

EFFECTS OF REDUCED WATER FLOW IN A RIPARIAN FOREST COMMUNITY: A CONSERVATION APPROACH

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VALE VS, SCHIAVINI I, ARAÚJO GM, GUSSON AE, LOPES SF, OLIVEIRA AP, PRADO-JÚNIOR JA, ARANTES CS & DIAS-NETO OC. 2015. Effects of reduced water flow in a riparian forest community: a conservation approach. Riparian forests promote several environmental services but are subject to many human impacts, for example, construction of dams. Dams reduce downstream water flow and directly affect riparian forests by the reduced outflow stretch. This study is one of the first works in the world which evaluated tree dynamics based on species annual rates of a riparian forest two and four years after reduction of water flow caused by dams. We hypothesised that several years of reduced river flow can alter the structure of tree community, reducing richness and diversity. We performed temporal soil moisture monitoring (at 0–10, 20–30 and 40–50 cm depth) to confirm reduction in soil moisture and tree community structure, richness and diversity (sampling trees with diameter at breast height \geq 4.77 cm) in 1.1 ha of forest. Three years after construction of the dam, soil moisture was reduced, especially in the dry season but tree richness and diversity showed no variation. However, in four years of study, the community dynamics had very high mortality rates (5.2% year⁻¹) and basal area loss (5.7% year⁻¹), demonstrating that water flow reduction had strong impact and severely modified the community. These changes were more intense in the understorey where generalists were better established. The water flow was reduced after dam construction and the forest would continue its changes, probably becoming structurally similar to a common seasonal forest.

Keywords: Dams, impoundment, mortality, tropical forest, vegetation dynamics

INTRODUCTION

In the world, at least 900,000 dams above 15 m high obstruct 60% of fresh water that flows to oceans (Nilsson et al. 2005). These dams are important to many human services but are also associated with many environmental problems (Sarkar & Karagoz 1995), especially for riparian systems. Many of these problems are related to water level elevation. Habitat becomes fragmented by water storage which eventually kills many flora and fauna elements and alters species richness and composition (Jansson et al. 2000).

However, some impacts in such constructions are poorly understood because most of the

studies conducted only comprised effects of water increase upstream of dam, neglecting problems associated with water flow reduction downstream, especially immediately after flow reduction. When dams are constructed, it is often necessary to divert the river but this will reduce water flow channels (Nilsson & Berggren 2000) and deplete water tables (Ward 1998). Nevertheless, there are no studies that show, with empirical data, how much soil moisture is reduced in these areas and implications to riparian systems. Only very few studies evaluate water flow reduction effects on riparian vegetation and these are

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conducted in temperate and low-biodiversity environments (Nilsson et al. 1991).

Considering the numerous ventures that reduce water available to riparian forests, this work aimed to supply some information about downstream effects on riparian forests and focused on tree dynamics after flow regulation by a dam in southern Brazil. A spillway controls water flow and a riparian forest, before near riverbed, is now 10 to 50 m away from river water. While some works show the influence of water discharge on river associated plants (Minshall et al. 1985) and the importance of soil moisture to species richness and riparian cover in these riparian systems (Naiman & Decamps 1997), we evaluated soil moisture reduction in riparian forest after flow reduction and its influence on riparian species and structure.

Our central hypothesis is that four years of reduced water flow are sufficient to alter tree community structure and floristic composition. We compartmentalised our central hypothesis into four hypotheses to better understand the final result, namely, (1) the river remoteness, due to water flow reduction, should affect riparian forest soil and, thus, significantly reduce moisture in layers up to 50 cm depth; (2) if soil moisture reduction is confirmed, it should be more severe in dry season because rain in wet season should help maintain soil moisture; (3) soil moisture will have negative effects on some water-associated species, reducing richness, alpha diversity and evenness of arboreal riparian flora and (4) net changes in riparian forest will be negative with mortality and outgrowth rates being larger than recruitment and ingrowth rates, and riparian forest would become less dense and support a smaller basal area.

MATERIALS AND METHODS

Study site

This study was conducted in a riparian forest (between 18° 47' S, 48° 08' W and 18° 47' S, 48° 08' W) located at the Amador Aguiar Dam in Minas Gerais, Brazil. During the dam construction, part of the river was diverted by a 27-m spillway, reducing the flow over a 10-km section beginning December 2005. Where water flow is reduced, the river section is called the reduced outflow stretch. The spillway reduced water flow from 359 to 7 m³ s⁻¹ (CCBE 2005).

Thus, riparian forest near the riverbed in 2005 is now about 10–50 m farther away from the direct water influence. Average altitude is 595 m with a low slope. Climate of the area is Aw (Koppen 1948) with dry winter (April till September) and rainy summer (October till March), while average annual temperature is 22 °C and average rainfall, 1595 mm (Santos & Assunção 2006).

Soil moisture changes

We carried out 10 soil collections in riparian forest at three distinct depths, namely, 0–10, 20–30 and 40–50 cm (total of 30 samples) along the riparian forest about 10 m from the riverside. Soil moisture was calculated based on EMBRAPA (1997). These depths are important because we try to evidence how water flow reduction affects soil moisture at different depths. We repeated soil sampling every three months for three years after damming to cover the middle and end of the rainy and dry seasons. Soil collections and determination of its moisture was carried out before the spillway construction in 2005 (T0), after completion of construction works in 2006 (T1) and during the third year of water flow reduction in 2008 (T3). These analyses were done to ascertain reduction in soil moisture due to dam impacts.

Since Lilliefors test showed that soil moisture data were not normally distributed, we used non-parametric Wilcoxon test to determine the possible difference between the data (near and far from shore together) over the years for the three soil depths. To compare effects of flow reduction on the seasons, we performed Kruskal–Wallis analysis followed by a post-hoc median test. All these analyses were performed in Systat 10.2 program (2002).

Plant sampling and community changes

The first survey (T0) was carried out in 2005 after the rainy season on 110 plots (each 10 m × 10 m) in riparian forest at 0–10 m and 10–20 m from the river. All trees with diameters at breast height (dbh, 1.3 m from the ground) of at least 4.77 cm were tagged with aluminum labels. Results of the first survey (T0) was published by Rodrigues et al. (2010). Second (T2) and third (T4) surveys were carried out in early 2008 and 2010 respectively two and four years after the spillway construction in the December of 2005. These

sampling methods followed the same procedure as in the first survey. New individuals that met the inclusion criteria (recruits) were measured and identified. Mortality refers to standing dead trees, fallen trees or individuals which were not found. All reproductive botanical material was deposited at the Uberlandense Herbarium, Institute of Biology, Uberlandia, Brazil and the species nomenclature and synonymies followed the Missouri Botanical Garden website (<http://www.tropicos.org/>).

Diversity

We calculated Shannon–Weaver and Simpson diversity indexes to measure changes in diversity over three measurement periods (T0–T2–T4). To compare changes in diversity, we performed statistical analyses between the three periods for each index. For Shannon-Weaver diversity index, we applied Hutcheson t-test (Hutcheson 1970) and for Simpson diversity index, we followed the procedures suggested by Brower et al. (1998). We conducted a Wilcoxon test between T0–T2, T2–T4 and T0–T4 on number of individuals and basal area using plots as samples.

Community dynamics rates

Community dynamics were based on annual mortality, recruitment, outgrowth and ingrowth rates. These were calculated in terms of annual exponential rates (Sheil et al. 1995, 2000). Outgrowth annual rate refers to basal areas of dead trees and dead branch of living trees (decrement) while ingrowth annual rate refers to basal area of recruits and growth in basal area of surviving trees (increment). Community dynamics rates were analysed for the most representative species (minimum 10 individuals). However, to compare community with studies which used logarithmic model, we performed the logarithmic model to ‘m’ (mortality) and ‘r’ (recruitment) rates (Condit et al. 1999).

Turnover and net changes

To evaluate changes in forest we computed turnover rates for individuals and basal area through mortality/recruitment rates and outgrowth/ingrowth rates (Oliveira-Filho et al. 2007) and evaluated the net changes to

individuals and basal area (Korning & Balslev 1994). Finally we developed an overall net change based on average net changes of individuals and basal area. All these analyses were conducted on each species with at least 10 individuals.

RESULTS

Soil moisture changes

Major significant differences between soil moisture occurred in the middle of the dry season at 0–10 cm depth (Table 1, Figure 1). During this time, the soil had higher moisture before flow reduction, but not at other depths. At the end of the dry season a clear reduction in moisture was observed at the three depths only one year after flow reduction.

In general, there were no significant differences in soil moisture contents between years. In all years, middle and end of rainy seasons were obviously more moist (Figure 1) at all three depths. However, before the dam construction soil at all depths in the middle of the dry season was as humid as in the rainy season of that year (T1 and T3) (Figure 1). Nevertheless, after dam construction and water flow reduction, in the middle of the dry season, soil became as dry as at the end of dry season. This effect was best demonstrated at 0–10 cm depth (Figure 1a) probably because this depth was more river dependent than deeper soil layers, the latter more influenced by moisture from groundwater. In rest of the layers, the effect was not significant (Figures 1b and c).

Plant sampling and changes in community floristic

After four years of water flow reduction the richness in riparian forest varied little (92 in T0 and T2, and 93 in T4). Two species were found in T0 and T2 (*Machaerium villosum* and *Rudgea virburnoides*) represented by a single tree, but these individuals died thereafter. Three new species were registered with single trees through T2–T4: *Chomelia sericea*, *Eugenia involucreta* and *Lonchocarpus cultratus*. Species richness and diversity were not affected by flow reduction even after four years. Shannon-Weaver index

Table 1 Wilcoxon test results for soil moisture in each season between different soil depths

p\Z values	0–10 cm			20–30 cm			40–50 cm		
	T0	T1	T3	T0	T1	T3	T0	T1	T3
Middle rainy season									
T0	–	1.478	-0.866	–	0.663	-0.357	–	0.968	-0.153
T1	0.139	–	-2.090	0.508	–	-0.663	0.333	–	-0.764
T3	0.386	0.370	–	0.721	0.508	–	0.878	0.445	–
End rainy season									
T0	–	0.459	1.580	–	-1.682	0.153	–	-0.764	0.968
T1	0.646	–	1.988	<i>0.093</i>	–	2.293	0.445	–	1.784
T3	0.114	0.047	–	0.878	0.022	–	0.333	<i>0.074</i>	–
Middle dry season									
T0	–	-2.803	-2.599	–	-0.764	-1.682	–	0.153	-0.255
T1	0.005	–	-0.051	0.445	–	-2.497	0.878	–	-0.357
T3	0.009	0.959	–	<i>0.093</i>	0.013	–	0.799	0.721	–
End dry season									
T0	–	-2.599	-1.172	–	-1.955	-1.580	–	-2.073	-1.172
T1	0.009	–	1.682	0.050	–	0.969	0.038	–	1.244
T3	0.241	<i>0.093</i>	–	0.114	0.333	–	0.241	0.214	–

T0 = before spillway construction, T1 and T3 = one and three years after flow reduction respectively; p = probability value, Z = test value for statistical comparison, values in bold = p < 0.05 and in italics, p < 0.10

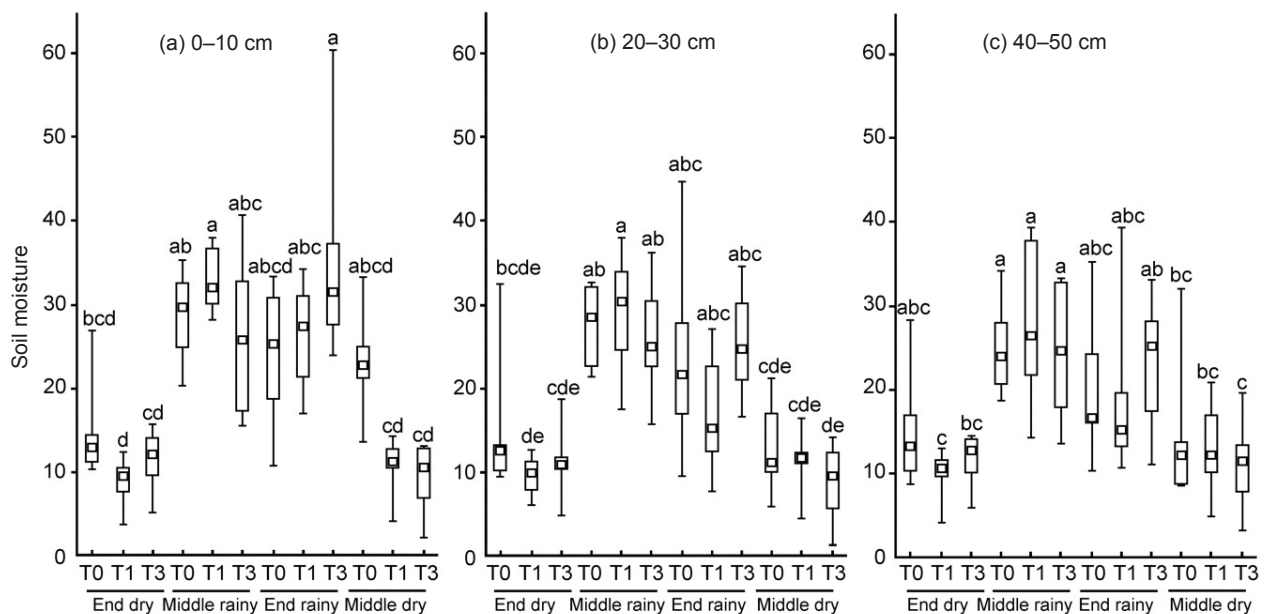


Figure 1 Box-plot representation to Kruskal–Wallis test to distinct depths before spillway construction (T0), one year after (T1) and three years after flow reduction (T3) in a riparian forest in southern Brazil; dashes = range, bars = interval between first and third quartile, square = median

varied from 3.66 in T0 to 3.71 and 3.69 in T2 and T4 respectively and the Simpson index varied from 0.95 in T0 to 0.96 in T2 and 0.96 in T4 but the differences were not significant (results not shown). For Shannon index the diversity was 3.25 in T0, 3.25 in T2 and 3.14 in T4 and for Simpsons index, 0.95 in T0 and T2 and 0.94 in T4 ($p > 0.100$, $t < 1.7$ for Hutcheson t-tests and $p > 0.100$, $t < 1.6$ for all Simpsons index comparisons between T0, T2 and T4).

Structural changes

The Wilcoxon test demonstrated reduction in number of individuals in T0–T4 ($p < 0.001$, $Z = -3.5$) and T2–T4 ($p < 0.001$, $Z = -3.6$). For T0–T2, result was only marginally significant ($p = 0.096$, $Z = -1.7$). Basal area reduction was only marginally significant in T0–T2 ($p = 0.092$, $Z = 2.0$) and T0–T4 ($p = 0.100$, $Z = 1.873$) but not significant in T2–T4 period ($p > 0.100$, $Z = 1.6$). There was reduction in number of individuals four years after water spillway construction (4.05%) and high basal area lost (3.04% in four years) (Table 2). These reductions were mainly due to high mortality (268 trees) and lower recruitment (151) along four measurement years (Table 2). Despite the high increment (7.68 m² in four years), high mortality caused greater loss in basal area than gain (Table 2).

Community dynamic rates

Tree dynamics presented higher mortality rates than recruitment (Table 2). Outgrowth annual rate was also higher than ingrowth rate due especially to low basal area of recruits, high mortality and high loss in basal area by trees with dead stems. High turnover rates of number of individuals and basal area are characteristics of a highly dynamic tree community (Table 2). High turnover occurred due to high negative net rates on number of individuals and basal area.

Some species showed slow dynamics with lower mortality and recruitment rates than the entire community (Figure 2a). Of species with high dynamics, only three had positive individual net change, meaning the number of trees recruited was more than those that died. A total of 14 species had negative individual net change. Thus, flow reduction in general affected more species negatively than positively.

Similar trend was observed in the ingrowth–outgrowth rates (Figure 2b) because eight species had rates lower than the entire community. Nine species had larger ingrowth than outgrowth rates and had positive basal area net change. However, 16 species had higher outgrowth rates than ingrowth and showed negative basal area net change. Hence, negative impacts of water flow reduction were intense for basal area and individuals in this riparian forest and surpassed any positive effects.

Turnover and net changes

Species with high individual turnover, i.e. > 3.5 (Table 3) were mostly from understorey or forest edge (*Siparuna guianensis*, *Myrcia laruotteana*, *Byrsonima laxiflora*, *Xylopia aromatica*, *Bauhinia unguolata*, *Coccoloba mollis*, *Cousarea hydrangeaeifolia*, *Erythroxylum daphnites*, *Matayba guianensis*, *Cordia sessilis*, *Alibertia edulis* and *Casearia sylvestris*), except for three subcanopy/canopy species (*Inga vera*, *I. laurina* and *Hirtella gracilipes*) which were related to moist environments (riparian and gallery forests). Species with low turnover rates, i.e. < 3.0 of individual turnover (Table 3) were all canopy species (*Apuleia leiocarpa*, *Terminalia glabrescens*, *Tabebuia roseo-alba*, *Ficus* sp.1, *Protium heptaphyllum*, *Copaifera langsdorffii*, *Hymenaea courbaril*, *Platypodium elegans*, *Pouteria torta*, *Andira anthelmia*, *Salacia elliptica* and *Acacia polyphylla*) except for one typical understorey species (*Cheiloclinium cognatum*).

Most of the high turnover species (11 of 15 of individual turnover) had negative balance between mortality/recruitment and outgrowth/ingrowth, except for *S. guianensis*, *B. laxiflora*, *E. daphnites* and *C. sessilis* (Table 3). However, some low turnover (7 of 13) species have zero/positive balance between mortality/recruitment and/or outgrowth/ingrowth. From these low turnover species analysed, four have negative balances (*Tapirira guianensis*, *Ormosia arborea*, *Zanthoxylum riedelianum* and *Myrcia splendens*) and one a zero/positive balance (*Unonopsis lindimani*). A total of 19 species had negative overall net rate while seven had negative overall net rate lower than 5% year⁻¹ (Table 3). Of the 14 species with positive overall net rate only *B. laxiflora* exceeded 5% year⁻¹ (Table 3).

Results of this study indicated that several species (mostly canopy species) were subjected

Table 2 Dynamics parameters for a arboreal community after four years of water flow reduction in a riparian forest in southern Brazil

Parameter	T0–T2	T2–T4	T0–T4
Mortality (N)	125	143	268
Recruitment (N)	89	62	151
Mortality (m ²)	2.80	3.26	6.07
Recruitment (m ²)	0.22	0.17	0.39
Decrement (m ²)	1.82	1.57	3.39
Increment (m ²)	3.55	4.13	7.68
Mortality rate (% year ⁻¹)	4.55	5.35	5.15
Recruitment rate (% year ⁻¹)	3.26	2.44	3.06
Outgrowth rate (% year ⁻¹)	5.20	5.55	5.65
Ingrowth rate (% year ⁻¹)	4.30	4.99	4.91
Individual turnover (% year ⁻¹)	3.91	3.90	4.11
Basal area turnover (% year ⁻¹)	4.75	5.10	5.28
Individual net change (% year ⁻¹)	-1.29	-3.00	-2.15
Basal area net change (% year ⁻¹)	-0.94	-0.61	-0.77

N = number of individuals, BA = basal area

to only minor changes and could be considered stable in this riparian forest even after flow reduction. However, most species experienced high death rates and/or loss of basal areas and demonstrated negative effects of lack of moisture. The most severe negative effects of moisture reduction occurred in the understorey species and those associated with water resources. Many species had major effects on community changes. *Hirtella gracilipes*, *I. vera*, *A. edulis* (water-associated subcanopy–understorey species), *I. laurina* (water-associated canopy species), *C. hydrangeaeifolia*, *C. mollis* and *P. torta* (water-associated understorey–subcanopy species) were very negatively affected species which strongly influenced the community density and/or basal area reduction. Only two species experienced major positive changes in this riparian forest, namely, *S. guianensis* and *A. leiocarpa*, both with high ingrowth rates (Table 3). Due to these values it is possible to summarise that layers below the canopy (understorey and subcanopy) are going through major restructuring of their features.

DISCUSSION

Soil moisture changes

Results from this study partly confirmed our hypotheses that spillway effected soil moisture in the dry season, but only in the 0–10 cm depth. Thus, only the soil surface layer was substantially affected by water flow reduction. Studies in riparian forests demonstrate groundwater importance and soil moisture storage to streamflow and vegetation (Fujieda et al. 1997). Thus, at deep layers (20–50 cm), the effect of spillway construction was not severe compared with soil at the surface. Soil moisture reduction was enough to cause structural modifications in this riparian forest. Many trees died after flow reduction and greater light penetration onto soil surface provided greater evaporation and loss of soil moisture. Trees increase water infiltration by retaining soil moisture and their absorption capacity (Joffre & Rambal 1993). Therefore, tree mortality also contributed to soil moisture reduction.

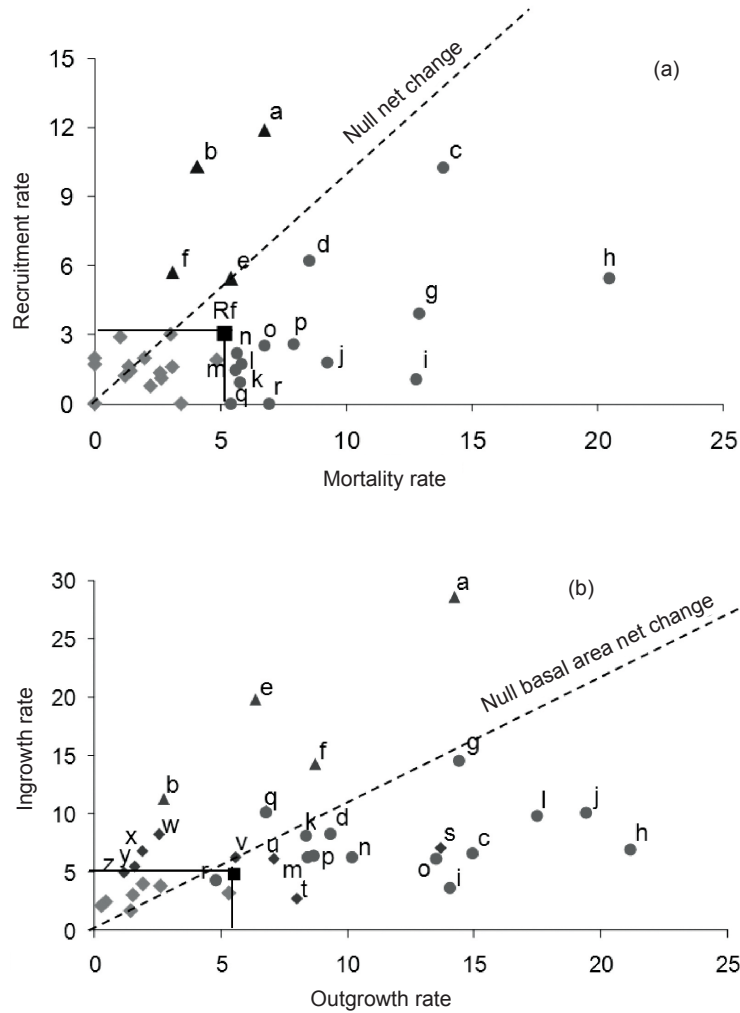


Figure 2 (a) Comparison of mortality/recruitment and (b) outgrowth/ingrowth rates in species with 10 or more individuals in a riparian forest in southern Brazil; square = community net change, triangles = species with positive individuals net changes, circles = species with negative individuals net changes, larger diamond = species with individual net changes lower than community, smaller diamond = species with individuals net changes lower than community but with area basal net change higher than community and Rf = rate for analysed forest; species legend in Table 3.

Absence of plant cover reduces water storage (Joffre & Rambal 1993), raises temperature in warmer months (Breshears & Barnes 1999) and raises water evapotranspiration (Breshears et al. 1997). Therefore, long dry periods following water flow reduction will probably change water cycle on the surface of the riparian forest. Even results of this study did not show strong soil moisture reduction in lower layers. There were clear trends of reduction especially at the end of the dry season at all depths. Despite soil surface being the most affected layer, at end of dry season very little water is stored in the soil from rain; average rainfall in each month in the region

during dry season is just 36.5 mm and during wet season, 236.5 mm (Silva & Ribeiro 2004). During these dry periods, deeper layers are dependent on moisture stemming from river and not from rains.

Structural changes

Contrary to our hypothesis, richness and diversity did not decrease after four years of reduction in river water flow. We have three explanations for this: (1) the time period of four years is not sufficient to provoke harsh changes on tree community and a longer study may clarify the

Table 3 Species dynamic rates between T0 and T4 in descending order of overall net change for species with 10 or more individuals in a riparian forest in southern Brazil

Code	Species	No. individuals				Basal area (m ²)				Dynamics rates				Turnover rate			Net change		Layer*
		T0	T2	T4	T0	T2	T4	M	O	R	I	TN	TBA	ChN	ChBA	ONC			
b	<i>Bysonima laxiflora</i>	13	12	17	0.21	0.25	0.26	4.09	2.73	10.31	11.24	7.20	6.98	6.94	5.45	6.19	U		
e	<i>Erythroxylum daphnites</i>	10	10	10	0.03	0.03	0.04	5.43	6.39	5.43	19.83	5.43	13.11	0.00	7.62	3.81	U		
a	<i>Siparuna guianensis</i>	78	91	98	0.34	0.40	0.37	6.74	14.23	11.91	28.54	9.33	21.38	5.87	1.62	3.74	I		
x	<i>Apuleia leiocarpa</i>	25	27	27	0.99	1.13	1.20	1.02	1.90	2.90	6.79	1.96	4.34	1.94	5.04	3.49	C		
y	<i>Ficus sp. 1</i>	12	13	13	2.31	2.23	2.71	0.00	1.61	1.98	5.47	0.99	3.54	2.02	4.04	3.03	C		
w	<i>Unonopsis lindmanii</i>	26	27	26	0.34	0.41	0.43	3.02	2.56	3.02	8.24	3.02	5.40	0.00	5.51	2.76	U		
f	<i>Cordia sessilis</i>	17	20	19	0.09	0.09	0.09	3.08	8.72	5.74	14.33	4.41	11.52	2.82	1.04	1.93	U		
z	<i>Tabebuia roseo-alba</i>	13	12	13	0.11	0.12	0.12	1.98	1.16	1.98	4.91	1.98	3.03	0.00	2.94	1.47	C		
-	<i>Cheilochinum cognatum</i>	14	14	15	0.29	0.30	0.31	0.00	2.62	1.71	3.87	0.86	3.24	1.74	1.13	1.43	U		
-	<i>Protium heptaphyllum</i>	94	96	95	3.23	3.38	3.50	1.36	1.92	1.62	4.04	1.49	2.98	0.26	2.09	1.18	C		
-	<i>Salacia elliptica</i>	12	12	12	0.62	0.65	0.67	0.00	0.28	0.00	2.18	0.00	1.23	0.00	1.95	0.97	I		
-	<i>Hymenaea cowbaril</i>	35	33	33	5.64	5.92	6.13	2.22	0.45	0.77	2.52	1.49	1.48	-1.46	2.11	0.32	C		
-	<i>Andira anhelmia</i>	21	22	21	0.80	0.83	0.81	1.21	1.43	1.21	1.75	1.21	1.59	0.00	0.22	0.11	C		
-	<i>Copaifera langsdorffii</i>	49	48	46	6.59	6.72	7.03	2.65	1.52	1.11	3.10	1.88	2.31	-1.57	1.61	0.02	C		
v	<i>Platypodium elegans</i>	20	20	19	0.52	0.52	0.53	2.60	5.61	1.34	6.32	1.97	5.96	-1.27	0.63	-0.32	C		
q	<i>Acacia polyphylla</i>	10	9	8	0.09	0.10	0.10	5.43	6.79	0.00	10.19	2.71	8.49	-5.43	3.79	-0.82	I		
u	<i>Tapirina guianensis</i>	61	60	54	1.77	1.87	1.69	4.85	7.09	1.91	6.16	3.38	6.62	-3.00	-1.24	-2.12	I		
d	<i>Matayba guianensis</i>	34	33	31	0.43	0.42	0.40	8.34	9.33	6.20	8.72	7.27	9.02	-2.28	-2.02	-2.15	I		
-	<i>Terminalia glabrescens</i>	23	22	20	1.59	1.61	1.46	3.43	5.31	0.00	3.26	1.72	4.29	-3.43	-2.12	-2.78	C		
k	<i>Myrcia splendens</i>	33	29	27	0.15	0.14	0.14	5.79	8.34	0.94	8.08	3.36	8.21	-4.89	-0.83	-2.86	U		
t	<i>Pouteria torta</i>	18	18	18	1.18	1.20	0.92	1.42	8.01	1.42	2.71	1.42	5.36	0.00	-5.85	-2.92	C		
m	<i>Coussarea hydrangifolia</i>	63	56	53	0.53	0.50	0.47	5.61	8.42	1.45	6.34	3.53	7.38	-4.23	-2.63	-3.43	U		
r	<i>Zanthoxylum riodelanum</i>	12	10	9	0.30	0.31	0.30	6.94	4.80	0.00	4.33	3.47	4.56	-6.94	-0.50	-3.72	C		
n	<i>Hirtella gracilipes</i>	174	171	151	4.41	3.78	3.68	5.63	10.20	2.23	6.30	3.93	8.25	-3.48	-4.45	-3.97	I		
c	<i>Casearia sylvestris</i>	25	22	20	0.18	0.16	0.15	7.88	8.65	2.60	6.37	5.24	7.51	-5.43	-3.26	-4.34	U		
s	<i>Ormosia arborea</i>	17	17	16	0.45	0.49	0.33	3.08	13.66	1.60	7.09	2.34	10.37	-1.50	-7.26	-4.38	C		
g	<i>Bauhinia unguilata</i>	40	40	27	0.23	0.27	0.21	12.92	14.44	3.93	14.60	8.42	14.52	-9.36	-1.74	-5.55	U		
l	<i>Inga laurina</i>	70	61	59	4.49	3.57	3.13	5.85	17.49	1.74	9.77	3.80	13.63	-4.18	-8.68	-6.43	C		
o	<i>Alibertia edulis</i>	74	68	62	0.70	0.53	0.49	6.73	13.49	2.51	6.16	4.62	9.83	-4.33	-8.81	-6.57	U		
c	<i>Xylopia aromatica</i>	20	19	17	0.37	0.27	0.24	13.88	14.94	10.31	6.97	12.10	10.96	-3.98	-10.29	-7.14	I		
j	<i>Coccoloba mollis</i>	59	52	43	0.61	0.52	0.38	9.26	19.41	1.79	10.11	5.53	14.76	-7.60	-11.05	-9.33	I		
i	<i>Inga vera</i>	38	29	23	1.00	0.86	0.63	12.77	14.03	1.11	3.60	6.94	8.81	-11.80	-10.90	-11.35	I		
h	<i>Myrcia lanuolteana</i>	10	9	5	0.14	0.10	0.07	20.47	21.19	5.43	6.91	12.95	14.05	-15.91	-16.14	-16.02	U		

Codes represent the species in Figure 2; M = mortality rate, O = output rate, R = recruitment rate, I = ingrowth rate, TN = individual turnover, TBA = basal area turnover, ChN = individual net change, ChBA = basal area net change, ONC = overall net change, U = understory, I = intermediary, C = canopy; *following Rodrigues et al. (2010)

moisture reduction effects on riparian tree flora, (2) intense rain during the rainy season was sufficient to keep the soil moist for majority of the species and (3) abundant species on soil with high moisture content will still have many individuals to support their presence in community for several years. Explanations 1 and 3 are most acceptable. Riparian trees are known to be sensitive to reduction in stream flow or groundwater availability (Schume et al. 2004) and many species present in this riparian forest are water dependent or at least, successful in riparian environments (*H. gracilipes*, *I. vera*, *A. edulis*, *I. laurina*, *C. hydrangeaeifolia*, *T. guianensis*, *P. heptaphyllum*) (Ferreira & Ribeiro 2001, Matos & Felfili 2010). High mortality of these species were main factor in density reduction over four years, therefore, in medium long (about 20 years) period with flow reduction and remoteness of riverbed, we believe there will be more severe changes in both richness and diversity. Water regime variations can strongly influence species composition, community structure and biological diversity (Vale et al. 2013) and this riparian forest will suffer drought effects and soil moisture reduction for several years. Reduction in water availability is the cause for extinction of moist dependent plant species from rivers and streams (Lopes & Schiavini 2007).

Community dynamics rates

Rapid mortality and outgrowth rates found in riparian forest confirmed our hypotheses and exemplified effects of drought due to water flow reduction. These rates were higher than any other tropical, semideciduous dry (Oliveira-Filho et al. 2007, Machado & Oliveira-Filho 2010), gallery (Felfili 1995, Lopes & Schiavini 2007), and deciduous (Swaine et al. 1990, Werneck & Francheschinelli 2004) forests. The values obtained in this study are higher than other long-term dynamics studies elsewhere (Korning & Balslev 1994, Phillips et al. 2004) or even studies on severe drought periods originated by El Niño events (Condit et al. 2004). These results elucidated the pronounced effect of water flow reduction on riparian forest. Moreover, these values proved the prolonged effects of drought in these forests because before the spillway construction, the river provided sufficient water supply to trees.

The length of dry periods and amount of annual rainfall are important determinants of plant distribution (Gitlin et al. 2006), but less intense droughts may not increase mortality (Condit et al. 2004). In riparian forests, dry periods may be milder and lower due river moisture. However, absence of the river clearly makes dry period more intense for trees with lower soil moisture. Reduction in soil moisture causes decrease in leaf area index, leaf water status, carbon fixation and gas exchange (Leuzinger et al. 2005, Orwig & Abrams 1997), which lead to lower photosynthetic, productivity and growth rates (Ciais et al. 2005) and occasionally the death of trees (Breshears et al. 2005, Gitlin et al. 2006) or, at least, the falling of branches. Thus, the fitness of trees are reduced and consequently surviving trees will become more vulnerable to pathogens, herbivores and wind. Falling of high branches and mortality result in great loss of basal area.

Turnover and net changes

Many species had high mortality and loss of basal area (outgrowth). However, some species had high recruitment (four species) and basal area gain (ingrowth) rates (eight species). Increase in number of individuals and basal area of some dry resistant species over water-associated species was noticeable in other works too (Breshears et al. 2005) and promotes high species turnover. However, high mortality leads to negative net changes in the most abundant species and this is confirmed in this study, i.e. number of individuals and basal area. High turnover species with negative overall net change are understorey species (except three subcanopy/canopy water related species). On the other hand, low turnover species are mostly canopy species. All species with negative net change (to basal area or individuals) are water-related (*H. gracilipes*, *I. laurina*, *A. edulis* and *I. vera*), or understorey/subcanopy (*C. hydrangeaeifolia*, *C. mollis* and *P. torta*) species, a clear impact of moisture reduction on the community.

Large-scale disturbances cause drastic negative effects on tree diversity (Oliveira et al. 1997). They also change forest structure and promote high turnover rates with sudden and dramatic changes in abundance and spatial arrangement of dominant plants (Gitlin et al.

2006). In our riparian forest, the four years of water flow reduction was not sufficient to cause reduction in diversity or richness, but clearly influenced structural changes in arboreal flora. More drought resistant species tend to reach low-water potential more rapidly than less resistant species (Ladiges 1975) and their physiological aspects should not be severely affected by drought. We did not evaluate seeds or saplings but the recruitment was apparently influenced with high recruitment of non water-dependent species, despite low recruitment of moist-dependent species.

CONSIDERATIONS

We conclude that the negative effects of water flow reduction in riparian forests far outweighed any positive effects on a few generalist species and important ecosystem services, such as carbon storage (reduction in basal area), soil protection (high mortality), as well as biodiversity (disadvantage for many moisture-dependent species and high mortality of understory species) and environmental (with increase in direct sunlight inside the forest) changes. On a larger scale, precipitation and temperature are the most important climatic factors controlling ecological processes (Liu et al. 2004). However, for riparian forest, water from the river clearly had great importance on ecological processes, of which would be lost or reduced. Floods create heterogeneity within riparian zone, favouring coexistence of different species (Naiman & Decamps 1997) and with river detachment, this area is lost and heterogeneity of the environment is clearly reduced.

With reduction in density and basal area, we can classify this riparian forest to be in degradation phase according to Machado and Oliveira-Filho (2010). Tree community dynamics in natural forests show that strong disturbance in natural forests can lead to loss of density and basal area (Machado & Oliveira-Filho 2010). However, the forest could still recover and become a forest with its initial density and basal area, returning to a stage of stability and resilience (Gunderson 2000).

Nevertheless, in our study area, this degradation phase will not recover to a mature successional stage due to the constant reduction in moisture content causing the forest to lose its

resilience. Many other riparian forests which have reduced riverbeds by deviations and damming will also face the same scenario. The constant disturbance causes droughts for several years. Riparian forest (with many moist-dependent species) will change to another physiognomy (with more generalist species), probably a semideciduous seasonal forest, which is strongly influenced by seasonal climatic changes. This study strongly contributes to understanding of consequences of human damming in riparian forests and provides invaluable insight into what may happen to riparian forests when river water is greatly reduced.

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