ADVANCES IN FORESTRY SCIENCE

OPEN ACCESS

Response groups of plants from deciduous and semi-deciduous forests based on dynamic rates: evaluating impacts imposed by dams

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Original Article

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Keywords:
Deciduous forest

Demographic rates

Semideciduous forest

Reservoir

Palavras-chave:
Floresta decídua

Taxas demográficas

Floresta semidecídua

Reservatório

Received in
2022/11/10

Accepted on
2023/09/11

Published in
2023/09/30

DOI:
http://dx.doi.org/10.34062/afs.v10i3.14648

ABSTRACT: The functional plant response groups can be useful to comprehend vegetation's reaction to an impact. The responses of tree species in seasonal forests under the influence of artificial damming were evaluated considering the hypothesis that deciduous forests may have more response groups due to their possession of species with higher tolerance to water deficit during the dry season than semi-deciduous forests, as it is an environment with greater water deficit during the dry season and possesses more species specialized in dry conditions. The hypothesis states that (1) increased water availability can hinder the maintenance and establishment of species adapted to dry environments, as they exhibit high tolerance to water deficit during dry seasons, and (2) deciduous forests will have more response groups with high demographic rates (recruitment, mortality, decrement, and increment) due to more dramatic changes in soil moisture. Response groups were detected by comparing dynamic rates of tree species near and far from the artificial lake's shore using Euclidean distance between species' dynamic rates and the Ward method. Few groups were formed away from the dams, and many groups emerged after the impact in both forests, indicating that changes resulting from damming were more prominent near the dam. More negative responses and groups affected by damming were formed in deciduous forests compared to semi-deciduous forests. Predicting the stabilization of these forests remains uncertain, necessitating long-term monitoring for obtaining robust data and additional explanations.

Grupos de resposta de plantas de florestas deciduais e semidecídua baseados em taxas dinâmicas: avaliando impactos impostos por barragens

RESUMO: Os grupos de resposta funcional das plantas podem ser úteis para compreender a reação da vegetação a um impacto. As respostas de espécies arbóreas em florestas sazonais sob a influência de represamento artificial foram avaliadas considerando a hipótese de que florestas decíduas podem ter mais grupos de resposta devido a possuírem espécies com maior tolerância ao déficit hídrico na estação seca do que florestas semidecíduas, por ser um ambiente com maior déficit hídrico durante a estação seca e possuir mais espécies especializadas em condições secas. A hipótese afirma que (1) o aumento da disponibilidade hídrica pode dificultar a manutenção e o estabelecimento de espécies adaptadas a ambientes secos, pois apresentam alta tolerância ao déficit hídrico nas estações secas, e (2) a floresta decídua terá mais grupos de resposta com altas taxas demográficas (recrutamento, mortalidade, decréscimo e incremento), devido às mudanças mais drásticas na umidade do solo. Grupos de resposta foram detectados comparando as taxas dinâmicas de espécies arbóreas próximas e distantes da margem artificial do lago usando a distância euclidiana entre as taxas dinâmicas das espécies e o método de Ward. Poucos grupos foram formados longe das barragens e muitos grupos após o impacto, em ambas as florestas, demonstrando que as mudanças resultantes do represamento foram mais proeminentes nas proximidades da barragem. Mais respostas negativas e grupos afetados pelo represamento foram formados na floresta decídua em comparação com a floresta semidecídua. Prever a estabilização dessas florestas permanece incerto, exigindo monitoramento de longo prazo para obter dados robustos e explicações adicionais.

Introduction

Responses to external factors, like light and soil moisture, led scientists to classify plant species into response groups. For example, some species on forest environments are classified according to light demand as shade-intolerant or shade-tolerant (Pearcy 1999; Swaine e Whitmore 1988); another possible classification use establishment under different water resources, namely, species tolerant and intolerant to drought, and those tolerant to high water saturation (Kozlowski e Pallardy 2002). These response group formations make it easier to understand a particular impact on a community because the interpretation a few groups is easier than analyzing a wide range of species (Petchey e Gaston 2000). Moreover, they can provide a clearer explanation of many systems, because species may be different in many locations, but the response to an impact tends to be similar on sites with a similar environment. Therefore, we believe that response groups may provide clues to proper interpretation, besides contributing to design better conservation and restoration projects aiming forests impacted by human disturbance.

Plants subjected to flooding undergo morphological and physiological changes to adapt to the flooded environment. They develop structures like aerenchyma, adventitious roots, and lenticels to enhance aeration and gas exchange under anaerobic conditions. Roots may also become shallower and more branched to absorb oxygen and nutrients. Physiologically, plants activate tolerance mechanisms such as fermentation and adjust the photosynthetic rate. These adaptations are crucial for plant survival and growth in flooded environments, enabling the exploration of specific ecological niches and the maintenance of biodiversity (Oliveira e Gualtieri 2017).

The use of species annual dynamic rates that take into account annual growth rate, establishment of recruits, and mortality (related to loss in the basal area, named outgrowth rates) have been considered an effective way to identify the formation of response groups based on disturbances. Among the most severe human impacts, two are closely related to water availability, a key abiotic resource in life: 1) changes caused by extreme weather events(Laurance et al. 2006); and 2) changes in the hydrological regime of watersheds through damming (Nilsson et al. 2005). The first one is related to carbon concentration in the atmosphere (Smith et al. 2000; Weltzin et al. 2003), leading to global temperature change, increasing rainfall frequency in some areas and causing prolonged drought in other ones (Walther et al. 2002).

The second one changes the watershed as a whole and forms huge artificial lakes, which cause a dramatic and quick increase in soil water availability leading changes in tree growth and survivor (Vale et al. 2013). Considering the progressive increase in human population and the increasing demand for electricity coming from reservoirs, these forests impacted by dams constitute an important object of study to evaluate the consequences of increased water availability at the ecosystem.

Even though the dams are distributed worldwide, mainly in biomes with high biodiversity (Nilsson et al. 2005), but the vast majority of studies were done in temperate countries (Bejarano et al. 2011; Nilsson e Berggren 2000; Dynesius et al. 2004) and there are few studies approach changes in tree species to tropical forests located in seasonal environments. In general, the impacts on forests are high mortality rates of species with no specialization for humid environments (Vale et al. 2015; Xu et al. 2009), impairs the dispersion of seeds and propagules (Sun et al. 2014), increase in species richness (Vale et al. 2013) and diversity (Xu et al. 2009) in few years after damming.

Previous studies show a rise in the basal area after damming (Vale et al. 2013) and species had different responses to increased soil moisture (Gusson et al. 2011; Vale et al. 2015), however, there are much more changes close to the dam compared to sites distant to the dams margin. Then the focus of this study was verified if it’s possible the formation of groups of species with same response to dams’ water to better understand the changes to these forests. These dry forests may be subdivided into two types, named deciduous and semideciduous forests (Oliveira-Filho e Ratter 2002). Both are seasonal, but the first implies more severe drought conditions because soil is shallower with steep slopes and retain less water during the dry season.

In this study we hypothesize that (1) since spatial and temporal availability of water has ecological and evolutionary implications (Schwinning e Ehleringer 2001), then, increased water availability can make the establishment of local specialized species in dry environments more difficult. Specialized species in these forest environments (with a high tolerance to water deficit on dry seasons) will be most negatively affected on patches closest to the dam. (2) The deciduous forest will have more response groups with high turnover of trees, due to more dramatic changes in soil moisture. Nevertheless, a semideciduous forest constitutes a milder environment and your species are less associated with drought tolerance or intolerance, and we may expect less severe responses of its species groups.

Material and Methods

Study area

This study was conducted at three dry forest patches (18°47´40”S, 48°08’57”W, 18°40’31’’ S, 42°24’30’’ W and 18°39’13’’ S, 42°25’04 W; see Fig. 1) located in the Amador Aguiar Dam Complex. The first dam finished flooding in 2005 and the second dam did it in 2006 (see Vale et al. 2013; Vale et al. 2015). The climate of the study area is Aw, according to the Koppen-Geiger classification (Alvares et al. 2003), with a dry winter (April to September), a rainy summer (October to March), an average annual temperature of 22°C, and an average rainfall around 1,595 mm (Santos e Assunção 2006).

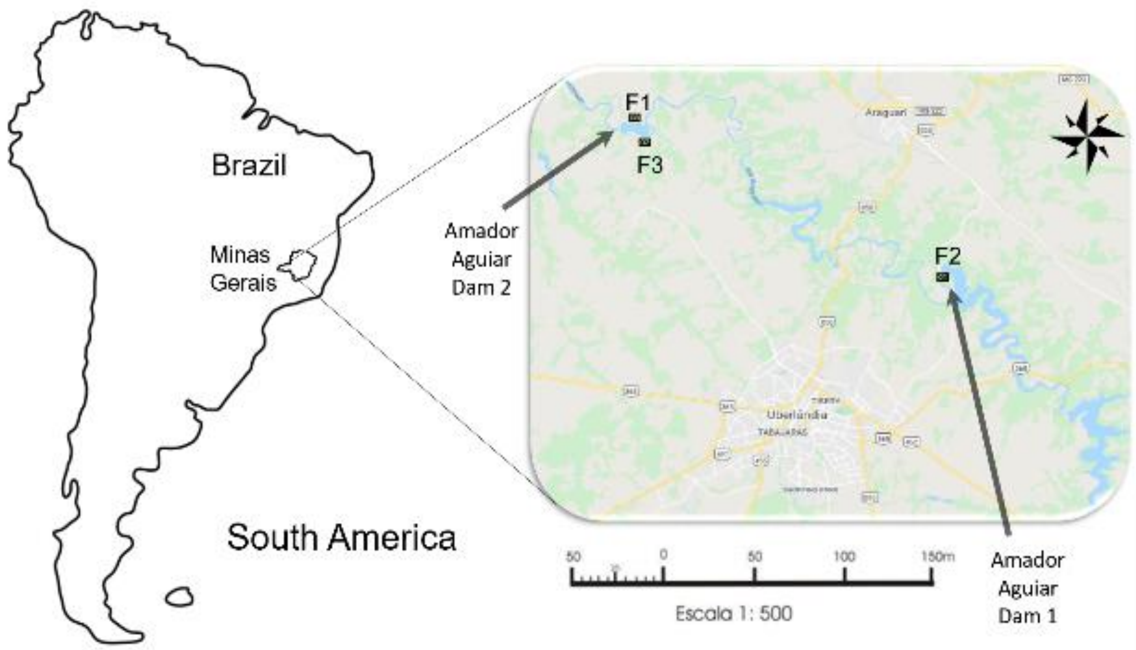

Figure 1. Location of three dry forests affected by the Amador Aguiar Dam Complex in Triângulo Mineiro, Minas Gerais, Brazil. Before dam construction, these forests were distant from water sources; now, they are on the edge of the artificial lake. F1 = Deciduous Forest 1, F2 = Deciduous Forest 2, F3 = Semideciduous Forest.

After damming, seasonally dry forests (deciduous forests with steep slopes and semideciduous forests with mild slopes), which were previously at least 200 m away from any water source, came close to the edge of the artificial lake (Figure 2). Deciduous forest occurs in rocky soils, which are more inefficient at retaining water (Oliveira-Filho e Ratter 2002). The number of deciduous trees is higher in deciduous forests compared to semideciduous forest and thus, the consequences of damming on these forests should be distinct. Damming increased the amount of water in the soil, mainly during the dry season (Vale et al. 2013) and their impacts on species within the first two years were severe (Vale et al. 2014). Previous studies (Vale et al. 2013; Vale et al. 2015) showed few community modifications to the plots located far from the water after damming (very few changes after damming Fig. 2a). Thus, we will use these plots as non-affected patches and compare them with forest patches changes closer to the artificial lake created by the dam, named dam-affected patches (plots near 0 to 30 m to the water, see Fig. 2b)

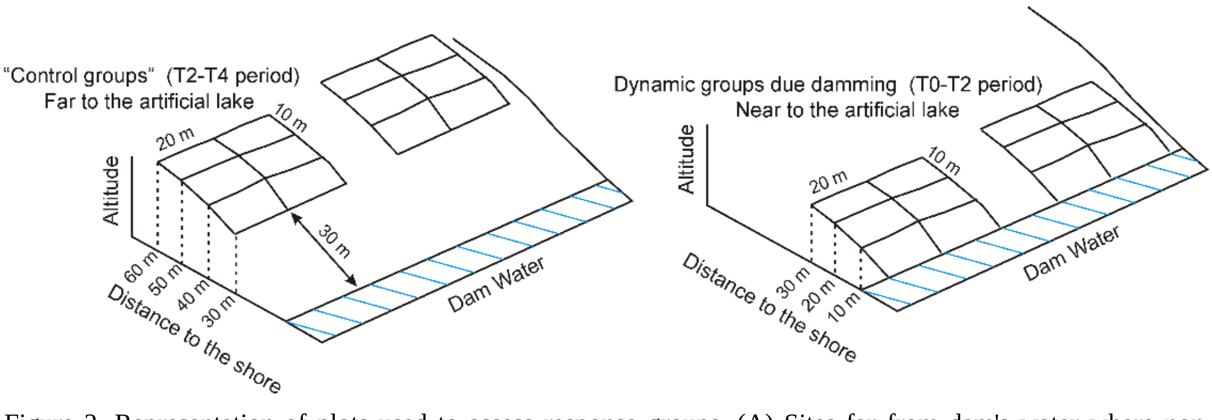

Figure 2. Representation of plots used to assess response groups. (A) Sites far from dam's water where non-dammed response groups were formed and (B) sites near dam’s water where dam-affected response groups were formed.

Plant sampling

The first inventory (T0) was carried out immediately after the start of the damming process before filling the reservoir. The second inventory (T2) was made two years after damming (two years after the first inventory) and a third inventory (T2-T4) was made four years after damming. We marked 120 permanent plots (20 × 10 m) in deciduous forests and 60 plots in semideciduous forests. Half were established close to the dams' margin (0-30m), and the remaining plots were established 30-60 m distant to the river margin. The T2-T4 period presented very few changes in the plots located far from damming and we use it as control to understand species responses to damming (Fig 2a). The T0-T2 period preseted the highest changes in the plots located near to the artificial lake and we use this period to compare with the control plots. All branches of all trees with a diameter at breast height (DBH) of 4.77 cm or higher were permanently tagged with aluminum labels. The stem diameter was measured at 1.30 m from the ground, and in case of multiple stems, all live trunks were also measured at 1.30 m and was considered only as one tree. All the live trunks had the basal area calculated and summarized to obtain one basal area for each tree. All samplings followed the same procedure as the first inventory (more information in Vale et al. 2013). The new individuals that met the inclusion criteria (recruits) were measured and identified, and mortality referred to standing dead trees or fallen trees.

Preliminary data analysis

We based the species dynamics on mortality, recruitment, outgrowth, and ingrowth rates. We calculated annual mortality (m) and recruitment (r) by exponential annual rates (see formulas in Sheil et al. 1995; 2000). Outgrowth annual rates (o) refer to the basal area of dead trees plus dead stems, and annual ingrowth rates (i) refer to basal area of recruits plus growth of the basal area of surviving trees. We evaluated each species regarding dynamic rates in the period (T0-T2): mortality, recruitment, outgrowth, and ingrowth rates (we focused on species with at least ten individuals, because the dynamic rates of species with few trees varies widely).

Response species groups

We performed analyses separately for deciduous and semideciduous forests. First, we evaluated the non-affected patches, and same procedures were performed to dam-affected ones. The response groups based on species rates were formed using the dynamic rates of each species (mortality, recruitment, outgrowth and ingrowth) with a minimum of ten trees. For this, we performed a cluster using simple Euclidean distance and the Ward's method. The cluster was performed using FITOPAC SHELL statistical program (Shepherd 2006) and we use 40 of Euclidian distance to groups formation to generate coherence groups (see below).

To assess the effectiveness of group formation, we performed a discriminant analysis, using the Statistica program (Statsoft 2005). The purpose of this analysis was testing significant differences between groups (in this case, those groups deriving from the cluster) and it determines discriminant functions that allow reclassifying species, when needed. This technique estimates the probability of correct classification and reclassifying species some species, ensuring more consistent groups (Gotelli e Ellison 2010).

After groups formation, we compare the groups formed on non-affected with dam-affected patches, calculating the dynamic rates used to each group summarizing data of all species used in the cluster. We calculated the mortality, recruitment, ingrowth, outgrowth rates, individuals' turnover by the equation $(m + r).2^{-1}$ and basal area turnover by the equation $(o + i).2^{-1}$ to each group. Based on all analysis we classified the groups in low turnover (turnover rates smaller than 5%.year^{-1}) and high turnover group (turnover rates surpass 5%.year^{-1}), negative (mortality rates higher than recruitment rates), positive (recruitment rates higher than mortality rates), very positive (recruitment rates much higher than mortality rates), unstable (turnover higher surpassing 15% .year^{-1}).

Results

Response species groups formed in the deciduous forest

The analysis allowed us to separate the species in several dynamic groups in non-affected and dam-affected areas. For the non-affected analysis, the cluster form three groups (Fig. 3a). The first group had 19 species with low dynamic rates, whose few species with rates superior to 6% year^{-1}(on supplementaty data, named low turnover group). The second group had four species with high ingrowth rates (close to 10%.year^{-1} – positive), but the mortality/recruitment and outgrowth/ingrowth were very similar (high turnover stable group), and one single species with extremely high mortality and outgrowth rates (high turnover negative group).

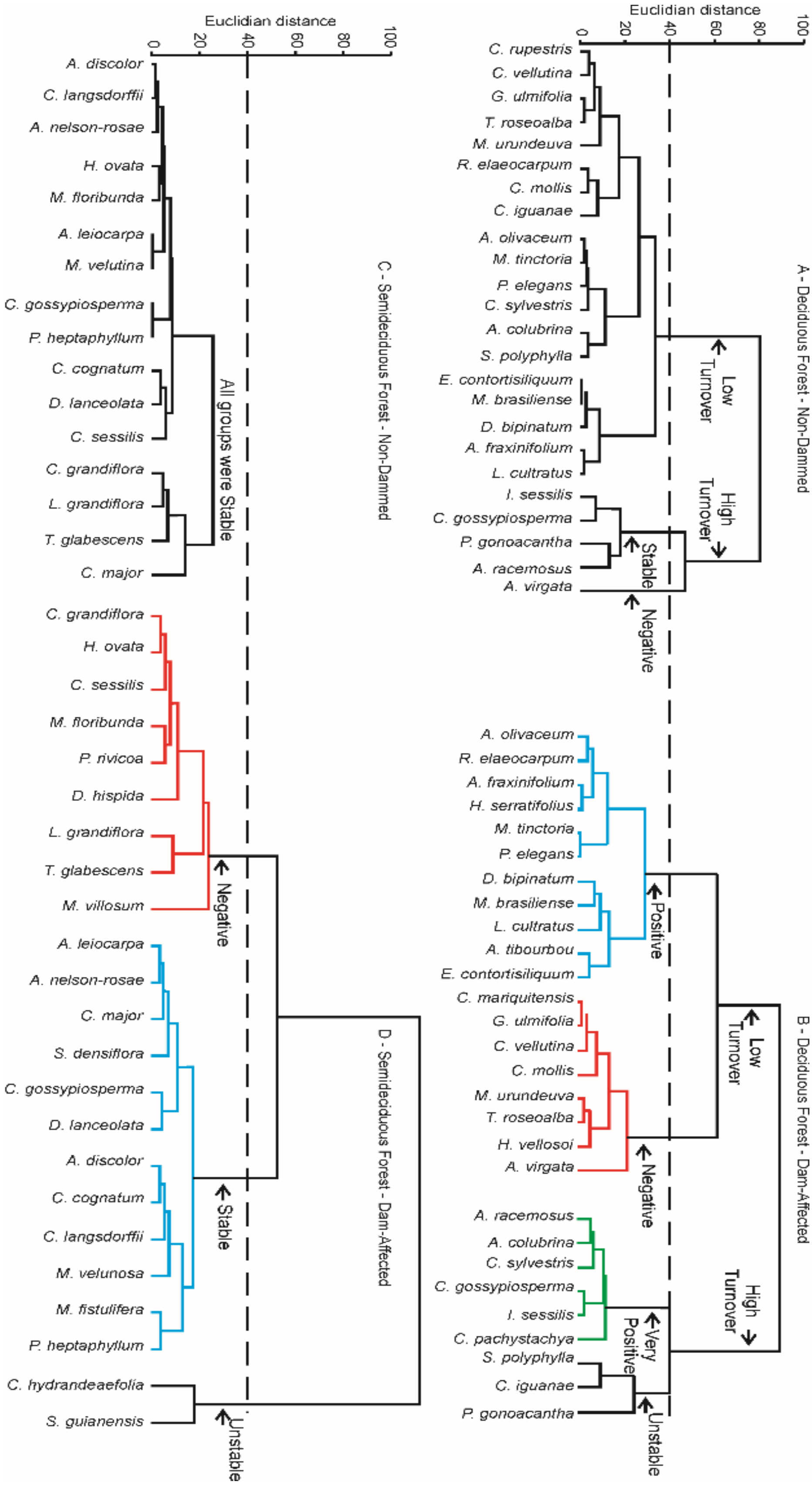

Figure 3. Cluster analysis by using Euclidian distance and the Ward's method. Groups were formed according to annual dynamic rates (mortality, recruitment, outgrowth, and ingrowth). (A) Deciduous forest non-affected response groups; (B) deciduous forest dam-affected response groups; (C) semideciduous forest non-affected response groups; (D) semideciduous dam-affected forest response groups.

The discriminant analysis confirmed cluster effectiveness (Tab. 1) and it did not reorganize any species, confirming the coherence of group formation by using the cluster technique ($F_{4,19}$ = 15.56, p < 0.001). However, only recruitment and ingrowth were significant regarding group formations (Tab. 1).

Table 1. Synthesis of discriminant function analysis of groups in the deciduous and semideciduous forest non-affected and dam-affected patches. In bold, p < 0.05; in italics, p < 0.10

		Wilks'	Partial	F-remove	p level
Deciduous Forests	Non-affected				
	Mortality	0.234	0.997	0.05	0.816
	Recruitment	0.600	0.391	29.63	**0.001**
	Outgrowth	0.236	0.992	0.15	0.412
	Ingrowth	0.254	0.922	1.61	**0.010**
	Dam-affected				
	Mortality	0.041	0.947	0.38	0.764
	Recruitment	0.122	0.321	14.76	**0.001**
	Outgrowth	0.076	0.519	6.48	**0.002**
	Ingrowth	0.054	0.731	2.57	*0.087*
Semideciduous Forests	Non-Affected				
	Mortality	0.183	0.990	0.112	0.744
	Recruitment	0.462	0.393	17.001	**0.002**
	Outgrowth	0.201	0.902	1.198	0.297
	Ingrowth	0.208	0.874	1.590	0.233
	Dam-affected				
	Mortality	0.042	0.693	3.761	**0.044**
	Recruitment	0.091	0.668	4.218	**0.032**
	Outgrowth	0.043	0.320	18.029	**0.001**
	Ingrowth	0.032	0.899	0.954	0.404

Table 2. Synthesis of discriminant function analysis of the first two discriminant roots in the deciduous and semideciduous forest non-affected and affected by damming. In bold, p < 0.05.

		Eigenvalue	Canonical R	Wilks'	Chi-square	df	p level
Deciduous Forest	Non-affected						
	Function 1	3.277	0.87	0.23	29.06	4	**0.001**
	Dam-affected						
	Function 1	5.73	0.92	0.04	74.43	12	**0.001**
	Function 2	2.19	0.83	0.26	30.59	6	**0.001**
Semideciduous Forest	Non-Affected						
	Function 1	4.508	0.90	0.181	20.47	4	**0.001**
	Dam-affected						
	Function 1	8.14	0.94	0.029	65.26	8	**0.001**
	Function 2	2.72	0.85	0.268	24.33	3	**0.001**

The first root was significant (Tab. 2), with a correlation of 87% to group formation. *Aloysia virgata* was not included because groups with only one species may not be included in discriminant analysis.

For the dam-affected analysis, the cluster formed four groups: the first had 11 species with high recruitment and ingrowth rates (sometimes surpassing 10% year^{-1} – named as positive group); the second group had eight species with high mortality and ingrowth rates (always below 10%.year^{-1} – negative); the third group had six species with very high recruitment and ingrowth rates (always surpassing 10%.year^{-1} –very positive) and the fourth group had three species with very high rates (sometimes surpassing 20%.year^{-1} – due this, we named this group as unstable) (Fig. 3b). Discriminant analysis confirmed cluster effectiveness and no species was reorganized (Fig. 4a), confirming the coherence of group formation by using the cluster technique ($F_{12,55} = 11.16$, $p < 0.001$). However, mortality rates were not significant regarding group formations (Tab. 1). The first two roots were significant with eigenvalue of 5.73 and 2.19 (Tab. 2, $p < 0.001$), with a correlation of 92% and 83% regarding group formations (canonical values – see Tab. 2).

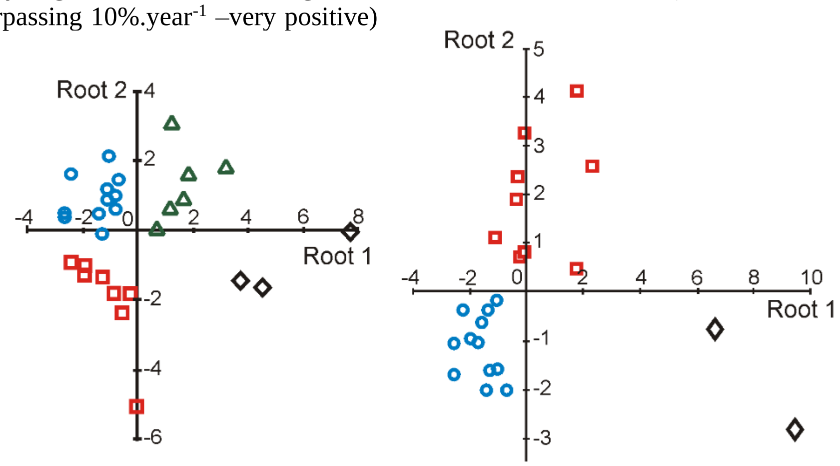

Figure 4**.** Discriminant analysis based on annual dynamic rates of species (mortality, recruitment, outgrowth, and ingrowth) affected by dam. (A) deciduous response groups. Red square = negative group; blue circles = positive group; green triangle = very positive group; and black diamond = unstable group. (B) semideciduous response groups. Red square = negative group; blue circles = stable group; black diamond = unstable group.

Response groups formed in the semideciduous forest

For non-affected analyses, the cluster formed two groups (one with 12 and another with four species), but there were small differences on dynamic rates between them (Fig. 3c). The discriminant analysis confirmed the existence of two groups ($F_{4,11} = 12{,}39$, $p < 0.001$), but the only variable separating groups was recruitment (Tab. 1). However, differences regarding the dynamic rates of these groups were tiny, besides, by using same procedure of the deciduous forest (40 of Euclidian distance), we may point out there is only one big group (Fig. 3c).

For dam-affected analysis, the cluster formed three groups (Fig. 3d) with different responses to dam impacts. The first group had 12 species with mortality and outgrowth rates higher than recruitment/ingrowth rates is about 4%.year^{-1} (negative). The second group had nine species with low rates (only ingrowth rates surpassing 5%.year^{-1} - stable). The third group with two species shows extremely high dynamic rates (all rates superior than 20%.year^{-1} - unstable). The discriminant analysis confirmed cluster effectiveness and no species was reorganized (Fig. 4b), confirming the coherence of group formation by using the cluster technique ($F_{8,34} = 20.55$, $p < 0.001$). Instead the deciduous forest, only ingrowth rates were not significant regarding group formations (Tab. 1). The first two roots were significant with eigenvalue of 8.14 and 2.72 (Tab. 2, $p < 0.001$). Then, the first two functions were highly correlated to group formations (94% and 85% of correlation; canonical values – see Tab. 2).

Deciduous groups remarks

Low turnover x High turnover groups – The analysis showed a division between groups with low and high turnover rates (Tab. 3). We considered a low turnover those groups that frequently had rates below 5%.year^{-1} and nerver surpass 10% year^{-1}. However, the low turnover group in non-affected patches had the smallest rates. The low turnover group in non-affected patches was a little different from the same group in dam-affected patches. Without direct dam influence, this group showed lower rates and it is considered stable. However, after dam construction, there was a clear separation between groups with high recruitment and groups with high mortality (positive and negative groups, respectively, see Tab. 3, Fig. 3b). Nevertheless, these rates were also lower than high turnover groups.

Table 3. Dynamic rates of response groups for deciduous and semideciduous forests. Non-affected refers to forest sites not affected by the dam; Dam-affected refers to forest sites near to the dams margin. M = mortality rate (%.year^{-1}); R = recruitment rate (%.year^{-1}); O = outgrowth rate (%.year^{-1}); I = Ingrowth (%.year^{-1}); Ind = turnover of individuals rates (%.year^{-1}); BA = turnover of basal area (%.year^{-1}); * = group with only one species.

		Average rates				Turnover	
	Groups	M	R	O	I	Ind	BA
Deciduous Non-affected	Low turnover	1.92	4.77	2.70	5.82	3.35	3.94
	Stable	5.35	0.00	7.19	9.35	13.89	8.27
	Negative*	18.35	22.43	26.52	1.05	9.18	13.78
Deciduous Dam-affected	Positive	1.62	4.01	1.00	16.19	2.82	8.60
	Negative	6.24	3.74	6.73	9.37	4.99	8.05
	Very positive	3.33	14.27	3.27	18.24	8.80	10.76
	Unstable	9.94	21.26	15.17	24.16	15.60	19.67
Semideciduous Non-affected	Stable	1.31	2.91	1.80	4.45	2.11	3.13
Semideciduous Dam-affected	Negative	8.73	3.65	12.01	7.08	6.19	9.55
	Stable	3.69	4.64	2.56	7.69	4.17	5.13
	Unstable	25.21	30.34	21.38	23.14	27.78	22.26

The high dynamic groups, those with rates near or superior to 10%.year^{-1}, had more species on dam-affected patches (nine against five in non-affected). Thus, closeness to water after damming accelerated the dynamics of this set of some species. When compare high turnover groups, on the dam-affected analysis (Fig. 3b) there is a group of six species with high growth and recruitment rates with low mortality and outgrowth rates (a very positive group, Tab. 3). Then, closeness to water did not affect all species negatively in these forests. Otherwise, three species with high rates had a high mortality, compensated by by high recruitment (named Unstable group, Fig. 3b, Tab. 3). This group was different from the stable group with high turnover, identified when analyzing the non-affected groups, because without dam influence, net change of the stable group was close to zero; with dam influence net change exceeds 15%.year^{-1}.

Comparing the species, *Rhamnidium elaeocarpum, Aspidosperma olivaceum, Platypodium elegans, Lonchocarpus cultratus, Astronium fraxinifolium, Dilodendron bipinatum* were into the stable group in non-affected area and goes to the positive response group in the dam-affected area. *Guazuma ulmifolia, Campomanesia velutina, Cocolloba mollis, Myracrodruon urundeuva, Tabebuia roseoalba* were grouped in low stable group in non-dammed area and were grouped in the negative group at dam-affected area.

Anadenanthera colubrina and *Casearia sylvestris* were grouped in the low stable group in non-dammed area. In dam-affected changed to the high turnover very positive group. *Senegalia polyphylla* and *Celtis iguanae* sylvestris were grouped in the low stable group in non-dammed area. In dam-affected area were grouped in high turnover unstable group.

Non-affected x dam-affected sites – On non-affected sites, only one group were negatively changing for both number of individuals and basal area (negative group – Tab. 3) and in the other groups the changes were tiny, and the overall net changes were near to zero. However, on dam-affected analysis, only one group had a negative balance for number of trees and no one for the basal area. Thus, the trees that survived the impacts of closeness to water increased their growth rates; therefore, all groups had a positive net change for the basal area. The overall changes were very positive for three groups (positive, very positive and unstable groups).

Semideciduous groups remarks

Stable non-affected x dam-affected groups **–** The analysis did not show clear response groups on semideciduous non-affected sites (Fig. 3c). Otherwise, three groups were identified on sites directly affected by damming (Fig. 3d). The single semideciduous group on non-affected sites had low dynamic rates, such as turnover rates and net change

(Tab. 3). One group on sites affected by damming remained stable, but other two groups did not: a group with negative responses to impact (high mortality and outgrowth rates) and an unstable group, with high mortality and outgrowth rates compensated by high recruitment and ingrowth rates (Tab. 3).

Semideciduous non-affected site had low rates and it seems to be stable. Thus, the formation of three response groups on dam-affected sites (two of them with rates > 10% year^{-1}) illustrated dam influence on the community (Tab. 1). Species in the "unstable group" had all high rates (*Siparuna guianensis* and *Coussarea hydrangeifolia*) confirming the existence of a group highly impacted by dams water.

The average dynamic rates synthetise dam impacts (Tab. 3). One group was negatively affected, and it lost many trees; the other two (stable and unstable) increased their importance in the community. Despite individual changes ingrowth was high in all groups on dam-affected sites. Those trees that survived impacts caused by closeness to water increased their growth rates. However, the basal area gain did not compensate the basal area lost by the negative group. Thus. Thus, only this group lost basal area on dam-affected sites, considering both forests.

Four species appears only in dam-affected area. *Handroanthus vellozoi*, *Handroanthus serratifolius* and *Apeiba tibourbou* were grouped with low turnover group. *Cecropia pachystachya* enter in the high turnover and very positive group.

Deciduous x semideciduous: dynamic groups, general aspects, and contrasts

The comparison between deciduous and semideciduous forests showed the formation of more dynamic groups of species in the deciduous forest, although both forests had some similar (not equal) groups. Negative and unstable groups occur more proeminent in sites affected by damming water, but the deciduous forest tend to suffer more alterations and had a group of species with high positive dynamic rates too. The unstable group occurred in both forests due to the dam influence and the dynamic rates were very high in both forests.

Discussion

Negative groups

We may claim that two response groups observed in both forests deriving from dam impacts: the negative and unstable groups. Instead of the community as a whole, which keeps a constant number of trees (Vale et al. 2013), many species had negative net change within the first two years after damming. Low recruitment rates indicate problems of group maintenance under new conditions. Mortality was concentrated on "young trees" (Vale et al. 2013); thus, many probable recruits died. Early life stages are likely to be sensitive and vulnerable to conditions of extreme water availability (Fenner et al. 1985; Leuzinger et al. 2005; Stefan et al. 2007), and even more to an environment without a pronounced dry period. This tendency was reinforced by low recruitment rates for the negative group in both physiognomies.

Many surveys on these sites reported the mortality of young trees and saplings of *Myracrodruon urundeuva* (Gusson et al. 2011) and *Guazuma ulmifolia* (Vale et al. 2014), two important species in the deciduous forest. Besides, other species considered specialized in dry forests and well distributed in these environments (Linares-Palomino et al. 2011) had high mortality rates: *Senegalia polyphylla*, *Celtis iguanae*, *Tabebuia roseoalba*, and *Aloysia virgata* the first two species in the unstable group and the last two in the negative group.

Water deficit is an ecological filter that favors plants adapted to low water saturation and species specialized in these environments tend to have less importance after damming. Growth and survival are associated to water availability and even few changes in soil moisture may lead to negative consequences to plant growth, such as root anoxia (Nilsson et al. 1997; White 2007), mainly among young trees. Having this group as a basis, we may infer the occurrence of changes in the lower layers of this community for many years.

The future consequences to these forests are unknown, but we believe in a decreased importance of species included in this group over the years. Even in the semideciduous forest (where this group keeps an equivalent number of trees), recruitment was lower than for other groups, suggesting a decreased importance. Other studies showed damming impacts on small trees and saplings (Xu et al. 2009), and many new species were observed four years after damming (Vale et al. 2013), so, major changes tend to occur.

Unstable, Positive groups and the "asleep resilience"

The presence of negatively affected groups was counterbalanced by the recruitment of new species, high recruitment rates of a positive and one very positive group in the deciduous forest and an unstable group in both forests. This unstable group has low abundant species that limit major conclusion. However, there were clear tendencies of density increase due to a rapid decrease in mortality rates after damming in the semideciduous forest; so, we conclude that these species tend to increase their importance in the coming years.

Instead, the unstable groups, the "positive" and the "very positive" groups contribute a lot to recruits, and their high recruitment rates lead to many changes in the deciduous community. We may argue that the positive groups (positive and very positive) and the unstable group represent an "asleep resilience". Resilience is the recovery capacity of a community after some disturbance (Walker 1992), but this concept is too wide. We observed that an entire community could respond positively to a certain disturbance, but few species can respond very positively to it. If there is no disturbance (in the case under study here, there was anthropogenic disturbance), these groups do not need to use their resilience capacity. Thus, we may claim that this group is "sleeping" regarding this kind of disturbance. However, if disturbance occurs, group resilience "wakes up" and start its positive response to disturbance. This phenotypic plasticity can change community characteristics after some disturbance and buffer the effects of soil changes (Burgess et al. 1998).

Phenotypic diversity increases the probability of species more positively affected by disturbance (Loreau 2000). Here, the very positively affected group consisted of only six species (only one of them is specialized in dry forests in South America, *Anadenanthera colubrina*; Linares-Palomino et al. 2011), but five of them are evergreen and not specialized in dry environments (*Allophylus racemosus*, *Casearia sylvestris*, *Casearia gossypiosperma*, *Inga sessilis*, and *Cecropia pachystachya*). Many new species sampled after four years of damming were evergreen. Thus, this trait has been selected after disturbance, two of them are water-associated species (*I. sessilis* and *C. pachystachya*) commonly found at riparian forest. *C. pachystachya* (Batista et al. 2008) and *I. sessilis* (Okamoto e Joly 2000), for example, can present morpho-anatomical alteration to enhance survival in flooded terrain such as increase in number of lenticels and reduction of root size.Some functional analysis show high recruitment of evergreeen species with low wood density in these deciduous forests affected by damming (Raymundo et al. 2019), confirming the tendency of high colonization of evergreen species.

This new forest "climax" will have a high basal area because all groups showed fast growth. Water deficit and several droughts decrease photosynthetic capacity and plant growth (Goulden et al. 1996; Reichstein et al. 2002). Thus, closeness to water due to damming and, as a consequence, increased soil moisture (Vale et al. 2013) eliminates this deficit. Mature moist forests tend to have a high basal area (Murphy e Lugo 1986), and we believe that these forests increase their basal area over the years, but it is difficult to predict when they will stabilize.

Stable and positive groups: implications to conservation and management

This instability changes the community. Only in the semideciduous forests, a stable group was observed within the first two years after damming and, however, in non-affected sites, 14 species in the deciduous forests and all semideciduous species were stable. We conclude that, despite changes after damming, there is still some resistance to disturbance, exemplified by the persistence of the stable group in the semideciduous forest. This ecological resistance promotes not only taxonomic maintenance but maintenance of forest characteristics. Even without a stable group in the deciduous forest, the "positive group" is mainly represented by deciduous and light demanding canopy species (typical traits of a tree community in the deciduous forest). So, not only stable groups could indicate community resistance, but also the increased importance of a set of species with typical traits.

The responses of a deciduous forest to dam impacts were higher than those of a semideciduous forest, both at the community (Vale et al. 2013; Vale et al. 2015) and species levels. The analysis of "species groups based on dynamic rates" confirms this tendency. Not only deciduous forest had different responses groups, but these groups showed an unstable period after damming. There were no a stable group in deciduous forest, and all dam-affected group had, at least, one dynamic rate surpassing 9%year^{-1}. Besides, rates were lower in the semideciduous, mainly in 12 species which form the stable group. Although dry forests have been floristically subdivided into seasonal deciduous and semideciduous forests (Oliveira-Filho e Ratter 2002) and they have a similar structure, dam effects showed different responses in these forests.

Different forest responses to disturbance imply different management and restoration projects. Resistance (lack of equilibrium following some disturbance) (Loreau 2000) in the semideciduous forest was high because this forest constitutes a less stressful environment. On the other hand, major changes in deciduous forests indicate less resistance to this disturbance and high adaptability to the new situation, as well as high complementarity.

Groups of species with different responses to an environment have different ecological niches (Walker et al. 1999). This ecological niche to water availability is different than functional groups on these areas (Vale et al. 2010), and it represents forest capacity to maintain its attributes for several years, even during a permanent disturbance. For instance, *Piptadenia gonoacantha*, *M. urundeuva* and *Platypodium elegans* have some traits in common: they are canopy trees, light-demanding, deciduous, and anemochoric species. However, these species have different responses to increased water soil. While *M. urundeuva* lost many individuals, *P. gonoacantha* recruited many trees and *P. elegans* remained constant in the environment, with high growth. Therefore, these characteristics will persist in the community.

Complementarity is not enough to maintain the importance of these traits in the forest community. There are no species with all traits mentioned above in the positive group, and many species were observed in the negative group. Thus, the importance of these traits in the deciduous forest will decrease. Otherwise, some zoochoric and perennial species had highly positive responses (*A. racemosus*, *C. sylvestris*, *I. sessilis*, *C. pachystachya*). We conclude that damming will change the dominant species and probably, the forests characteristics too. Within a few years these changes will not lead to several changes in the community, however, as damming is a permanent condition, these changes will keep occurring (the recruitment rates of these species is still high, > 10% year^{-1}) and functions will change, too.

We predict changes for the coming years, and the deciduous forests will become more evergreen and zoochoric and more similar to semideciduous forests in terms of number of trees with these traits. The impact on deciduous forests affects patches up to 60 m away from the edge of the lake (see positive group on non-affected sites), also favouring evergreen zoochoric species (*I. sessilis* and *A. racemosus*). So, damming effects constitute very invasive and changes in the deciduous forest tend to be more extensive than in the semideciduous forest.

Moreover, the most important group of individuals in the semideciduous forest was the “stable group”, while in the deciduous forest the most important group was that “negatively affected”. This scenario leads to several future changes in the deciduous forest for many decades. In natural forests, the disturbance regime is primarily driven by tree fall (Clark e Clark 1996), and high community mortality rates open space to new trees. In many cases, high mortality rates are associated to high recruitment rates (Gourlet-Fleury et al. 2005); high turnover is expected for pioneering species and low turnover is expected for non-pioneering species (Kohler et al. 2000).

Nevertheless, many adversely affected species in both forests (negative group) are old non-pioneering important canopy species such as *M. urundeuva*, *T. roseoalba*, *G. ulmifolia* (deciduous forest) and *Pouteria rivicoa*, *Terminalia glabescens* and *Machaerium villosum* (semideciduous forest). This imbalance makes sudden soil moisture increase a singular disturbance to dry forest, by affect species independently from light demanding.

Conclusions

Stressful environmental changes may lead to a complete reformulation of communities, and this poses a problem to deciduous forests. This endangered forest physiognomy (Espirito-Santo et al. 2009; Miles et al. 2006) often occurs in mountainous regions, the most effective sites to hydropower production (Truffer et al. 2003). So, many other deciduous forest areas may have similar responses. Therefore, the analysis based on “dynamic response groups” has proved to be satisfactory because, in the world, the floristic diversity is too high (Pennington et al. 2009), but the condition of low water forests on dry season occurs largely on Earth. Besides, this unique impact is not a simple transitory kind of disturbance that can be reversed, but a permanent disturbance, leading to a reorganization of this forest. We may not predict the stabilization of these forests, so, there is a need for monitoring this kind of forest over many years, to obtain robust data and provide further explanation.

Acknowledgements

The authors thank the Foundation for Research Support of the State of Minas Gerais (FAPEMIG) for financial support. The authors thank the Coordination for the Improvement of Higher Education Personnel (Process 2498/09-0) (CAPES), State University of Goiás (BIP-UEG) and PACCSS-FAPEMIG (Processo CRA-30058-12) for financial support.

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