Shifting species and functional diversity due to abrupt changes in water availability in tropical dry forests

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Abstract
1. Recent insights show that tropical forests are shifting in species composition, possibly due to changing environmental conditions. However, we still poorly understand the forest response to different environmental change drivers, which limits our ability to predict the future of tropical forests. Although some studies have evaluated drought effects on tree communities, we know little about the influence of increased water availability.

2. Here, we evaluated how an increase in water availability caused by an artificial reservoir affected temporal changes in forest structure, species and functional diversity, and community-weighted mean traits. Furthermore, we evaluated how demographical groups (recruits, survivors and trees that died) contributed to these temporal changes in tropical dry forests.

3. We present data for the dynamics of forest change over a 10-year period for 120 permanent plots that were far from the water’s edge before reservoir construction and are now close to the water’s edge (0–60 m). Plots close to the water’s edge had an abrupt increase in water availability, while distant plots did not.

4. Plots close to the water’s edge showed an increase in species and functional diversity, and in the abundance of species with traits associated with low drought resistance (i.e., evergreen species with simple leaves and low wood density), whereas plots far from the water’s edge did not change. Changes in overall community metrics were mainly due to recruits rather than to survivors or dead trees. Overall stand basal area did not change because growth and recruitment were balanced by mortality.

5. Synthesis. Our results showed that tropical dry forests can respond quickly to abrupt changes in environmental conditions. Temporal changes in vegetation metrics due to increased water availability were mainly attributed to recruits, suggesting that these effects are lasting and may become stronger over time. The lack of

These authors have contributed equally to this study.

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1 | INTRODUCTION

Climate change and other human impacts on abiotic conditions are causing global shifts in ecosystem dynamics, even in old-growth tropical forests, thought to be in a stable state (Meir & Ian Woodward, 2010, Brienen et al., 2015, van der Sande et al., 2016). Abiotic conditions can shift in multiple ways (e.g., increased drought, rain or temperature), each of which can result in distinct changes in the vegetation. Since the future climate of tropical regions remains uncertain (Carlton et al., 2016), it is important to understand the influence of different drivers on tropical forests. Here, we evaluate the response of species and trait diversity and community-mean traits to an abrupt and lasting increase in water availability in tropical dry forests.

Although the prevailing expectation is that the tropics will become warmer, much uncertainty remains regarding changes in rainfall patterns, and hence in water availability (IPCC, 2014). What seems clear is that extreme conditions—both drought and wet events—will increase in frequency and intensity (Cook, Ault, & Smerdon, 2015; Gloor et al., 2013). Furthermore, human influences other than climate change can affect local abiotic conditions. For example, increased drought can be caused by reduced water recycling due to deforestation (Bagley, Desai, Harding, Snyder, & Foley, 2014; Costa & Pires, 2010; Lee & Berbery, 2012), and locally increased water availability can be caused by the creation of artificial water reservoirs for hydroelectric power (Finer & Jenkins, 2012), agricultural irrigation systems (Fitzhugh & Richter, 2004; López, Vincent, & Rap, 2015), and navigability and recreation activities (Graf, 1999). Some studies have shown strong effects of drought on tropical forests (Brienen et al., 2015; Chatet et al., 2012; Nepstad, Tohver, Ray, Moutinho, & Cardinot, 2007), but few studies have evaluated the effect of increased water availability (but see Liu, Liu, Liu, Song, & Zhang, 2013, Vale et al., 2013).

The creation of water reservoirs may have abrupt and long-term impacts on the composition and diversity of the surrounding vegetation (Vale et al., 2013) by favouring species that can more efficiently use water (Nilsson & Svedmark, 2002, van der Sande et al., 2017). Most studies that evaluate the effect of increasing water availability (due to the construction of artificial reservoirs or other human influences) on plant communities were conducted in temperate regions with low diversity, and evaluated ecosystems dominated by grasses, herbs or shrubs (Jansson, Nilsson, Dynesius, & Andersson, 2000; Mallik & Richardson, 2009; Nilsson, Jansson, & Zinko, 1997). Yet, most reservoirs are located in tropical regions and are surrounded by highly diverse tropical forests (Nilsson, Reidy, Dynesius, & Revenga, 2005) that fulfill an important role in global ecosystem functions, such as climate change mitigation (Chazdon et al., 2016; Guo, Li, Xiao, Zhang, & Gan, 2007; Soares-Filho et al., 2010). It is, therefore, important to understand how major human interferences influence tropical forest dynamics.

Tropical dry forests (TDF) are ideal ecosystems to test the effect of increasing water availability, because they are dominated by species that possess a suite of traits associated with drought avoidance and/or resistance such as deciduousness and high wood density (Prado-Junior et al., 2016). Plant species in TDF should, therefore, respond markedly to an increase in water availability. TDF experience a mean annual rainfall ranging from 250 to 2,000 mm (4–6 months with precipitation <100 mm; Holdridge, 1967, Tropical Science Center) and the annual ratio of potential evapotranspiration to precipitation exceeds 1 (Dirzo, 2011; Murphy & Lugo, 1986), indicating that water is strongly limiting. Because of the strong seasonality in water availability, TDF have lower tree density, basal area and species diversity compared with wet and moist tropical forests (Lohbeck et al., 2013). After a water reservoir construction, however, the increased water availability should reduce the effect of the drought barrier, allowing less drought-resistant species to colonize and establish (Knapp et al., 2002; O’brien, 2000). This should cause a shift in species and trait composition towards higher abundance of less drought-resistant species, an increase in stem number and plot basal area, and an increase in species and functional diversity (Chave et al., 2009; Lohbeck et al., 2013; Lohbeck, Poorter, Martinez-Ramos, & Bongers, 2015; Poorter et al., 2017).

Here, we evaluated how the increase in water availability due to the construction of an artificial reservoir affected temporal changes in community structure, species diversity and functional diversity in tropical dry forests. We assessed these temporal changes for the whole community, as well as for demographic groups (recruits, surviving trees and trees that died), using dynamics data of 120 permanent plots that were initially far from the water’s edge before reservoir flooding, and close to the water’s edge after flooding.
(between 0 and 60 m). We asked three questions: first, does water availability (soil moisture) show the strongest increase in plots located close to water’s edge, compared with plots located far from it? We hypothesized that after the reservoir construction, water availability is higher in plots close to the water’s edge and similar between dry and wet seasons. Second, how do overall community metrics change over time as a result of increased water availability? We hypothesized that plots closer to the water’s edge should experience an increase in tree density, basal area, species diversity, functional diversity and a marked compositional change towards a high abundance of species exhibiting trait values associated with low drought resistance (i.e., lower wood density, higher specific leaf area, and evergreen and simple leaf species). Third, how do new recruits, trees that survive and trees that die contribute to any temporal changes in overall community metrics? We hypothesized that an increase in water availability should favour the recruitment of fast-growing species at the expense of drought-resistant species, but should not necessarily increase the mortality of drought-resistant species. Hence, in plots close to the water’s edge, temporal changes in overall community metrics should mainly be determined by the recruits, resulting in high species and functional diversity, and high abundance of traits associated with low drought avoidance and/or resistance.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was based on 120 plots in two seasonal tropical dry forests in the Minas Gerais state, Southeastern Brazil (Figure 1). The plots were affected by the construction of a hydroelectric plant reservoir (Amador Aguiar Dam Complex), which separates the two studied forest sites (2 km apart) (Figure 1). The reservoir flooding occurred in the end of 2006, covering an area of approximately 45.11 km². Before reservoir flooding, the studied sites were located at least 700 m from the riverside, and since the reservoir flooding,
they are located close (0–60 m) to the water’s edge (Figure 1). The reservoir of the study area is stable, and the water level had no strong seasonal fluctuations.

The region experiences a tropical savanna climate (Aw Megathermic climate of Köppen), characterized by rainy summers (October to March) and dry winters (April to September). Mean annual rainfall is 1,524 mm, dry season length varies from 4 to 6 months (period with <100 mm rainfall) and mean annual temperature is 21°C (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; https://www.worldclim.org/bioclim). Soil type in the studied areas is primarily podsol, with 84% sand content, pH around 5.7, and soil CEC around 5.6 cmol/kg according to the Harmonized World Soil Database (HWSD version 1.2). These areas were secondary forests with an estimated 50 years of agricultural abandonment before the first sampling in 2005 (Kilca, Schiavini, Araújo, & Fagg, 2009). We did not find any signs of logging (e.g., tree stumps), fire or cattle grazing since our plots were established.

2.2 | Experimental design and plots

Before reservoir construction, a topographic study estimated the level where water should reach after flooding (Kilca et al., 2009), allowing us to establish our plots in locations where they should remain between 0 and 60 m from the water’s edge after flooding. In the first census (T₀, 2005, before reservoir flooding), in each of the two sites, 60 permanent plots (20 × 10 m) were established in core forest areas (1.2 ha in total per forest) (Figure 1). The plots were located along several transects (12 transects in Forest 1 and 15 transects in Forest 2) that varied in length from 20 to 60 m (i.e., transects with two plots up to transects with six plots) (see Appendix S1). Before the reservoir construction, the beginning of the transects was at a distance of 700 m from the river for one forest and at 540 m for the other (Figure 1a). All trees with stem diameter at breast height (DBH, measured at 1.30 m above-ground) ≥5 cm were tagged, identified to species level, their diameters were measured, and heights were estimated. After the reservoir flooding, our plots (originally in core forest areas) were located along a distance gradient from the reservoir edge (0–60 m). All plots were re-measured after flooding in 2007, 2009 and 2015, and surviving, dead and recruiting trees were evaluated. Here, we used the first (T₀, 2005) and last (T₁₀, 2015) census to evaluate a 10-year time period, and used the census data from T₂ and T₄ to incorporate individuals that recruited and died within the 10-year time period in the estimates of recruitment and mortality (see Demographical groups).

2.3 | Spatial and temporal changes in soil moisture

To evaluate to what extent soil water availability increased after reservoir flooding, soil moisture samples were collected before (2005) and after (2007) the reservoir flooding at different distances from the water’s edge (5 and 15 m) and in different seasons (end of dry and end of rainy season). Soil samples were collected from 0 to 40 cm soil depth within 10 plots (5 in each site) close to the water’s edge (5 m) and within 10 plots far from water’s edge (15 m) in both the wet and dry seasons. Hence, this resulted in 2 years (before and after flooding) × 2 distances × 2 seasons × 10 plots = 80 soil samples. In the field, soil samples were sieved with a 2-mm sieve to remove roots and stones and were put into hermetic containers. Soil mass was determined before and after the soil samples were oven-dried (120°C), and soil moisture percentage was calculated as: (soil fresh mass – soil dry mass)/soil fresh mass × 100. Besides distance to the water’s edge, water availability can be lower for plots that are on a slope. We, therefore, determined the slope within the plots based on the Pythagoras theorem, assuming that each plot fits in a rectangle triangle. We measured the altitude of the lower and upper left corner of each plot and calculated the difference (upper altitude–lower altitude) to estimate the opposite leg (a). The hypotenuse side of the triangle (i.e., the tilted side) had a value (b) of 10 m for all plots (Figure 1). To then assess the slope angle of each plot, we used: sin (slope) = (a/b), which is equal to: slope = arsin (a/b). The altitude values were obtained with a GPS (Garmin Etrex 20).

2.4 | Demographical groups

To evaluate how changes in overall vegetation metrics (i.e., based on all live individuals in T₀ and T₁₀) are related to its underlying demographical groups, we split the data into: trees that survived between T₀ and T₁₀; trees that recruited into the ≥5 cm DBH size class between T₀ and T₁₀; and trees that died between T₀ and T₁₀. To account for individuals that recruited and died within the 10-year period, we used the census data from T₂ and T₄. Individuals that recruited or died between the 10-year period (T₂ and T₄) were included in each respective demographical group to avoid underestimation of the values for dead trees (102 trees, which represented 11% of all dead trees and 13% of all recruits). All vegetation metrics explained below were calculated for the overall community (i.e., all live trees) and for the three demographical groups separately. Note that the metrics for the overall community yield two values per plot (at T₀ and T₁₀), and the metrics for the demographical groups yield one value per plot (calculated using the time interval between T₀ and T₁₀).

2.5 | Forest structural, species diversity and similarity metrics

Per plot for the overall community (i.e., at T₀ and T₁₀) and for each demographical group (recruits, survivors and trees that died), we described structural metrics as tree density (number of individuals) and basal area (m²), species diversity metrics as species richness (S) and rarefied species richness (S`). S’ for the overall community was based on a random sampling of 12 individuals, as this was the minimum number of individuals found in all plots, and S’ for the three demographical groups was based on a random sampling of six individuals, as this was the minimum number of individuals that died or recruited in most plots (75% of plots used for dead trees and 80% of plots used for recruited trees). We used rarefied species richness to account for the effect of number of individuals on species richness.
We acknowledge that the number of individuals used to calculate rarefied species richness may be close to the lower part of the species rarefaction curve, rather than to the asymptote. To evaluate the difference between estimates from a higher number of individuals, we performed correlations between rarefaction with 12 individuals (based on the overall community) and rarefaction with more individuals (i.e., 20, 25 and 30 individuals). The correlation coefficients were >0.94, suggesting that rarefied richness at different number of individuals were comparable, and so we, henceforth, present rarefied richness results based on 12 individuals.

We assessed changes in species composition between $T_0$ and $T_{10}$ per plot using the Horn similarity index. This index weights all individuals equally and thus weighs each species according to its abundance, and is, therefore, less sensitive to dominant species than other indices. Horn similarity index values range from 0 (nonoverlapping species composition between $T_0$ and $T_{10}$) to 1 (same species composition between $T_0$ and $T_{10}$). All parameters were calculated in R 3.1.2 (R Development Core Team, 2013), using the “vegan” (Oksanen et al., 2014) and “spadetR” packages (Chao, Ma, Hsieh, & Chiu, 2016). Additional information on structure, species diversity and species composition metrics can be found in Appendix S2.

### 2.6 | Functional traits

We evaluated four functional traits that are associated with drought avoidance and/or resistance and can potentially affect demographical processes, and hence should indicate species responses to changes in water availability (van der Sande et al., 2016, Chave et al., 2009): a stem trait (wood density, WD) and three leaf traits (specific leaf area, SLA; deciduousness, and compound/simple leaves). Wood density is positively related with plant carbon storage and drought resistance (Pérez-Harguindeguy et al., 2013; Santiago et al., 2004). Specific leaf area is the ratio between leaf area and its oven-dried mass, and it is positively related to photosynthetic rates, leaf light interception efficiency and transpiration rates (Bakker, Carreño-Rocabado, & Poorter, 2011). Deciduousness is an important trait related to drought avoidance and shorter growth length period and was calculated as the percentage of deciduous individuals per plot ($\%_{\text{Dec}}$) (Poorter & Markesteijn, 2008). Compound leaves are associated with desiccation avoidance, as leaflets can be folded to avoid water loss or tilted to avoid overheating due to direct sunlight (Poorter & Markesteijn, 2008). Moreover, compound leaves have generally smaller leaflet size, which increases convective heat loss and should provide an advantage in high-light conditions (van der Sande et al., 2016, Lohbeck et al., 2013, Lohbeck et al., 2015). We acknowledge that the size of the minimum photosynthetic unit (i.e., leaves or leaflets) would be a more direct and accurate measure of convective heat cooling, but unfortunately, we lacked these data. This trait was calculated as the percentage of individuals with compound leaves per plot ($\%_{\text{Comp}}$).

Plant traits were evaluated for most of the 133 species found in the plots (100% for deciduousness and compound leaves; 97% for WD; 56% for SLA) and on average 86% (range 54%–100%) of the individuals in each sampling plot had data for all four traits. Wood density data were obtained from the global wood density database (WD, g/cm$^3$, Zanne et al., 2009; available online) at the species level, and when this was not available, at the genus level. Data on SLA and deciduousness were obtained from previous studies in the area (Prado-Junior et al., 2016), and the classification of species into compound or simple leaves was obtained from the Herbarium Uberlandensis (HUFU) collection, according to their phylotaxy. Hence, all traits were quantified at the species level. Additional information on species functional traits can be found in Appendix S2.

### 2.7 | Community-weighted mean traits and functional diversity indices

Community-weighted mean (CWM) trait values and functional diversity indices (FD) were calculated per plot for the overall community (at $T_0$ and $T_{10}$) and the three demographical groups. We weighted by species abundance to equally weight recruiting and dying trees on changes in CWM values (van der Sande et al., 2016). CWM values were calculated for WD and SLA. For deciduousness and compound leaves, which are categorical traits, we calculated the percentage of deciduous individuals and the percentage of individuals with compound leaves per plots in $T_0$ and $T_{10}$.

For functional diversity, we used two indices: functional richness ($\text{F}_{\text{ric}}$) and functional dispersion ($\text{F}_{\text{dis}}$). $\text{F}_{\text{ric}}$ indicates the volume of multivariate trait space occupied by the community, which is strongly driven by the extreme trait values and does not incorporate species abundances (Villéger, Mason, & Mouillot, 2008). $\text{F}_{\text{dis}}$ indicates the average distance in multidimensional trait space of individual species to the centroid of the whole community, taking into account species abundance (Laliberté & Legendre, 2010). Functional indices (CWM and FD indices) were calculated using the “FD” package in R (Laliberté & Shipley, 2011). Additional information on CWM and FD indices per plot can be found in Appendix S1.

### 2.8 | Data analyses

For our first question, we evaluated how relative changes in soil moisture changed over time and depended on distance to the water’s edge, slope and season. To test this, we used a linear mixed model including time (before and after reservoir flooding), distance to the water’s edge, slope, and season (dry and rainy) as fixed factors, and site and plot as random factors to account for the possible lack of independence of soil samples within sites, and to account for the two measurements (before and after the reservoir flooding) per plot. Changes in soil moisture, however, did not depend on slope (Appendix S3), and we, therefore, excluded the slope effect from further analyses.

For our second question, we evaluated the effect of distance to the water’s edge on overall relative changes in community structure (tree density and stand basal area), species diversity ($S$, $S'$), species similarity (Horn index), functional diversity ($\text{F}_{\text{ric}}$ and $\text{F}_{\text{dis}}$) and CWM trait values (WD, SLA, $\%_{\text{Dec}}$ and $\%_{\text{Comp}}$) in dry forests. Relative changes ($\Delta$) in overall community metrics between $T_0$ and $T_{10}$ were calculated as:

$$\Delta = \frac{(T_{10} - T_0)}{T_0}$$

with positive values indicating an increase over time.
and negative values a decrease over time (except for species similarity, which was calculated as one value per plot). Relative changes rather than absolute changes were used to control for differences in the initial values of the metrics among plots. We used distance of plots to the water’s edge as indicator of temporal increase in water availability. That is, plots close to the water’s edge experienced strongest increase in water availability over time, whereas plots far from the water’s edge experienced little change in water availability over time. To evaluate the effect of increasing water availability (i.e., distance to the water’s edge) on temporal changes in these community metrics, we used one linear mixed model per metric, including distance to the water’s edge as fixed factor and site as random factor.

For our third question, we evaluated how demographical groups (trees that recruited, died and survived) contributed to shifts in the overall community metrics. Similar linear mixed models were used as for changes in overall community metrics, but this time with metrics per demographical group as response variable. When necessary, data were log_{10} or square root transformed prior to analysis to meet the assumptions of normality, homoscedasticity, to control for the effect of outliers, and to account for possible nonlinear relationships between variables. Mixed models were performed in R 3.1.2 (Team, 2013) using the lmer function from the “lme4” package (Bates, Maechler, & Bolker, 2012).

To test for potential nonindependence of plots, we assessed the degree of spatial autocorrelation in our linear mixed model residuals using the Moran’s I test. A p-value <0.05 indicates that the model residuals show spatial autocorrelation. For the models that showed spatial autocorrelation (i.e., Moran’s I p-value <0.5; see Appendix S4), we performed simultaneous autoregressive SAR models including a second error term for spatial autocorrelation (Kissling & Carl, 2008), based on the geographical coordinates of the plots. The SAR model approach has been used as an efficient tool to handle models with spatial autocorrelation (Raymundo et al., 2018; Zhang, Nielsen, Mao, Chen, & Svenning, 2016). In SAR models, it is necessary to define a minimum-weighted neighbourhood structure to fit the spatial structure of the models residuals. We used a neighbourhood distance of 0.00013 decimal degrees (~10 m), because this was the minimum distance between plots, and was sufficient to consider plots of different patches as nonneighbour plots (Dormann et al., 2007). Moran’s I tests for the SAR model residuals showed that the autocorrelation had been removed in all models (Appendix S4). The SAR models produced standardized coefficients that were similar to the nonspatial mixed effect models (Appendix S4), and we, therefore, focused on the nonspatial path coefficients throughout the manuscript. SAR error analyses were performed in R 3.1.2 (Team, 2013), using ”spdep” package.

3 | RESULTS

Soil moisture contents generally increased after reservoir flooding, especially in the dry season and for plots close to the reservoir (Table 1). In the dry season, soil moisture increased 126% (from 8.42% to 19.06%) in plots close to the reservoir (5 m) and did not significantly change (from 7.56% to 8.05%) at 15 m from the reservoir (Table 1).

In the rainy season, soil moisture increased 16.4% (from 18.86% to 21.96%) in plots close to the reservoir and decreased 30% (from 18.92% to 13.14%) in plots far from the reservoir. Hence, after reservoir construction, soil moisture differences were markedly reduced between seasons in plots close to the reservoir (Table 1). Because annual rainfall in the first soil sampling (before reservoir flooding, 2005) was higher (1.713 mm) than in the second soil sampling (after reservoir flooding, 2007, 1.369 mm), the increase in soil moisture in plots close to the water’s edge was due to the reservoir, rather than to differences in annual rainfall between years (Table 1). In plots far from the water’s edge, decreasing soil moisture in the rainy season was probably due to lower annual rainfall during the second soil sampling (Table 1).

The increasing water availability in plots close to the reservoir and nonsignificant, or even decreasing (in the rainy season) water availability in plots far from the reservoir, imposed a strong gradient in water availability among our plots. Distance to the water’s edge was, therefore, used as a proxy to evaluate the effect of changing water availability on relative changes (Δ) in overall community metrics and metrics of each demographical group (recruits, survivors and trees that died). For the overall community metrics, we found a significant negative effect of distance on relative changes (Δ) in species richness (Figure 2c) and functional richness (Figure 2f), meaning that plots with strongest increase in water availability (i.e., close to the water’s edge) showed strongest temporal increase in diversity, whereas plots with little change in water availability did not change in diversity (95% confidence interval contained zero). We found a significant positive effect of distance on species similarity between T0 and T10, indicating that stronger changes in species composition occurred in plots close to the water’s edge (Figure 2e). We found a significant positive effect of distance on relative changes (Δ) in CWM wood density (CWM_{wdf}, Figure 2h), CWM-specific leaf area (CWM_{slaf}, Figure 2i), and percentage of individuals with compound leaves (%_comp, Figure 2j), although relative changes in these variables were not significantly different from zero across the whole distance gradient. We found, however, no effect of distance to the water’s edge on changes in overall community stand basal area, tree density, rarefied species richness, functional dispersion and percentage of individuals belonging to deciduous species (%_dec) (Figure 2a,b,d,g,k).

For trees that recruited and trees that died, we found a significant negative effect of distance to the water’s edge on tree density and

| TABLE 1 | Mean percentage of soil moisture before and after dam construction, in dry and rainy seasons and close and far from the water’s edge |
| Season | Distance | Before dam (T0: 2005) | After dam (T1: 2007) | Change (%) |
|--------|---------|----------------------|----------------------|------------|
| Dry    | Close   | 8.42^d              | 19.06^b              | 126.5      |
|        | Far     | 7.56^d              | 8.05^f              | 6.5        |
| Rainy  | Close   | 18.86^b             | 21.96^a             | 16.4       |
|        | Far     | 18.92^b             | 13.14^c             | 30.5       |
| Rainfall |        | 1.713               | 1.369               | 20.1       |

Annual rainfall (mm) before and after damming are also given. Letters indicate significant differences (p < 0.05) among the parameters.
FIGURE 2  Bivariate relationships between distance to the water’s edge and temporal changes ($\Delta$) in stand basal area (a), density (b), species richness (c), rarefied species richness (d), Horn similarity index (e), functional richness (Fric, f), functional dispersion (Fdis, g), and community-weighted mean of wood density (WD, h), specific leaf area (SLA, i), percentage of individuals with compound leaves (j), and percentage of deciduousness (k) of whole community in a secondary dry forest that was affected by a reservoir construction. Changes were calculated by comparing just before and 10 years after reservoir flooding. Forest patches were included as random effect in the linear models to account for the nestedness of the plots within sites, and distance was log-transformed. Continuous lines represent significant relationships, dashed lines represent nonsignificant relationships, and grey areas represent the 95% confidence intervals.
FIGURE 3  Bivariate relationships between distance to the water’s edge and metrics per demographic group: stand basal area (a), density (b), species richness (c), rarefied species richness (d), functional richness (e), functional dispersion (f), and community weighted mean of wood density (WD, g), specific leaf area (SLA, h), percentage of individuals with compound leaves (i), and percentage of deciduousness (j) of trees that survived (narrow dashed line), died (broad dashed line) and recruited (continuous line) after the increase in water availability due to a reservoir construction. The increase in water availability decreased with distance to the water’s edge (i.e., close to the water’s edge experienced strong changes in water availability, and far from the water’s edge experienced little change in soil moisture). The two forest sites were included as random effect in the linear regression models to account for the nestedness of the plots within sites, and distance was log-transformed. Lines with $R^2$ values had a nonsignificant slope.
species richness (Figure 3b,c), indicating more marked changes in forest structure and diversity in plots with higher increase in water availability. Additionally, for recruiting trees, distance to the water’s edge significantly negatively affected stand basal area (Figure 3a), rarefied species richness (Figure 3d) and functional richness (Figure 3e), and significantly positively affected most CWM trait values (CWM$_{wat}$, %$_{comp}$, and %$_{SLA}$, Figure 3g,i,j), indicating a higher recruitment of evergreen species with lower wood density and simple leaves in plots with higher increase in water availability. For trees that died, we found no effect of distance to the water’s edge on CWM trait values, and for surviving trees, we found no effect of distance on any of the metrics (Figure 3). These results indicate that the temporal changes in overall community metrics were mainly due to recruiting trees.

4 | DISCUSSION

We evaluated how an abrupt and lasting increase in water availability, due to the creation of an artificial reservoir, influenced relative changes in water availability and overall community structure, diversity (species and functional), species composition and community-mean trait values in tropical dry forests. Furthermore, we evaluated the contribution of recruits, survivors and trees that died to temporal changes in community metrics. We found that plots experiencing the strongest increase in water availability (i.e., plots close to the water’s edge) increased in species and functional diversity, showed highest dissimilarity (lower values of Horn index) in species composition between $T_0$ and $T_{10}$, and tended to decrease in community-weighted mean (CWM) wood density (CWM$_{wat}$), specific leaf area (CWM$_{SLA}$), and in the percentage of individuals with compound leaves (%$_{comp}$). These changes in plots with strong increase in water availability were mainly caused by the new recruits, which were more diverse and had traits associated with low drought resistance (i.e., species that are evergreen and have low wood density and simple leaves) compared with recruits in plots with little change in water availability.

4.1 | Water availability increases species and functional diversity, but does not affect structural metrics

We hypothesized that plots close to the water’s edge should experience a more marked increase in water availability than plots far from the water’s edge, and that the water availability between rainy and dry season should be similar. We indeed found that, in plots close to the water’s edge, water availability increased over time and was similar between the rainy and dry season, indicating a reduced seasonality in water availability. We hypothesized that plots with strongest increase in soil moisture (i.e., close to the water’s edge) should have a stronger increase in species and functional diversity than plots with little change in water availability, and that these changes should be mainly due to recruits. For plots with the strongest increase in water availability, we indeed found an increase in species and functional richness of the whole community (Figure 2c,f) and a strong dissimilarity in species composition between $T_0$ and $T_{10}$ (Figure 2e). However, plots exhibiting little change in water availability (i.e., far from the water’s edge) showed only slight changes in these community metrics. We also found that plots with a marked increase in water availability had higher species richness of recruits and trees that died (Figure 3c) and high functional richness of recruits (Figure 3e). As expected, species and functional richness were higher for recruits than for trees that died in these plots, indicating that recruits notably contributed to the overall increase in species and functional diversity. The strong reduction in seasonality in plots close to the water’s edge (Table 1) probably facilitated the successful establishment of species that are less adapted to drought stress and so changed species composition to a more diverse community (i.e., higher species and functional richness).

We hypothesized that increasing water availability leads to an increase in stand basal area and tree density (van der Sande et al., 2017). However, we found that changes in overall community tree density and stand basal area were not related to distance to the water’s edge, possibly because in plots with strongest increase in water availability, high recruitment was balanced out by high mortality (Figure 3a,b). Although spatial variation in water availability is usually positively related to community stand basal area in tropical forests (Mahi, 2012; Poorter et al., 2015), an abrupt increase in water availability may also cause higher mortality (Pillet et al., 2018), leading to nonsignificant changes in stand basal area.

4.2 | Water availability increases abundance of drought-vulnerable species

We hypothesized that plots close to the water’s edge should experience a decrease in the abundance of species with traits related to drought avoidance and/or resistance (i.e., high WD, low SLA, deciduousness and compound leaves), and that such changes should be mainly due to recruits. We indeed found a significant positive effect of distance to the water’s edge on relative changes in CWM$_{wat}$, and %$_{comp}$ of the overall community (i.e., a decrease in the abundance of these traits close to the water’s edge), but, contrary to our expectations, we found a positive effect of distance to water’s edge on relative changes in CWM$_{SLA}$ of the overall community (i.e., an increase in abundance of species with high SLA close to the water’s edge, although these changes were not significantly different from zero) (Figure 2h–j). High wood density enhances cavitation resistance (Markesteijn, Poorter, Bongers, Paz, & Sack, 2011) and is an important trait in dry forest species given that drought-induced cavitation is considered the main cause of tree mortality in dry habitats (Cavender-Bares, Kitajima, & Bazzaz, 2004). When water availability increases, however, soft-wooded species with higher hydraulic conductivity and growth potential (Chave et al., 2009) can take advantage of higher water availability and outperform drought-tolerant species. Compound leaves can enhance heat loss through convective cooling and desiccation avoidance as leaflets can be folded to avoid water loss (Poorter & Markesteijn, 2008; van der Sande et al., 2016). The decrease in CWM$_{SLA}$ in plots close to the water’s edge for the overall community (Figure 2) could have been caused by edge effects created by the construction of the reservoir. These open conditions could
increase light intensity (Harper et al., 2015), temperature variation (Arroyo-Rodríguez, Saldana-Vazquez, Fahrig, & Santos, 2017) and wind speed (Wuyts, Verheyen, Schrijver, Cornelis, & Gabriels, 2008) in plots close to the water's edge, benefitting plants with tough leaves (i.e., low SLA) adapted to such harsh conditions. Alternatively, CWM_{SLA} might decrease as a result of the increased abundance of evergreen species, which have generally lower SLA values than deciduous species.

We also found that CWM_{wd} %_{dec} and %_{comp} for recruits were significantly lower in plots with the most marked increase in water availability compared with plots with slight change in water availability (Figure 3g,i,j), indicating that recruitment was dominated by evergreen species that have a year-round ability to photosynthesize. Conversely, in plots far from the water's edge, CWM_{wd} %_{dec} and %_{comp} were higher for recruits than for surviving and dead trees. Surprisingly, CWM trait values of surviving and dead trees were not related to changes in water availability. A possible explanation is that, in dry forests, small trees (i.e., recruits) are more exposed to elevated risk of desiccation than larger trees (i.e., many surviving and dead trees) that usually have root systems that can reach a water supply from deeper soil layers (Hoover, Duniway, & Belnap, 2017; Ma & Chen, 2017). An increase in water availability, therefore, more strongly impacts the type of species that can recruit than the type of species that survive and die. Despite the increased mortality in plots close to the water's edge (Figure 3b), the dead trees showed no directional shifts over time in diversity and traits, indicating that mortality remained a predominantly random process. Although no significant relative changes were found in CWM traits for the overall community (95% confidence interval of Δ contained zero over the whole gradient, Figure 2h-k), the significant positive relationships for CWM_{wd} and %_{comp} indicate that overall changes are following the trend found for recruits. Although recruits are a small portion of the overall community, they represent the potential future individuals of the forest. A consistent recruitment of species that are functionally different from the resident community may, therefore, lead to stronger and significant CWM changes in the overall community on longer time-scales.

4.3 | Concluding remarks

Our study can be summarized in three main results. First, over our 10-year study period, increased water availability increased species richness, functional richness and the abundance of traits less adapted to drought stress (i.e., low wood density, evergreen and simple leaves species). These changes, which may become more apparent at longer time-scales, highlight the potential ability of tropical forests to respond quickly to changes in climatic conditions. Second, although the increase in water availability increased basal area of recruits, in relative terms, it also increased basal area of dead trees, leading to nonsignificant overall changes in stand basal area. This, in combination with the increased abundance of soft-wooded species, could reduce total carbon storage and sequestration capacity of the community. Moreover, the decreasing abundance of drought-tolerant species may increase the forest’s vulnerability to extreme climate events that are predicted to become more common (Drijfhout et al., 2015), although long-term studies are needed to further understand this process. Third, an increase in water availability led to changes in metrics especially for recruits. Since recruits are the trees of the future, this indicates long-lasting effects on tropical forest composition, diversity and resistance to extreme climate events.

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AUTHORS’ CONTRIBUTIONS

D.R., J.P.-J., F.A.C., V.S.V. and P.E.O. conceived the ideas and designed methodology; D.R., J.P.-J. and V.S.V. collected the data; D.R. and J.P.-J. analysed the data; D.R., J.P.-J. and M.T.v.d.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.f1q5870 (Raymundo, 2018).

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