increase in number of individuals of plants on both forests, along with increase in richness, mainly zoochoric and evergreen species. Closeness to water probably relieved the effects of the dry period common in seasonal environments, allowing new trees and different species to establish themselves on the forests.

Keywords: human impact, impoundment, seasonal forests, deciduousness, seed dispersal syndrome.

Resumo Mudanças locais causadas por represas podem ter drásticas consequências para os ecossistemas, porém raros são os estudos que avaliam suas consequências para a regeneração de espécies arbóreas. Assim, avaliamos as consequências de uma represa na

regeneração de duas florestas estacionais secas, uma floresta decídua e outra semidecídua, localizadas no sudeste do Brasil. Estas florestas se situam em uma região de clima estacional que possui um inverno seco, e muitas espécies possuem adaptações a este ambiente seco, como a deciduidade foliar e a sementes dispersas pelo vento, no entanto, a proximidade com a linha de água pode suavizar os impactos da estação seca e espécies com outras características podem colonizar o local, em detrimento das espécies típicas deste tipo florestal. Logo, nossa hipótese central é de que três anos de represamento são suficientes para aumentar a riqueza local e o estabelecimento de espécies sempre-verdes e zoocóricas, uma vez que a disponibilidade hídrica passou a não ser mais uma restrição. Plotamos, 40 parcelas de 5 x 5 m nas margens da represa e todas as plantas com circunferência menores que 15 cm foram catalogadas antes da construção da represa e três anos após o represamento, e tiveram sua deciduidade e síndrome de dispersão bibliografadas. Houve um aumento no número de plantas e espécies em ambas as florestas, sobretudo devido ao estabelecimento de espécies zoocóricas e sempre-verdes. A presença de água constante provavelmente atenua os efeitos da estação seca e permite que novos indivíduos, sem fortes adaptações a estação seca, possam se estabelecer nas comunidades.

Palavras-chaves: florestas estacionais, impactos antrópicos, represas, deciduidade, síndrome de dispersão de sementes.

Introduction

Changes in plant communities are critical, as they're primary producers and basal components in most food webs on ecosystems (Loreau *et al.* 2001), and then . This way, it's crucial to monitor vegetation changes after human disturbances, in order to evaluate

impacts on the ecosystem. Taking into account that most of the world's large rivers have a regular flow (Nilsson *et al.* 2005), studies on plant community must clarify damming impacts on the various environments. Moreover, these forests are located on mountainous areas (Nilsson and Bergreen 2000), just where the most dams are built to generate electric power (Truffer *et al.* 2003).

Among the various impacts which may be caused by dams, trapped water form huge artificial lakes and they increase mountain soil moisture, leading to various vegetation changes (Nilsson and Bergreen 2000) as plant basal area increase, mortality of non-moisture tolerant species and recruitment of new species which tolerate these conditions (Vale *et al.* 2013). This increase in soil moisture may be critical, because even small changes in water regime level induce modifications in vegetation structure (Vale *et al.* 2013). Most studies are focused on grass and herbs in temperate environments with a low species diversity (Jansson *et al.* 2000), although most dams are built on woody plant tropical systems with a high species diversity (Nilsson *et al.* 2005).

The woody plant community in forests has, at least, two components: well-established trees – many papers on tropical forests considering trees with circumference at breast height (CBH) ≥ 15 cm (Oliveira-Filho *et al.* 1994; Chazdon *et al.* 2005; Lopes *et al.* 2012); and regeneration trees – seedlings, saplings, and young trees with CBH < 15 cm (Condit *et al.* 1999). In this case, the evaluation of regeneration layer is particularly important, because a change in this forest layer tends to be faster than changes on the arboreal layer (Milhomen *et al.* 2013). Therefore, studies on the regeneration layer may provide information enough to predict the structure and composition of a woody plant community in the future (Pare *et al.* 2009).

Given the above, this paper chose to evaluate upstream dam effects on regeneration plants, in two dry tropical forests, three years after the construction of a dam. These forests are associated to mountainous or, at least, steep terrains, and they constitute an excellent study object to understand changes related to damming. These dry forests may be subdivided into two types, named deciduous and semideciduous forest (Oliveira-Filho and Ratter 2002). Water restriction is an usual event in these seasonal environments during the dry winter, but it's stronger in deciduous forests than within semideciduous ones. In deciduous forests, the soil drought is more prominent, due to the rocky soils, high slopes and well-drained terrain and then, runoff is greater, occurring less water retention in the soil, thus, most of their species are dispersed by wind. Deciduousness and dispersal by wind are two usual plant traits facilitating the establishment of trees in dry environments.

Deciduousness prevents water loss during the dry period and dispersion by wind shows to be effective in low moisture environments, due to the long distance seeds can reach (Yamamoto *et al.* 2007). When soil moisture increases, the constraints posed by the dry season decrease, and it's predicted that species with other adaptive traits may settle in the community. So, deciduous

and anemochoric species, typical of dry forests, may present a disadvantage when compared to evergreen and zoochoric species, because closeness to water is usually attractive to fauna (Heinzenknecht and Paterson 1978) and an increased water availability tends to favor evergreen species, since photosynthesis is carried on throughout the year (Eamus 1999).

Therefore, this paper hypothesized that the changes in deciduous forests are due to the construction of a dam may be greater after water closeness. Flora from the two dry forests was used as reference to a restoration program funded by Consorcio Capim Branco Energia (CCBE), the company which manages the dam, since 2006. Some studies on the germination of these plants were conducted in laboratory by the "Germoplasm Rescue Program", developed by CCBE; however, no field studies were carried out to investigate the ability of these species to settle under the new conditions posed by damming. So, our focus isn't only understanding changes in these forests, but also indicating good species to restore areas with similar physical features, in order to constitute patterns for reforestation projects, as many species found in these locations are used for this purpose in Brazil.

Methods

Study area

This study was carried out in two dry forests, a deciduous forest and a semideciduous forest ($18^{\circ} 40' 31''$ S, $42^{\circ} 24' 30''$ W and $18^{\circ} 39' 13''$ S, $48^{\circ} 25' 04''$ W, respective), at the Amador Aguiar Dam 2 (located in the Araguari River), which is 55 m deep. These forests are associated to mountainous or, at least, steep terrains and, thus, they constitute a valuable study object for thinking through changes in forests subject similar impacts. These forests are physiognomically identical in terms of structural parameters – canopy height, tree density, and basal area (Vale *et al.* 2010) –, but the deciduous forest grows on rocky soils, which are ineffective to retain water (Oliveira-Filho and Ratter 2002). The IBGE (2012) classification separates these two types of forests based on the percentage of foliar deciduousness on the dry season: the deciduous forest has more than 50% of foliage loss whereas the semideciduous forest has 20-50% the trees are deciduous.

Both areas have sloped terrains; however, the deciduous forest slope (at some plots it was $> 30^{\circ}$) was much higher than in the semideciduous forest. The predominant soil types were dystrophic and eutrophic podzolic soils and dystrophic cambisols with basalt outcrops, micaxist, and biotite-gnaiss (Baccaro *et al.* 2004). The Amador Aguiar Dam 2 (AAD2) finished flooding in 2006, it's 565 m high and its flooded area is 45.11 km² (CCBE 2006).

These forests were about 200 m far from any fluvial water resource, however, after damming, they became close to the lakeshore created by the reservoir and an impact on soil moisture

started to be observed (Vale *et al.* 2013). Unlike other dams, the water level is controlled through the water flow of an upstream dam; thus, there're no water fluctuations and no floods during any period of the year. The climate is Aw (Kottec 2006), with a dry winter (April to September) and a rainy summer (October to March), an average annual temperature of 22°C, and an average rainfall around 1,595 mm (Santos and Assunção 2006).

Regeneration layer

The first survey (T0) was carried out in 2006, close to AAD2 in both forests, and the second survey was conducted 3 years after damming (T3). We plotted 40 samples of 5 x 5 meters of close to the lakeshore within the woody plant layer, 0-10 m far from the lakeshore. All plants had their individuals catalogued and their species identified, however, adult trees with a circumference at soil level > 15 cm weren't analyzed, because they are plants well-established within the community. The relative density of all species was calculated and a ranking of species was developed, having their absolute density within the T0 and T3 periods as a basis.

Diversity and similarity

We calculated the Shannon-Weaver diversity index (Shannon 1948), in order to estimate diversity changes over the regeneration layer measurement periods (T0-T3) in both forests. We also applied Hutcheson's t test (Hutcheson 1970), in order to compare T0 richness to T3 richness. Moreover, the Jaccard similarity coefficient and the Morisita-Horn index were calculated for the regeneration layer before and after damming (comparing T0 to T3), and the same procedure was undertaken with regard to the regeneration layer at T3 and T0 and the woody plant layer at T0 (comparing T0 regeneration layer to T0 woody plant layer and T3 regeneration layer to T0 woody plant layer).

Ecological traits

Two ecological traits were analyzed: deciduousness and dispersion syndrome. Deciduousness is a major characteristic in seasonal environments, because it's related to canopy openness and litter release (Percy *et al.* 2014); we distinguish deciduous species from evergreen species. Dispersion syndrome is related to tree capacity for spreading their seeds as far as possible from the parent plant and, in seasonal environments, seeds dispersed by wind are more usual than in moist environments, due to easiness of dispersal during the dry season. Thus, we distinguished three dispersion syndrome types: anemochory (species dispersed by wind), autochory (species dispersed by ballistic mechanisms), and zoochory (species dispersed by fauna). Information on these ecological attributes were surveyed in scientific papers and technical books and obtained by means of field observations, specialist conferences, and the analyses previously conducted on the structure of tree communities. Still, to classify the species

in generalist, non-generalist or supertramp of dry forests we used the Linares-Palomino *et al.* (2011) classification about the species occurrence on these forests.

Results

General changes

The dam's impacts on the regeneration component were high in both forests. There was a strong rise in the number of individuals (from 375 to 697 in the deciduous forest and from 586 to 1,196 in the semideciduous forest) in 1,000 m² sampled in each forest. In the deciduous forest, 11 species found at T0 weren't sampled at T3, and 15 new species were sampled (Table 1). Similar results was showed in the semideciduous forest, whereas 9 species found at T0 weren't sampled at T3, and 21 new species were sampled at T3 (Table 2). Nevertheless, the number of species at T0 and T3 varied just a little in the deciduous forest (only 4) and the same occurred with regard to the Shannon index (3.05 at T0 and 3.03 at T3), then, Hutcheson's t test shows no statistical difference ($t = 0.29$, $p > 0.05$). Otherwise, the semideciduous forest had a high increase in the number of species (12), leading to a significantly higher Shannon's diversity at T3 (from 3.43 to 3.71), something proven through Hutcheson's t test ($t = 5.08$, $p < 0.001$).

Table 1 Regeneration layer parameters of 2 dry forests before (T0) and 3 years after (T3) dam's construction in southeastern Brazil.

| | Deciduous forest | | Semideciduous forest | |
|-----------------------|------------------|------|----------------------|-------|
| | T0 | T3 | T0 | T3 |
| Number of individuals | 375 | 697 | 584 | 1,196 |
| Richness | 47 | 51 | 65 | 77 |
| Shannon index | 3.06 | 3.03 | 3.43* | 3.71* |
| Species loss | - | 11 | - | 9 |
| New species | - | 15 | - | 21 |

Jaccard's similarity (presence/absence) between T0 and T3 in the regeneration layer was 0.581 in the deciduous forest and 0.632 in the semideciduous forest. These values were lower than Jaccard's similarity not only with regard to the presence of species, but also taking into account their abundance (Morisita-Horn): 0.743 in the deciduous forest and 0.770 in the semideciduous forest.

Species changes

Some species greatly varied with regard to their absolute density at the regeneration layer before damming. In the deciduous forest, 8 species were clearly impacted: *Guazuma ulmifolia*, *Acrocomia aculeata*, *Aloysia virgata*, *Celtis iguanae*, *Cedrela fissilis*, *Handroanthus impetiginosus*, *Croton* sp. and *Senna* sp. All these species significantly lost positions in the ranking of species

Table 2 Data on the regeneration layer of a deciduous dry forest before (T0) and 3 years after (T3) dam's construction in southeastern Brazil, organized by order of abundance in T0.

| R | T0 | T3 | Species | Authors | Ni T0 | Ni T3 | %T0 | %T3 | DS | DC |
|---|-----|-----|--------------------------------------|------------------------------------|-------|-------|-------|-------|-----|-----|
| | 1 | 3 | <i>Inga sessilis</i> | (Vell.) Mart. | 68 | 73 | 18.13 | 10.55 | Zoo | Evg |
| - | 2 | 8 | <i>Guazuma ulmifolia</i> | Lam. | 46 | 29 | 12.27 | 4.19 | Aut | Dec |
| + | 3 | 1 | <i>Anadenanthera colubrina</i> | (Vell.) Brenan | 34 | 141 | 9.07 | 20.38 | Aut | Dec |
| + | 4 | 2 | <i>Casearia rupestris</i> | Eichler | 26 | 79 | 6.93 | 11.42 | Zoo | Dec |
| - | 5 | <20 | <i>Acrocomia aculeata</i> | (Jacq.) Lodd. ex Mart. | 21 | 0 | 5.60 | 0.00 | Zoo | Evg |
| - | 6 | 18 | <i>Aloysia virgata</i> | (Ruiz & Pav.) Juss. | 21 | 8 | 5.60 | 1.16 | Ane | Dec |
| + | 7 | 5 | <i>Allophylus sericeus</i> | Radlk. | 15 | 40 | 4.00 | 5.78 | Zoo | Evg |
| - | 8 | 16 | <i>Celtis iguanae</i> | (Jacq.) Sarg. | 13 | 9 | 3.47 | 1.30 | Zoo | Dec |
| | 9 | 12 | <i>Myracrodruon urundeuva</i> | Allemão | 11 | 11 | 2.93 | 1.59 | Ane | Dec |
| | 10 | 12 | <i>Xylopia aromatica</i> | (Lam.) Mart. | 11 | 11 | 2.93 | 1.59 | Zoo | Evg |
| + | 11 | 9 | <i>Rhamnidium elaeocarpum</i> | Reissek | 9 | 24 | 2.40 | 3.47 | Zoo | Evg |
| + | 12 | 4 | <i>Campomanesia velutina</i> | (Cambess.) O. Berg | 8 | 43 | 2.13 | 6.21 | Zoo | Dec |
| - | 13 | <20 | <i>Cedrela fissilis</i> | Vell. | 8 | 3 | 2.13 | 0.43 | Ane | Dec |
| - | 14 | <20 | <i>Handroanthus impetiginosus</i> | (Mart. ex DC.) Mattos | 8 | 0 | 2.13 | 0.00 | Ane | Dec |
| + | 15 | 6 | <i>Coccoloba mollis</i> | Casar. | 6 | 35 | 1.60 | 5.06 | Zoo | Dec |
| - | 16 | <20 | <i>Croton</i> sp. | L. | 6 | 0 | 1.60 | 0.00 | Ane | - |
| | 17 | 12 | <i>Dilodendron bipinnatum</i> | Radlk. | 6 | 11 | 1.60 | 1.59 | Zoo | Dec |
| - | 18 | <20 | <i>Senna</i> sp. | Mill. | 6 | 0 | 1.60 | 0.00 | Aut | Dec |
| | 19 | 18 | <i>Luehea grandiflora</i> | Mart. | 5 | 8 | 1.33 | 1.16 | Ane | Evg |
| + | 20 | 12 | <i>Myrcia splendens</i> | (Sw.) DC | 5 | 11 | 1.33 | 1.59 | Zoo | Evg |
| | <20 | <20 | <i>Astronium fraxinifolium</i> | Schott ex Spreng. | 4 | 4 | 1.07 | 0.58 | Ane | Dec |
| | <20 | <20 | <i>Lonchocarpus cultratus</i> | (Vell.) A.M.G. Azevedo & H.C. Lima | 4 | 2 | 1.07 | 0.29 | Aut | Dec |
| | <20 | <20 | <i>Enterolobium contortisiliquum</i> | (Vell.) Morong | 3 | 2 | 0.80 | 0.29 | Zoo | Dec |
| | <20 | 18 | <i>Machaerium brasiliense</i> | Vogel | 3 | 8 | 0.80 | 1.16 | Ane | Dec |
| | <20 | <20 | <i>Senegalia polyphylla</i> | (DC.) Britton | 2 | 6 | 0.53 | 0.87 | Aut | Dec |
| | <20 | <20 | <i>Aspidosperma parvifolium</i> | A. DC. | 2 | 2 | 0.53 | 0.29 | Ane | Dec |
| | <20 | <20 | <i>Casearia gossypiosperma</i> | Briq. | 2 | 3 | 0.53 | 0.43 | Zoo | Dec |
| | <20 | <20 | <i>Cordia alliodora</i> | (Ruiz & Pav.) Cham. | 2 | 0 | 0.53 | 0.00 | Ane | Dec |
| | <20 | <20 | <i>Handroanthus chrysotrichus</i> | (Mart. ex A. DC.) Mattos | 2 | 1 | 0.53 | 0.14 | Ane | Dec |
| | <20 | <20 | <i>Albizia niopoides</i> | (Spruce ex Benth.) Burkart | 1 | 1 | 0.27 | 0.14 | Aut | Dec |
| | <20 | <20 | <i>Aspidosperma subincanum</i> | Mart. ex A. DC. | 1 | 6 | 0.27 | 0.87 | Ane | Dec |
| | <20 | <20 | <i>Casearia sylvestris</i> | Sw. | 1 | 4 | 0.27 | 0.58 | Zoo | Evg |
| | <20 | <20 | <i>Cestrum</i> sp. | L. | 1 | 0 | 0.27 | 0.00 | - | - |
| | <20 | <20 | <i>Chomelia ribesoides</i> | Benth. ex A. Gray | 1 | 0 | 0.27 | 0.00 | Zoo | Evg |
| | <20 | <20 | <i>Maclura tinctoria</i> | (L.) D. Don ex Steud. | 2 | 3 | 0.53 | 0.42 | Zoo | Dec |
| + | <20 | 7 | <i>Cordia trichotoma</i> | (Vell.) Arráb. ex Steud. | 1 | 30 | 0.27 | 4.34 | Ane | Dec |
| + | <20 | 11 | <i>Cupania vernalis</i> | Cambess. | 1 | 14 | 0.27 | 2.02 | Zoo | Evg |
| | <20 | <20 | <i>Genipa americana</i> | L. | 1 | 1 | 0.27 | 0.14 | Zoo | Evg |
| | <20 | <20 | <i>Guarea guidonia</i> | (L.) Sleumer | 1 | 1 | 0.27 | 0.14 | Zoo | Evg |
| | <20 | <20 | <i>Machaerium nyctitans</i> | (Vell.) Benth. | 1 | 0 | 0.27 | 0.00 | Ane | Dec |
| | <20 | <20 | <i>Machaerium stipitatum</i> | (DC.) Vogel | 1 | 2 | 0.27 | 0.29 | Ane | Dec |
| | <20 | <20 | <i>Psidium guajava</i> | L. | 1 | 0 | 0.27 | 0.00 | Zoo | Evg |
| | <20 | <20 | <i>Sweetia fruticosa</i> | Spreng. | 1 | 0 | 0.27 | 0.00 | Ane | Dec |
| | <20 | <20 | <i>Tapirira guianensis</i> | Aubl. | 1 | 4 | 0.27 | 0.58 | Zoo | Evg |
| | <20 | <20 | <i>Trichilia pallida</i> | Sw. | 1 | 2 | 0.27 | 0.29 | Zoo | Evg |
| | <20 | <20 | <i>Zanthoxylum rhoifolium</i> | Lam. | 1 | 7 | 0.27 | 1.01 | Zoo | Dec |
| | <20 | <20 | <i>Aegiphila integrifolia</i> | (Jacq.) B.D. Jacks. | 0 | 1 | 0.00 | 0.14 | Zoo | Dec |
| | <20 | <20 | <i>Apeiba tibourbou</i> | Aubl. | 0 | 2 | 0.00 | 0.29 | Aut | Dec |
| | <20 | 16 | <i>Attalea phararata</i> | Mart. ex Spreng. | 0 | 9 | 0.00 | 1.30 | Zoo | Evg |
| + | <20 | 10 | <i>Cecropia pachystachya</i> | Trécul | 0 | 20 | 0.00 | 2.89 | Zoo | Evg |
| | <20 | <20 | <i>Cordia sessilis</i> | (Vell.) Kuntze | 0 | 4 | 0.00 | 0.58 | Zoo | Evg |
| | <20 | <20 | <i>Erythroxylum daphnites</i> | Mart. | 0 | 3 | 0.00 | 0.43 | Zoo | Evg |
| | <20 | <20 | <i>Eugenia florida</i> | DC. | 0 | 2 | 0.00 | 0.29 | Zoo | Evg |
| | <20 | <20 | <i>Eugenia ligustrina</i> | Kiaersk. | 0 | 1 | 0.00 | 0.14 | Zoo | Evg |
| | <20 | <20 | <i>Handroanthus serratifolius</i> | (Vahl) S. O. Grose | 0 | 1 | 0.00 | 0.14 | Ane | Dec |
| | <20 | <20 | <i>Jacaranda caroba</i> | (Vell.) A. DC. | 0 | 1 | 0.00 | 0.14 | Ane | Dec |
| | <20 | <20 | <i>Piptadenia gonoacantha</i> | (Mart.) J.F. Macbr. | 0 | 1 | 0.00 | 0.14 | Ane | Dec |
| | <20 | <20 | <i>Pouteria gardneri</i> | (Mart. & Miq.) Baehni | 0 | 1 | 0.00 | 0.14 | Zoo | Evg |
| | <20 | <20 | <i>Tocoyena formosa</i> | (Cham. & Schltdl.) K. Schum. | 0 | 1 | 0.00 | 0.14 | Zoo | Evg |
| | <20 | <20 | <i>Unonopsis guatterioides</i> | R.E. Fr. | 0 | 3 | 0.00 | 0.43 | Zoo | Evg |
| | <20 | <20 | <i>Zanthoxylum riedelianum</i> | Engl. | 0 | 3 | 0.00 | 0.43 | Zoo | Dec |

R = species response to damming; Ni = number of individuals; DS = dispersion syndrome; DEC = deciduousness; Zoo = zoochoric species; Aut = autochoric species; Ane = anemochoric species; Evg = evergreen species; Dec = deciduous species; + = high increase in the number of individuals; - = high decrease in the number of individuals; < 20 = not among the 20 most abundant species.

Table 3 Data on the regeneration layer of a semideciduous dry forest before (T0) and 3 years after (T3) dam's construction in southeastern Brazil, organized by order of abundance in T0.

| R | T0 | T3 | Species | Authors | NI T0 | NI T3 | %T0 | %T3 | DSI | DEC |
|---|-----|-----|------------------------------------|--|-------|-------|-------|------|-----|-----|
| - | 1 | 2 | <i>Senegalia polyphylla</i> | (DC.) Britto | 100 | 86 | 17.12 | 7.19 | Aut | Dec |
| - | 2 | 15 | <i>Myrciaria glanduliflora</i> | (Kiaersk.) Mattos & D. Legrand | 49 | 27 | 8.39 | 2.26 | Zoo | Evg |
| + | 3 | 4 | <i>Casearia grandiflora</i> | Cambess. | 35 | 75 | 5.99 | 6.27 | Zoo | Dec |
| + | 4 | 5 | <i>Erythroxylum daphnites</i> | Mart. | 23 | 53 | 3.94 | 4.43 | Zoo | Evg |
| + | 5 | 1 | <i>Siparuna guianensis</i> | Aubl. | 23 | 92 | 3.94 | 7.69 | Zoo | Evg |
| + | 6 | 11 | <i>Terminalia glabrescens</i> | Mart. | 24 | 32 | 3.11 | 2.68 | Ane | Dec |
| + | 7 | 3 | <i>Astronium nelson-rosae</i> | Santin | 22 | 76 | 3.77 | 6.35 | Ane | Dec |
| + | 8 | 12 | <i>Cheiloclinium cognatum</i> | (Miers) A.C. Sm. | 22 | 30 | 3.77 | 2.51 | Zoo | Evg |
| - | 9 | 25 | <i>Bauhinia unguolata</i> | L. | 20 | 15 | 3.42 | 1.25 | Aut | Evg |
| + | 10 | 7 | <i>Matayba guianensis</i> | Aubl. | 17 | 42 | 2.91 | 3.51 | Zoo | Evg |
| | 11 | <20 | <i>Aspidosperma discolor</i> | A. DC. | 16 | 21 | 2.74 | 1.76 | Ane | Dec |
| | 12 | <20 | <i>Callisthene major</i> | Mart. | 15 | 20 | 2.57 | 1.67 | Ane | Evg |
| | 13 | <20 | <i>Qualea multiflora</i> | Mart. | 15 | 20 | 2.57 | 1.67 | Ane | Evg |
| | 14 | <20 | <i>Luehea grandiflora</i> | Mart. | 14 | 15 | 2.40 | 1.25 | Ane | Dec |
| + | 15 | 6 | <i>Mabea fistulifera</i> | Mart. | 14 | 45 | 2.40 | 3.76 | Aut | Dec |
| + | 16 | 13 | <i>Cordia sessilis</i> | Kuntze | 13 | 29 | 2.23 | 2.42 | Zoo | Evg |
| | 17 | <20 | <i>Duguetia lanceolata</i> | A. St.-Hil. | 10 | 11 | 1.71 | 0.92 | Zoo | Evg |
| + | 18 | 9 | <i>Cupania vernalis</i> | Cambess. | 9 | 38 | 1.54 | 3.18 | Zoo | Evg |
| | 19 | <20 | <i>Ocotea corymbosa</i> | (Meisn.) Mez | 9 | 10 | 1.54 | 0.84 | Zoo | Evg |
| + | 20 | 14 | <i>Protium heptaphyllum</i> | (Aubl.) Marchand | 9 | 29 | 1.54 | 2.42 | Zoo | Evg |
| + | <20 | 17 | <i>Pouteria gardneri</i> | (Mart. & Miq.) Baehni | 8 | 23 | 1.37 | 1.92 | Zoo | Evg |
| | <20 | <20 | <i>Virola sebifera</i> | Aubl. | 8 | 14 | 1.37 | 1.17 | Zoo | Evg |
| | <20 | <20 | <i>Apuleia leiocarpa</i> | (Vogel) J.F. Macbr. | 7 | 15 | 1.20 | 1.25 | Ane | Dec |
| | <20 | <20 | <i>Casearia gossypiosperma</i> | Briq. | 7 | 3 | 1.20 | 0.25 | Zoo | Dec |
| + | <20 | 16 | <i>Coussarea hydrangaeifolia</i> | (Benth.) Benth. & Hook. f. ex Müll. Arg. | 7 | 24 | 1.20 | 2.01 | Zoo | Evg |
| + | <20 | 18 | <i>Heisteria ovata</i> | Benth. | 6 | 22 | 1.03 | 1.84 | Zoo | Evg |
| + | <20 | 18 | <i>Simira viridiflora</i> | (Allemão & Saldanha) Steyerm. | 6 | 22 | 1.03 | 1.84 | Ane | Dec |
| | <20 | <20 | <i>Trichilia catigua</i> | A. Juss. | 6 | 3 | 1.03 | 0.25 | Zoo | Evg |
| | <20 | <20 | <i>Ixora brevifolia</i> | Benth. | 5 | 4 | 0.86 | 0.33 | Zoo | Evg |
| | <20 | <20 | <i>Psidium rufum</i> | DC. | 5 | 0 | 0.86 | 0.00 | Zoo | Evg |
| | <20 | <20 | <i>Micropholis venulosa</i> | (Mart. & Eichler) Pierre | 4 | 0 | 0.68 | 0.00 | Zoo | Evg |
| + | <20 | 10 | <i>Myrcia splendens</i> | (Sw.) DC. | 4 | 38 | 0.68 | 3.18 | Zoo | Evg |
| | <20 | <20 | <i>Myrcia tomentosa</i> | (Aubl.) DC. | 4 | 4 | 0.68 | 0.33 | Zoo | Evg |
| | <20 | <20 | <i>Agonandra brasiliensis</i> | Miers ex Benth. & Hook. f. | 3 | 0 | 0.51 | 0.00 | Zoo | Dec |
| | <20 | <20 | <i>Inga laurina</i> | (Sw.) Willd. | 3 | 7 | 0.51 | 0.59 | Zoo | Evg |
| | <20 | <20 | <i>Rudgea viburnoides</i> | (Cham.) Benth. | 3 | 4 | 0.51 | 0.33 | Zoo | Evg |
| | <20 | <20 | <i>Trichilia pallida</i> | Sw. | 3 | 0 | 0.51 | 0.00 | Zoo | Evg |
| | <20 | <20 | <i>Bauhinia rufa</i> | Graham | 2 | 3 | 0.34 | 0.25 | Aut | Evg |
| | <20 | <20 | <i>Cardiopetalum calophyllum</i> | Schtdl. | 2 | 6 | 0.34 | 0.50 | Zoo | Evg |
| | <20 | <20 | <i>Copaifera langsdorffii</i> | Desf. | 2 | 14 | 0.34 | 1.17 | Zoo | Dec |
| | <20 | <20 | <i>Diospyros hispida</i> | A. DC. | 2 | 17 | 0.34 | 1.42 | Zoo | Dec |
| + | <20 | 8 | <i>Eugenia ligustrina</i> | (Sw.) Willd. | 2 | 40 | 0.34 | 3.34 | Zoo | Dec |
| | <20 | <20 | <i>Hirtella gracilipes</i> | (Hook. f.) Prance | 2 | 1 | 0.34 | 0.08 | Zoo | Evg |
| | <20 | <20 | <i>Hymenaea courbaril</i> | L. | 2 | 1 | 0.34 | 0.08 | Zoo | Dec |
| | <20 | <20 | <i>Maprounea guianensis</i> | Aubl. | 2 | 8 | 0.34 | 0.67 | Aut | Evg |
| | <20 | <20 | <i>Sweetia fruticosa</i> | Sprenng. | 2 | 0 | 0.34 | 0.00 | Ane | Dec |
| | <20 | <20 | <i>Aspidosperma cylindrocarpon</i> | Müll. Arg. | 1 | 2 | 0.17 | 0.17 | Ane | Dec |
| | <20 | <20 | <i>Campomanesia velutina</i> | (Cambess.) O. Berg | 1 | 6 | 0.17 | 0.50 | Zoo | Dec |
| | <20 | <20 | <i>Casearia sylvestris</i> | Sw. | 1 | 3 | 0.17 | 0.25 | Zoo | Evg |
| | <20 | <20 | <i>Chrysophyllum marginatum</i> | (Hook. & Arn.) Radlk. | 1 | 3 | 0.17 | 0.25 | Zoo | Evg |
| | <20 | <20 | <i>Eriotheca candolleana</i> | (K. Schum.) A. Robyns | 1 | 0 | 0.17 | 0.00 | Ane | Evg |
| | <20 | <20 | <i>Eugenia florida</i> | DC. | 1 | 11 | 0.17 | 0.92 | Zoo | Evg |
| | <20 | <20 | <i>Handroanthus impetiginosus</i> | (Mart. ex DC.) Mattos | 1 | 1 | 0.17 | 0.08 | Ane | Dec |
| | <20 | <20 | <i>Handroanthus serratifolius</i> | (Vahl) S. O. Grose | 1 | 0 | 0.17 | 0.00 | Ane | Dec |
| | <20 | <20 | <i>Matayba elaeagnoides</i> | Radlk. | 1 | 0 | 0.17 | 0.00 | Zoo | Evg |
| | <20 | <20 | <i>Miconia albicans</i> | (Sw.) Steud. | 1 | 10 | 0.17 | 0.84 | Zoo | Evg |
| | <20 | <20 | <i>Myracrodruon urundeuva</i> | Allemão | 1 | 1 | 0.17 | 0.08 | Ane | Dec |
| | <20 | <20 | <i>Qualea dichotoma</i> | (Mart.) Warm. | 1 | 3 | 0.17 | 0.25 | Ane | Dec |
| | <20 | <20 | <i>Rhamnidium elaeocarpum</i> | Reissek | 1 | 7 | 0.17 | 0.59 | Zoo | Dec |
| + | <20 | <20 | <i>Siphoneugena densiflora</i> | O. Berg | 1 | 20 | 0.17 | 1.67 | Zoo | Evg |
| | <20 | <20 | <i>Smilax</i> sp. | L. | 1 | 0 | 0.17 | 0.00 | - | - |
| | <20 | <20 | <i>Sorocea bonplandii</i> | (Baill.) W.C. Burger, Lanj. & Wess. Boer | 1 | 3 | 0.17 | 0.25 | Zoo | Evg |
| | <20 | <20 | <i>Tocoyena formosa</i> | (Cham. & Schtdl.) K. Schum. | 1 | 9 | 0.17 | 0.75 | Zoo | Evg |
| | <20 | <20 | <i>Zanthoxylum rhoifolium</i> | Lam. | 1 | 1 | 0.17 | 0.08 | Zoo | Dec |
| | <20 | <20 | <i>Aegiphila integrifolia</i> | (Jacq.) B.D. Jacks. | 0 | 6 | 0.00 | 0.50 | Zoo | Dec |
| | <20 | <20 | <i>Casearia rupestris</i> | Eichler | 0 | 2 | 0.00 | 0.17 | Zoo | Dec |
| + | <20 | <20 | <i>Cecropia pachystachya</i> | Trécul | 0 | 12 | 0.00 | 1.00 | Zoo | Evg |
| | <20 | <20 | <i>Ceiba speciosa</i> | (A. St.-Hil.) Ravenna | 0 | 1 | 0.00 | 0.08 | Ane | Dec |
| | <20 | <20 | <i>Coccoloba molis</i> | Casar. | 0 | 8 | 0.00 | 0.67 | Zoo | Dec |

R = species response to damming; Ni = number of individuals; DS = dispersion syndrome; DEC = deciduousness; Zoo = zoochoric species; Aut = autochoric species; Ane = anemochoric species; Evg = evergreen species; Dec = deciduous species; + = high increase in the number of individuals; - = high decrease in the number of individuals; < 20 = not among the 20 most abundant species.

Table 3 cont. Data on the regeneration layer of a semideciduous dry forest before (T0) and 3 years after (T3) dam's construction in southeastern Brazil, organized by order of abundance in T0.

| R | T0 | T3 | Species | Authors | NI T0 | NI T3 | %T0 | %T3 | DSI | DEC |
|---|------|------|-------------------------------|------------------------------------|-------|-------|------|------|-----|-----|
| | < 20 | < 20 | <i>Dilodendron bipinnatum</i> | Radlk. | 0 | 2 | 0.00 | 0.17 | Zoo | Dec |
| | < 20 | < 20 | <i>Dipterix alata</i> | Vogel | 0 | 5 | 0.00 | 0.42 | Ane | Evg |
| | < 20 | < 20 | <i>Guapira opposita</i> | (Vell.) Reitz | 0 | 2 | 0.00 | 0.17 | Zoo | Evg |
| | < 20 | < 20 | <i>Guazuma ulmifolia</i> | Lam. | 0 | 1 | 0.00 | 0.08 | Aut | Evg |
| | < 20 | < 20 | <i>Inga sessilis</i> | (Vell.) Mart. | 0 | 2 | 0.00 | 0.17 | Zoo | Evg |
| | < 20 | < 20 | <i>Jacaranda cuspidifolia</i> | Mart. ex A. DC. | 0 | 1 | 0.00 | 0.08 | Ane | Dec |
| | < 20 | < 20 | <i>Lonchocarpus cultratus</i> | (Vell.) A.M.G. Azevedo & H.C. Lima | 0 | 1 | 0.00 | 0.08 | Aut | Dec |
| | < 20 | < 20 | <i>Machaerium villosum</i> | Vogel | 0 | 3 | 0.00 | 0.25 | Ane | Evg |
| | < 20 | < 20 | <i>Maclura tintorica</i> | (L.) D. Don ex Steud. | 0 | 1 | 0.00 | 0.08 | Zoo | Dec |
| | < 20 | < 20 | <i>Myrsine umbellata</i> | Mart. | 0 | 2 | 0.00 | 0.17 | Zoo | Evg |
| + | < 20 | < 20 | <i>Ouratea castaneifolia</i> | (DC.) Engl. | 0 | 12 | 0.00 | 1.00 | zoo | Evg |
| | < 20 | < 20 | <i>Pouteria torta</i> | (Mart.) Radlk. | 0 | 2 | 0.00 | 0.17 | Zoo | Evg |
| | < 20 | < 20 | <i>Schefflera morototoni</i> | (Aubl.) Maguire, Steyerm. & Frodin | 0 | 1 | 0.00 | 0.08 | Zoo | Evg |
| | < 20 | < 20 | <i>Sterculia striata</i> | A. St.-Hil. & Naudin | 0 | 1 | 0.00 | 0.08 | Zoo | Dec |
| | < 20 | < 20 | <i>Symplocos</i> sp. | Jacq. | 0 | 1 | 0.00 | 0.08 | Zoo | Evg |
| | < 20 | < 20 | <i>Tapirira guianensis</i> | Aubl. | 0 | 1 | 0.00 | 0.08 | Zoo | Evg |
| + | < 20 | < 20 | <i>Xylopia aromatica</i> | (Lam.) Mart. | 0 | 10 | 0.00 | 0.84 | Zoo | Evg |

R = species response to damming; Ni = number of individuals; DS = dispersion syndrome; DEC = deciduousness; Zoo = zoochoric species; Aut = autochoric species; Ane = anemochoric species; Evg = evergreen species; Dec = deciduous species; + = high increase in the number of individuals; - = high decrease in the number of individuals; < 20 = not among the 20 most abundant species.

(Table 2) and 5 of them are generalist or supertramp species from dry forests (species broadly distributed in dry forests), therefore, adapted to hydric stress. Moreover, out of these 8 species, 6 are deciduous and/or have abiotic dispersion (anemochoric or autochoric), 2 important traits of many species adapted to environments with low water availability. Otherwise, 10 species clearly enhanced their importance within the community (Table 2), including the dry forest supertramp *Anadenanthera collubrina* and the dry forest generalist *Cordia trichotoma* (both abiotic-dispersed and deciduous species), however, the other 8 positively affected species are non-widespread species in the dry forest (all of them are zoochoric and 5 are evergreen species).

In the semideciduous forest, few species decrease their abundance: *Senegalia polyphylla*, *Myrciaria glanduliflora*, *Baubinia unguolata* (Table 3). Only the first one is a generalist species from neotropical seasonal dry forests. The significant increase in abundance of 21 species was even more unusual, out of which 19 species, at least, doubled their number (Table 3). Few of them had very low abundance before damming (T0), such as *Eugenia ligustrina*, *Siphoneugena densiflora*, and *Cecropia pachystachia*, but they had many plants sampled at T3. Out of these 19 species, 15 are species with a zoochoric dispersal syndrome and 13 are evergreen species; therefore, these traits increased their abundance 3 years after damming.

Ecological traits

Regarding both analyzed traits, several changes occurred after damming. Concerning the dispersion syndromes, more zoochoric species occurred at T3 in both forests, 8 in the deciduous forest and 9 in the semideciduous forest, but there were no major changes in anemochory and autochory (Table 4). However, the number of individuals increased in all syndromes (Table 4), but the highest

addition occurred in the zoochoric syndrome (> 100% increase in the number of individuals) in both forests. Abundance of autochorous species also practically doubled in the deciduous forest, but there were little changes in the semideciduous forest. The anemochoric species had a small increase in the deciduous forest, when compared to other syndromes (Table 4), but they had a high increase in the semideciduous forest.

Several changes in deciduousness were noticed, too. More evergreen species colonized both forests (Table 4), representing an increase of 6 species in the deciduous forest and 8 species in the semideciduous forest. The same occurred to deciduousness, even though the rise was much smaller in the deciduous forest. Despite there was a small colonization of new species, the establishment of new deciduous trees was high in both forests, almost doubling their number. This increase also occurred to evergreen species in both forests, and this demonstrates the influence of closeness to water on the establishment of plants. Undoubtedly, damming

Table 4 Number of species and individuals in the ecological groups of the regeneration layer in 2 dry forests before (T0) and 3 years after (T3) dam's construction in southeastern Brazil.

| | Number of species | | | | Number of individuals | | | |
|------------|-------------------|-------|--------|--------|-----------------------|-------|--------|--------|
| | DecT0 | DecT3 | SemiT0 | SemiT3 | DecT0 | DecT3 | SemiT0 | SemiT3 |
| Anemochory | 16 | 14 | 16 | 16 | 77 | 86 | 127 | 238 |
| Autochory | 6 | 6 | 5 | 7 | 93 | 181 | 138 | 159 |
| Zoochory | 23 | 31 | 43 | 54 | 203 | 425 | 318 | 799 |
| Deciduous | 29 | 30 | 25 | 30 | 225 | 455 | 266 | 506 |
| Evergreen | 15 | 21 | 39 | 47 | 142 | 237 | 317 | 690 |

Dec = deciduous forest; Semi = semideciduous forest.

reduced the influence of the strong seasonality on plants in both areas, causing fast colonization after only 3 years.

Discussion

Many parameters, as richness, diversity, number of individuals and changes on functional traits illustrate the vegetation changes after the dam's construction. The most dramatic change occurred to abundance, which almost doubled in both forests. Dry environments, such as neotropical seasonal dry forests, present long winter season and net primary productivity (Pregitzer e Euskirchen 2004), perhaps due to many problems posed for the establishment of seedlings and saplings. Long drought hinders photosynthetic capacity and plant growth (Churkina e Running 1998) due to stomatal closure (Tyree *et al.* 1994); besides, embolism on xylem due to intense dry periods can kill the plant (Choat *et al.* 2005). Many of these problems were relieved through new conditions posed by damming, providing water even during dry seasons (Vale *et al.* 2013, Gusson *et al.* 2011), thus, many individuals of several species may meet good condition to settle.

The increase in the number of individuals had consequences on richness because, with more seedlings and saplings, the chance for an individual of a new species establish will be higher. However, the species composition changes greatly after 3 years of damming, much more than expected. In the species composition, at least 40% of changes were observed in the deciduous forest and 35% in the semideciduous forest, having the Jaccard similarity index between T0 and T3 as a basis, with a high turnover after only 3 years. It's possible to present some explanations for these formidable changes. Regarding the new species, the first plausible explanation is that the germination of seeds can't overcome the intense dry period in this seasonal environment. Studies showed that small differences in soil moisture sometimes results in strong differences in seed germination and, thus, in communities richness (Keddy e Ellis 1985), once that the soil moisture in these forests had a > 100% increase after damming in the dry season at 0-10 cm deep into the soil (Vale *et al.* 2013). Therefore, is possible that many species can now overcoming this environmental filter, due to the dam's construction, and the number of trees, as well species richness, becomes higher in both forests.

Other feasible explanation for these new species is the dispersion by fauna derived from other areas. With plenty of water throughout the year and a permanent water resource, more animals can disperse seeds close to the lakeshore. The occurrence of many new zoochoric

species after damming validates this hypothesis. Other studies showed that, in arid areas, damming may attract fauna (Heinzenknecht and Paterson 1978), favoring the presence of birds and mammals (Nilsson and Dynesius 1994), something which supports this hypothesis.

The species turnover, however, isn't just due to the occurrence of more species, but because some species weren't found after damming. Outra explicação possível para estas novas espécies é a dispersão pela fauna para outras áreas too (e.g. *Acrocomia aculeata* and *Handroanthus impetiginosus*, for instance). The increase in soil moisture can cause plant mortality by drowning, because the waterlogged soil becomes anoxic and this leads to oxygen stress, sometimes killing the root system (Nilsson and Berggren 2000). Therefore, it's possible to conclude that damming cause several changes to seedlings and saplings close to the lakeshore; first by mortality of non-water adapted species, second by colonization by water-tolerant species, and third by new kinds of seed dispersal by fauna. The mortality was lower in the semideciduous forest and few species underwent negative damming effects, probably because the low water stress wasn't a severe filter before damming. Otherwise, closeness to water clearly favors the settlement of new species and, thus, an increased diversity in this forest type.

Detailing of species

Changes influence not only on species richness, but also on species composition. The abundance of the regeneration layer changed greatly. In the deciduous forest sampled, *Anadenanthera collubrina* had a notorious increase in the abundance of new plants, unlike some important species found before damming, such as *Guazuma ulmifolia*, which had a decrease in its abundance. These species are similar in many aspects in the study area: both are deciduous, light demanding, autochoric, and they're frequently found in the forest canopy; however, their responses to damming were different. Despite having similar functional attributes, *A. colubrina* tolerates the new conditions in a better manner, increasing the number of individuals and establishment after the dam impact. Species with similar ecological functions may react differently to disturbances (Walker *et al.* 1999), and this becomes clear with regard to these species, at last in the regeneration layer. For example, other regeneration study shows that *M. urundeuva* (other common deciduous species abiotically dispersed) had a high reduction in its number of individuals after damming (Gusson *et al.* 2011). This means that, even if many changes occur in the forest in the future, it's still maintaining part of its primary structure and function. Indeed, the similarity in structure (Morisita-Horn) was high in both forests, when compared to floristic similarity (Jaccard).

Nevertheless, the regeneration analysis shows a tendency of both forests to become more evergreen and more zoochoric over the years (see Table 4). Undoubtedly, these changes will be noticed

only in the future, when the seedlings become adult trees, and the regeneration layer may be regarded as a predictor of future changes in woody plant characteristics. If that's true, the impacts of damming may be regarded as a huge impact on these forests, not only on richness increase and species changes, but as a landscape modifier. As an evergreen forest becomes more attractive to wildlife, the landscape may seem more traditional with the existence of a riparian forest. However, this new forest will never play exactly the same ecological roles as a traditional riparian forest. Even an increased richness and/or diversity won't mean a "total" conversion of these dry forests into typical riparian forests, due to the maintenance of most species in the community and the lack of high species loss.

It's believed that restoration programs shouldn't try reproducing a natural riparian forest in these environments, neither use only species from dry forests, but a mix of species which is tolerant to closeness to water after damming. This way, this study shows that it's important, because some projects about "seed collection" aimed at the restoration of areas affected by the construction of this dam use species which don't show a good response to their natural environment (*Guazuma ulmifolia*, *Handroanthus impetiginosus*, *Acrocomia aculeata*, *Myracrodruon urundeuwa*, and *Senegalia polyphylla*, for instance). This represents money loss and useless work. Otherwise, many species show a good response after damming and their seeds should be used in restoration programs, such as *Anadenanthera colubrina*, *Casearia rupestris*, *Allophylus sericeus*, *Rhamnidium elaeocarpum*, *Cordia trichotoma*, *Cecropia pachystachya*, *Cupania vernalis*, *Casearia grandiflora*, *Siparuna guianensis*, and *Matayba guianensis*.

Our results show the importance of this kind of study for improving the design of restoration programs in areas undergoing similar impacts. Many projects use typical species from a determined system without evaluate they regeneration potential and the functional attributes after a possible human impact. We need to focus on experimental and field works able to evaluate not only the growth and establishment of species under determined environmental conditions, but also their ecological attributes. In this work, the new conditions imposed by dam were clearly harmful not only for many species, but also for many functional attributes of dry deciduous forests. However, the same impact facilitated the survivorship of species with others traits, many evergreen and dispersed by fauna, which means a change of floristic and role of these forests to the ecosystem. We think that new restoration programs should focus on the functional traits, and species, which better established after damming. This paper helps understanding the impacts of damming on seasonal forests. Undoubtedly, not all changes in these forests can be documented, but it's clear that the damming impacts are very significant and deserve further study.

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