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Functional organization of woody plant assemblages along precipitation and human disturbance gradients in a seasonally dry tropical forest

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Abstract

Chronic anthropogenic disturbances (CAD) and rainfall are important drivers of plant community assembly, but little is known about the role played by inter- and intraspecific trait variation as communities respond to these pervasive forces. Here, we examined the hypothesis that lower precipitation and higher CAD reduce both intra- and interspecific trait variation in Caatinga dry forests. We sampled woody plants across 15 plots along precipitation and CAD gradients and measured resource-use traits. The effects of precipitation and CAD on RaoQ functional diversity were decomposed into species turnover and intraspecific variability. We used "T-statistics" to assess the trait sorting from the regional pool to local communities (i.e., external filtering), and within-community forces leading to low trait overlap (i.e., internal filtering) at individual and species levels. Intraspecific variability explained at least one-third of the total trait variation and 46% of variation in multitrait diversity across communities. Increasing disturbance reduced multitrait diversity, while precipitation affected some particular traits, such as wood density. Overall, precipitation determined species sorting across communities, while disturbance relaxed internal filters, leading to higher trait overlap within communities due to higher intraspecific variability. Our results suggest that the woody Caatinga flora contains a substantial amount of both inter- and intraspecific trait variation. This variation is not randomly distributed within and across communities, but varies according to rainfall conditions and disturbance intensity. These findings reinforce the emerging idea that human disturbances can reorganize plant communities at multiple scales and highlight trait variability as a key biological asset for the resilience of dry forests.

KEYWORDS

Caatinga, environmental filtering, functional diversity, functional traits, intraspecific variation, species coexistence, T-statistics

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1 | INTRODUCTION

Community organization at multiple spatial scales remains a key topic in ecology as natural and human-induced environmental changes are expected to alter community functional profiles with impacts on ecosystem functioning and provision of ecological services (Carreño-Rocabado et al., 2016; Laliberté et al., 2010). In this perspective, functional traits have been shown to mediate both species responses to environmental conditions and their effects on ecosystems (Diaz & Cabido, 2001; Westoby, Falster, Moles, Vesk, & Wright, 2002), and thus have been scaled up to the community level to address patterns of species coexistence, community assembly, and ecosystem functioning along environmental gradients (Le Bagousse-Pinguet et al., 2017; McGill, Enquist, Weiher, & Westoby, 2006; Suding et al., 2008). While the focus on trait differences among species is motivated by the aim of generalized predictability (McGill et al., 2006), recent evidence points to a substantial contribution from plant intraspecific trait variability (ITV) in determining patterns of trait variation within and across communities (Albert et al., 2010; Siefert et al., 2015). Although the effects of within-species trait variation on community dynamics and ecosystem functioning are being increasingly investigated (de Bello et al., 2011; Kichenin, Wardle, Peltzer, Morse, & Freschet, 2013; Sfair, Bello, França, Baldauf, & Tabarelli, 2018; Violle et al., 2012), the understanding of the contexts in which plant ITV is relevant, and how such variation relates to measurable environmental and disturbance gradients to determine community functional patterns, still remains poorly understood (Shipley et al., 2016).

Among the forces shaping community assembly, stress and disturbance (i.e., resource availability and biomass destruction, sensu Grime, 2001) have long been recognized as important for plant performance (Grime, 1979; Grime & Pierce, 2012; Huston, 1979; Tilman, 1988). For instance, the Competitor (C), Stress-Tolerator (S), Ruderal (R), that is, CSR strategy scheme (Grime, 1979, 2001, but see Grime & Pierce, 2012), suggests that plant strategies have evolved in response to different levels of stress and disturbance. Although variation in such factors can indeed define species' primary adaptive strategies (Grime, 2001; Pierce et al., 2017), the wide distribution of species along abiotic gradients suggests a large intraspecific variation in traits related to such selective pressures, caused either by genetic variability or by phenotypic plasticity (Albert, Grassein, Schurr, Vieilledent, & Violle, 2011; Valladares, Gianoli, & Gómez, 2007). Substantial trait variation is also evident within communities as a result of microenvironmental heterogeneity or species interactions, as niche differentiation may reduce competition and thus favor coexistence among individuals or species (Clark, 2010; Violle et al., 2012). However, while some propose that ITV should be reduced under strong environmental filtering (Hulshof et al., 2013; Valladares et al., 2007), others have suggested that unfavorable conditions may enhance the expression of phenotypic variation (Hoffmann & Merila, 1999; Siefert et al., 2015). The coexistence of plants with contrasting functional strategies may promote high functional diversity, niche complementarity, and increased resilience to human-induced disturbances (Tilman et al., 1997; Valencia et al., 2015). Therefore, understanding the drivers of trait variation at both individual and species levels along stress and disturbance gradients is not only a theoretical challenge, but also of great importance to conservation.

In the case of seasonally dry tropical forests (SDTFs, sensu Pennington, Lavin, & Oliveira-Filho, 2009), water availability is a factor that influences the physiology, fitness, and distribution of individuals and species (Engelbrecht et al., 2007; Maestre et al., 2016). Additionally, most SDTFs are exploited by humans for products such as firewood and fodder (Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal, 2015; da Silva, Leal, & Tabarelli, 2017). Such a continuous removal of small portions of biomass (i.e., chronic anthropogenic disturbance—CAD; sensu Singh, 1998) can directly impact plant fitness but also change environmental conditions, that is, microclimate, water availability, and nutrient availability (Pereira, Andrade, Sampaio, & Barbosa, 2006; Ribeiro et al., 2015; Rito, Arroyo-Rodríguez, Queiroz, Leal, & Tabarelli, 2017a). Decreasing resource availability is expected to favor increasing dominance of *stress-tolerant* strategies able to conserve resources by growing slowly and producing dense, durable tissues (Reich, 2014), while frequent disturbances tend to favor *ruderal* strategies with high colonization abilities and fast growth (Grime & Pierce, 2012). Moreover, evidence suggests that precipitation and CAD have the potential to operate as synergistic forces of taxonomic community organization (Rito, Arroyo-Rodríguez, et al., 2017a). However, the emerging patterns, baseline mechanisms, and consequences for functional organization remain poorly investigated in SDTFs (Ribeiro et al., 2019; Sfair et al., 2018) despite the increasing level of human disturbance in these ecosystems (da Silva et al., 2017).

The Caatinga dry forest is the largest expanse of SDTFs in the Neotropics, with plant communities stretched over a variety of environmental gradients such as those caused by changes in precipitation (500 mm up to 1,000 mm of rainfall; da Silva et al., 2017). Moreover, slash-and-burn agriculture and the exploitation of forest products have converted most of the Caatinga old growth forest into a mosaic of forest patches exposed to varying levels of chronic disturbance (Ribeiro et al., 2015; da Silva et al., 2017; Sobrinho et al., 2016). Recent studies in the Caatinga have documented the influence of CAD and changes in precipitation levels as drivers of plant community organization, including taxonomic (Ribeiro et al., 2015; Ribeiro-Neto, Arnan, Tabarelli, & Leal, 2016; Rito, Arroyo-Rodríguez, et al., 2017a; Siqueira et al., 2018), phylogenetic (Ribeiro et al., 2016), and functional patterns (Ribeiro et al., 2019; Sfair et al., 2018). Overall, these findings suggest environmental filtering and intraspecific trait variation as key drivers of the spatial distribution of plants along environmental and disturbance gradients. Yet, the relative contribution of inter- and intraspecific trait variation in determining community assembly and functional diversity patterns along such gradients in SDTFs has not been assessed to date.

This study investigates the role played by CAD and changes in precipitation levels as drivers of plant community organization in a human-modified landscape covered by the Caatinga dry forest, northeast Brazil. We test the hypothesis that lower levels of precipitation and higher chronic anthropogenic disturbance reduce plant community functional diversity by affecting both intra- and interspecific trait variation from local to regional scales. Specifically, we expected changing precipitation conditions to reduce cross-community trait overlap due to species sorting, while disturbance should drive niche differentiation and species coexistence at the local scale. We examine variation in resource-use traits (e.g., wood density, specific leaf area) that have been widely recognized to confer the ability for plants to cope with reduced water availability and disturbance (O'Brien et al., 2017; Reich, 2014; Sfair et al., 2018). To reveal potential mechanisms driving coexistence patterns within and across communities, we decompose the effects of precipitation and CAD on community functional diversity into species turnover and intraspecific variability components. Additionally, we consider ratios of trait variance across scales, as evidence of trait filtering from the regional pool to local communities (i.e., external filtering), and within-community forces leading to low trait overlap (i.e., internal filtering) at the individual and species levels (i.e., "T-statistics," sensu Violle et al., 2012). We highlight the relative contribution of within- and among-species trait variation, the strength and direction of functional diversity responses along precipitation and disturbance gradients, and the consequences for species assembly, community organization, and resilience of seasonally dry tropical forests.

2 | METHODS

2.1 | Study area

The study was carried out in the Catimbau National Park, located in the municipalities of Buíque, Tupanatinga, and Ibimirim, in Pernambuco State, Brazil (8° 24'00" and 8°36'35" S and 37°09'30" and 37°14'40" W) (Figure 1). This is one of the few protected areas that include Caatinga, with an area of *c*. 60,000 ha. The climate is semiarid, Bsh (Koppen's classification), with an average temperature of 25 °C and a high variation of annual precipitation (from 480 to 1,100 mm) at the landscape scale. The park is mainly composed of lithosols, characterized by coarse-grained sandstones (sandy soils), and the vegetation is mainly composed of shrubs and small trees (Rito, Arroyo-Rodríguez, et al., 2017a). The Caatinga region has a long history of human-induced disturbance, and people living inside the park still use local natural resources for their livelihoods, such as firewood extraction and extensive livestock ranching (da Silva et al., 2017). There are *c*. 300 families living in the park, but others living outside its borders are landowners inside the park (Specht et al., 2019).

2.2 | Sampling design

We established 15 plots (20 × 50 m) at least 2 km apart from each other, in sites dominated by old growth vegetation exposed to chronic anthropogenic disturbance along a precipitation gradient (from 510 to 940 mm per year). To control for potential effects of terrain slope and soil characteristics on species responses, all plots were located in areas with the same soil type (sandy soil) and on flat terrain. In each plot, during the rainy season in 2015, we sampled and identified to species level all woody plants with diameter at soil ≥ 3 cm and height ≥ 1 m. Details on the floristic inventory can be found in Rito, Arroyo-Rodríguez, et al. (2017a).

2.3 | Environmental and disturbance gradients

We downloaded precipitation data for each plot from the updated WorldClim global climate data repository with monthly average data over all available years (1970–2000) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), with a resolution of 30 arc seconds (i.e., 1 km^2). The precipitation of each plot was calculated by interpolation of data from climatic stations near the studied areas, using the *maptools* package for R (Bivand & Lewin-Koh, 2015). Mean annual precipitation ranged from 510 to 940 mm among the sampling plots (see Figure 1).

To estimate intensity across a gradient of human-induced disturbance, we adopted a multimetric disturbance index (sensu Arnan et al., 2018), which was computed from the integration of three different indices for the main types of CAD affecting the Caatinga dry forest: *people pressure*, *livestock pressure*, and *wood extraction*. The indices were computed using the formula originally proposed by Legendre and Legendre (1998) to get an overall level of land-use intensity.

$$I = \frac{\sum_{i=1}^{n} (y_i - y_{\min}) / (y_{\max} - y_{\min})}{n} \times 100$$

where *I* is the disturbance intensity index, *yi* is the observed value for a given disturbance metric in plot *i*, *ymin* is the minimum observed value for the disturbance metric considering all plots, *ymax* is the maximum observed value for the disturbance metric considering all plots, and *n* is the number of individual disturbance metrics included in the index. This formula allows the different metrics (which may present different units) to be combined into an overall index, as they are standardized to take on a value between 0 and 1 (for more details about the computation of these indices, see Arnan et al., 2018).

The livestock pressure index includes measurements of goat trail length and density of goat and cattle dung, which were combined into one variable by means of PCA (both variables were highly and positively correlated with the first PCA axis, which explained 88% of the variation). The wood extraction index estimates live wood extraction from the basal area of all cut stems, and firewood collection from the ratio of aboveground biomass of living plants to woody debris in the plot, in which a higher ratio indicates that wood debris were more extracted for firewood (see Arnan et al., 2018). The people pressure index included indirect measures related to geographic variables, such as "proximity to houses," "proximity to villages," and "proximity to roads," and measures related to socio-ecological context, such as

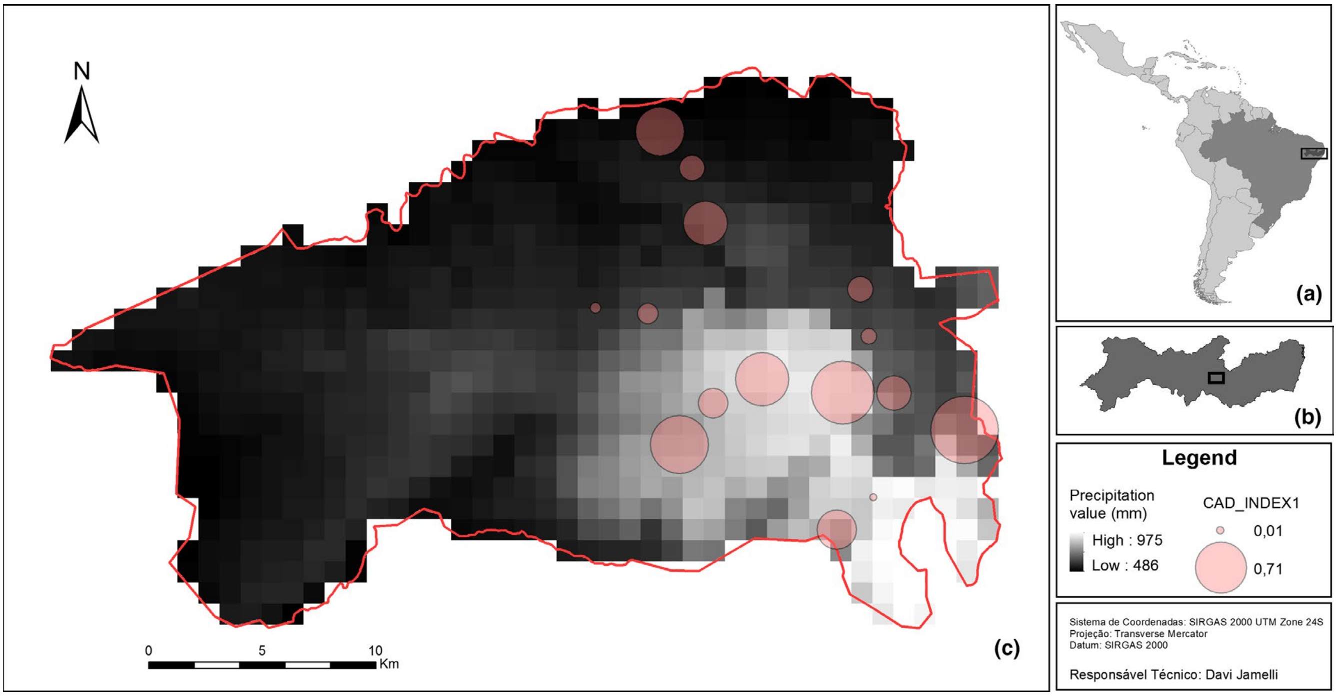

FIGURE 1 (a) Study area in the northeast of Brazil. (b) Catimbau National Park, Buíque, Pernambuco. (c) Variation of values of precipitation in gray scale and chronic anthropogenic disturbance intensity represented by circular area. The circular areas also correspond to the locations of the 15 plots of 20 × 50 m (0.1 ha) along the precipitation and chronic anthropogenic disturbance gradients

"the number of people with a direct influence on the plot," which were estimated using 69 interviews with local families. Since these variables may not be independent from one another, they were also integrated into one variable by means of a PCA. As the values of the "people pressure index" computed by PCA and by the disturbance intensity index (sum approach) were highly correlated (Pearson $r = .94$, $p < .0001$), the values computed from the summed approach were used. We then used PCA coordinates and integrated all three indices into a "global multimetric CAD index" (see formula above), which varies from 0 to 100 (from low- to high-intensity disturbance).

2.4 | Trait data

We sampled resource-economy plant traits (stem density, WD; specific leaf area, SLA; leaf dry matter content, LDMC; leaf area, LA; and leaf thickness, Lth) for 1,008 individuals from 61 species (48% of the sampled species across all plots), which accounted for 24% of the total abundance of shrubs and trees across our sampling units. We selected these traits due to their recognized ability to describe plant responses to disturbances and drought (Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter, 2010; Mason, Bello, Doležal, & Lepš, 2011; Reich, 2014; Westoby et al., 2002; Wright, Reich, & Westoby, 2001). Some of the traits considered are expected to be correlated as they are related to common trade-offs (Reich, 2014), but correlation among individual traits was weak overall (Table S1). Specifically, we tried to sample 10 individuals of each species in each plot. In the case of less abundant or rare species, we sampled at least two individuals (Table S2). Common species that evolved to occur throughout environmental gradients may sometimes account for most of the intraspecific variation across communities, but our trait sampling encompassed both common and rare species with either low or high intraspecific variation (Table S2). We used sections of about 2 cm length of 1-cm-thick stem (excepting young branches) and two randomly selected leaves (among those sun-exposed, well-expanded, and undamaged) for each sampled individual to measure the traits using the methodology reported in Pérez-Harguindeguy et al. (2013). Specifically, we collected plants in the rainy season (February to April) in 2016, always before 10 a.m. to avoid dehydration. Then, we rehydrated leaf samples to measure the leaf-saturated area and weight, as required for calculating SLA and LDMC (Pérez-Harguindeguy et al., 2013).

2.5 | Data analysis

Total trait variation may result from intrinsic variation among species, or intraspecific variation. To assess the relative amount of variation in each of these components, we decomposed the total variation of each trait into between-species variability (BSV) and within-species variability (WSV), by applying linear models, with trait values per individual (i.e., species observation in each plot) as the response variables and species name as a factor. The between-species variability consists in the coefficient of determination (R^2) of such models, while the proportion of variation within species is denoted by 1-R^2 (Carlucci, Debastiani, Pillar, & Duarte, 2015).

We assessed the relative contribution of species turnover and intraspecific variability in determining variation in RaoQ functional diversity (FD) of each trait separately and all traits together (multitrait) across communities, based on the partitioning approach proposed by de Bello et al. (2011). For this, we calculated FD from both species mean trait values ($\mathrm{FD}_{\mathrm{inter}}$) and individual trait values ($\mathrm{FD}_{\mathrm{whole}}$). Species turnover is the only possible cause of variation in community functional properties calculated from species mean trait values, while variation in FD based on individual variation may be related to species turnover, intraspecific variability, or both. In turn, the "intraspecific variability effect" ($\mathrm{FD}_{\mathrm{intra}}$) was determined by subtracting the interspecific components from measures based on the whole variability (de Bello et al., 2011; Carlucci et al., 2015). Finally, the relative effects of environmental and disturbance variables on FD were determined from the decomposition of the sum of squares of three ANOVAs for linear regression based on each component (i.e., between-species variability, intraspecific variability, and whole-community variation). This reveals the proportion of cross-community variation explained by species turnover, intraspecific variability, and the covariation between these two components, as well as the relative effects of precipitation and CAD on each of these variation components. Species turnover and intraspecific variation may correlate positively or negatively along the environmental gradients, what determines their covariation effects (Carlucci et al., 2015; Lepš, Bello, Šmilauer, & Doležal, 2011).

Finally, we assessed the role of large-scale environmental variation driving trait sorting across communities (i.e., external filters) and within-community forces promoting niche differentiation among co-occurring individuals and species (i.e., internal filters) in structuring communities along precipitation and chronic disturbance gradients, by using the "T-statistics" proposed by Violle et al. (2012). These are based on ratios of trait variance across scales and organizational levels, considering variation among individuals within each population (i.e., species) occurring in a given community ("IP"), among all individuals occurring in a given community ("IC") or across all communities in the region ("IR"); and among species (mean trait values) in a given community ("PC") or in the regional pool ("PR"), as follows:

- TIP/IC (variance individuals within species/variance community): the ratio of mean within-species variance to total variance within community—this is a measure of niche packing among the species within a community and reflects internal filtering (e.g., competition, facilitation) at the individual level; lower values denote stronger internal filtering, and thus relatively low trait overlap among species within a given community;
- TIC/IR (variance individuals within community/variance regional pool): the ratio of community-wide variance to total variance in the regional pool among individuals, which measures external filtering at the individual level (i.e., the selection of individuals along environmental gradients); lower values indicate stronger external filtering, suggesting relatively high functional similarity among individuals in a given community compared to those across other communities;
- TPC/PR (variance species within community/variance regional pool): the ratio of community-wide variance to total variance in the regional pool among species, which is an indication of external filtering at the species level (i.e., the selection of species along environmental gradients); lower values indicate that individuals from a given community tend to have more similar species mean trait values than individuals drawn randomly from the regional species pool.

After calculating the T-statistics for each trait, we compared the observed values with values based on 999 randomly generated communities. For this, we calculated the standard effect size (SES) as a measure of deviation from what would be expected at random (more negative values indicate stronger filters for each measure), as follows: $\mathrm{SES} = (\text{T-stat}_{\mathrm{obs}} - \text{T-stat}_{\mathrm{null}})/\text{T-stat}_{\mathrm{SD}}$, where $\text{T-stat}_{\mathrm{obs}}$ is the value observed in a given community, while $\text{T-stat}_{\mathrm{null}}$ and $\text{T-stat}_{\mathrm{SD}}$ are the mean value and standard deviation, respectively, of the null distribution of T-stat values generated for each community (Gotelli & Graves, 1996). We used specific randomization procedures for each of the T-statistics, following Taudiere and Violle (2016). Accordingly, for $T_{\mathrm{IP/IC}}$ we randomized individual trait values within each community; for $T_{\mathrm{IC/IR}}$, we drew individual trait values without replacement from the regional pool; and for $T_{\mathrm{PC/PR}}$, after defining species-level trait values to each individual across communities, we drew values without replacement from the regional pool for each community, keeping the actual number of individuals in each community (Taudiere & Violle, 2016). Finally, after calculating SES values, we assessed how the direction and magnitude of the deviations of T-statistics from a null expectation (i.e., SES) vary across the gradients considered, by applying multiple regression models.

All analyses were performed using the software R (http://www.R-project.org). Specifically, we used the "FD" package (Laliberté & Legendre, 2010) to calculate FD, the "trait.flex.ANOVA" function (Lepš et al., 2011) to decompose CWM and FD variation along the gradients into species turnover and intraspecific components, and the "cati" package (Taudiere & Violle, 2016) to calculate T-statistics and their deviation from null expectations.

3 | RESULTS

We recorded 4,138 individual trees (275 ± 101 trees per sampling unit; mean ± *SD*) from 128 species (27 ± 9) across 15 plots (i.e., local communities). Species mean and individual trait values presented a wide range, with intraspecific trait variation explaining at least one-third of the total variation (Table 1). Moreover, most of the variation (46%) in multitrait diversity (RaoQ with all traits) across local communities was explained by intraspecific variability, while species turnover explained only 24%, and the remaining variation (30%) correlated positively with the covariation between these two components (Table 2). Considering traits individually, species turnover and intraspecific trait variability in general accounted for similar portions of cross-community variation in diversity scores, except for wood density. For this trait, species turnover explained most of the variation in diversity and presented a negative covariation with

TABLE 1 Trait range at species and individual levels, and between-species (BSV) and within-species variability (WSV) of five plant functional traits for seasonally dry tropical forest species ($N_{species}$ = 61, $N_{individuals}$ = 1,008) in the Catimbau National Park, Pernambuco State, northeast Brazil. BSV and WSV were determined from decomposition of total variation across individuals using a linear model

Trait	Species mean trait range	Individual trait range	Individual mean	BSV (%)	WSV (%)
Wood density (g/cm^3)	0.18–0.88	0.11–1.25	0.65	63.6	36.4
Leaf area (cm^2)	0.89–121.02	0.32–472.16	24.49	66.6	33.4
Specific leaf area (cm^2/g)	41.96–334.12	17.08–618.52	148.65	46.1	53.9
Leaf dry matter content (g/g)	0.18–0.59	0.12–0.82	0.37	68.0	32.0
Leaf thickness (mm)	0.07–0.48	0.01–0.76	0.22	59.5	40.5

intraspecific variability (Table 2). LDMC and leaf-thickness diversity were also determined by a negative covariation between species turnover and intraspecific variability, while for the other traits, such components of diversity covaried positively (Table 2).

Overall, multitrait diversity was correlated with the environmental/disturbance gradients (45% in the whole gradient; Table 2). More specifically, functional diversity considering both inter- and intraspecific variation decreased with increasing disturbance (Figure 2). For individual traits, changes in diversity as a response to gradients differed considerably, with an appreciable effect from the precipitation gradient on diversity related to interspecific trait variation. For instance, 34% of the variation in the diversity of SLA was determined by species turnover, from which more than half was explained by variation in precipitation (Table 2). Also, the precipitation gradient accounted for 43% of the total variation in the diversity of wood density across plots, from which three-quarters were explained by species turnover (Table 2). Specifically, the total diversity of wood density tended to decrease with increasing precipitation, while the interspecific variability of SLA and leaf area, as well as the total diversity of SLA, was positively related to the precipitation gradient (Figure 2). On the other hand, the disturbance gradient was significantly related to intraspecific variability of leaf area across local communities and explained 24% of the total variation in the diversity of this trait (Table 2). Both components of leaf-area diversity decreased with CAD intensity (Figure 2). For leaf dry matter content and leaf thickness, diversity across plots was very poorly explained by the gradients considered here (79% and 96% of unexplained variance, respectively; Table 2).

Finally, the departure of the T-statistics from randomly expectation was consistent among traits (Figure 3). Specifically, SES values for $T_{IP/IC}$ were very low across communities, implying low overlap of trait values between co-occurring populations. On the other hand, although some extreme values also occurred for the other T-statistics (i.e., $T_{IC/IR}$ and $T_{PC/PR}$), the mean of the SES values across communities was not significantly different from the null distribution for these statistics (Figure 3), suggesting a weak effect of external filters across communities for most traits. In general, variations in T-statistics were weakly related to the gradients considered here, but some strong relationships emerged (Table 3). Specifically, the stronger the disturbance, the weaker the internal filters within communities (i.e., higher $T_{IP/IC}$) for leaf area and specific leaf area, suggesting a higher overlap of trait values between co-occurring populations under high levels of disturbance (Table 3, Figure 4). Furthermore, variation in precipitation presented a strong and positive relationship with the intensity of external filters at the species level for wood density (i.e., inversely related to $T_{PC/PR}$; Table 3, Figure 4), indicating the selection of species with more similar values of wood density under high precipitation.

4 | DISCUSSION

Our results suggest that plant communities along stress (i.e., precipitation level) and disturbance (i.e., CAD) gradients in the Caatinga dry forest exhibit extensive trait variation, with the intraspecific component accounting for a substantial proportion of total trait variation and greatly affecting the patterns of community-level functional diversity. Both intra- and interspecific trait variation respond to precipitation and human-induced disturbance, with impacts on community-level functional diversity, but these impacts are trait specific. Although some traits are not responsive, CAD reduces multitrait diversity. Overall, changes in precipitation appear to affect interspecific trait variation, while CAD mainly affects intraspecific variation. Finally, from local to regional/landscape scale, the role of both species sorting due to habitat filtering (i.e., external filtering) and niche differentiation (i.e., internal filtering) in the organization of plant communities is evident, although only a few traits—such as wood density and specific leaf area—are responsive. While chronic disturbance relaxes niche differentiation (i.e., increased trait overlaps among species within communities), precipitation affects cross-community trait overlap, increasing the strength of habitat filtering (i.e., species sorting from the regional pool to local communities). Finally, communities exposed to high levels of precipitation and CAD tend to support ecologically similar individuals and species in the case of responsive traits such as wood density and leaf area.

Our results reinforce the notion that both CAD and variation in precipitation operate as species assembly and community-level organizing forces in SDTFs (Rito, Arroyo-Rodríguez, et al., 2017a), even if not synergistically. Yet, in the Caatinga dry forest they influence the spatial distribution and values of some traits within populations

TABLE 2 Variation partitioning of Rao's functional diversity of five plant functional traits together and in isolation, in seasonally dry tropical forest patches ($n = 15$). Partitioning follows the approach of Lepš et al. (2011) and de Bello et al. (2011). Values represent the proportion of variability associated with individual components, and their parts were explained by environmental and disturbance gradients (i.e., sum of squares associated with each component/variable divided by total sum of squares; see Methods for further details). Significance of testable effects was evaluated via repeated-measures ANOVA for each component, and significant values are indicated in bold (*$p \le .05$, **$p \le .01$)

	Species turnover	Intraspecific variability	Covariation	Total
RaoQ (all traits)				
Precipitation	0.041	0.021	0.058	0.120
Disturbance	**0.058***	0.110	0.161	**0.329***
Precipitation × disturbance	0.028	0.007	0.028	0.064
Residuals	0.111	0.326	0.051	0.487
Total	0.238	0.464	0.298	1.000
RaoQ Wood density				
Precipitation	0.305	0.010	0.112	**0.427****
Disturbance	0.108	0.00001	−0.002	0.106
Precipitation × disturbance	0.00005	0.002	−0.001	0.001
Residuals	1.258	0.814	−1.606	0.466
Total	1.670	0.827	−1.497	1.000
RaoQ leaf area				
Precipitation	**0.052***	0.035	0.085	0.171
Disturbance	0.045	**0.075***	0.117	**0.237***
Precipitation × disturbance	0.032	0.030	0.062	0.124
Residuals	0.123	0.121	0.224	0.468
Total	0.252	0.261	0.487	1.000
RaoQ specific leaf area				
Precipitation	**0.181****	0.021	0.124	**0.326***
Disturbance	0.007	0.023	0.026	0.057
Precipitation × disturbance	0.019	0.031	−0.048	0.002
Residuals	0.129	0.256	0.231	0.616
Total	0.336	0.331	0.333	1.000
RaoQ leaf dry matter content				
Precipitation	0.627	0.455	−1.068	0.014
Disturbance	0.222	0.001	−0.024	0.198
Precipitation × disturbance	0.0001	0.001	−0.001	0.001
Residuals	2.588	2.971	−4.772	0.787
Total	3.437	3.428	−5.865	1.000
RaoQ leaf thickness				
Precipitation	0.071	0.039	−0.105	0.005
Disturbance	0.028	0.106	−0.109	0.025
Precipitation × disturbance	0.003	0.020	−0.015	0.008
Residuals	0.545	0.513	−0.096	0.962
Total	0.646	0.678	−0.324	1.000

(intraspecific variation) and between species (interspecific variation), with predictable effects on patterns of community-level trait diversity (Sfair et al., 2018). In accordance with previous studies (Lôbo, Leão, Melo, Santos, & Tabarelli, 2011; Ribeiro-Neto et al., 2016; Rito, Tabarelli, & Leal, 2017b), increased human pressure tended to cause community-level biotic homogenization, which in most cases results from the proliferation of a few disturbance-adapted species—that is, *winners* (sensu Tabarelli, Peres, & Melo, 2012). Here, we offer evidence for a complementary force: increased trait overlaps among co-occurring populations.

Precipitation and chronic anthropogenic disturbance appear to affect the basic mechanisms of species assembly and community

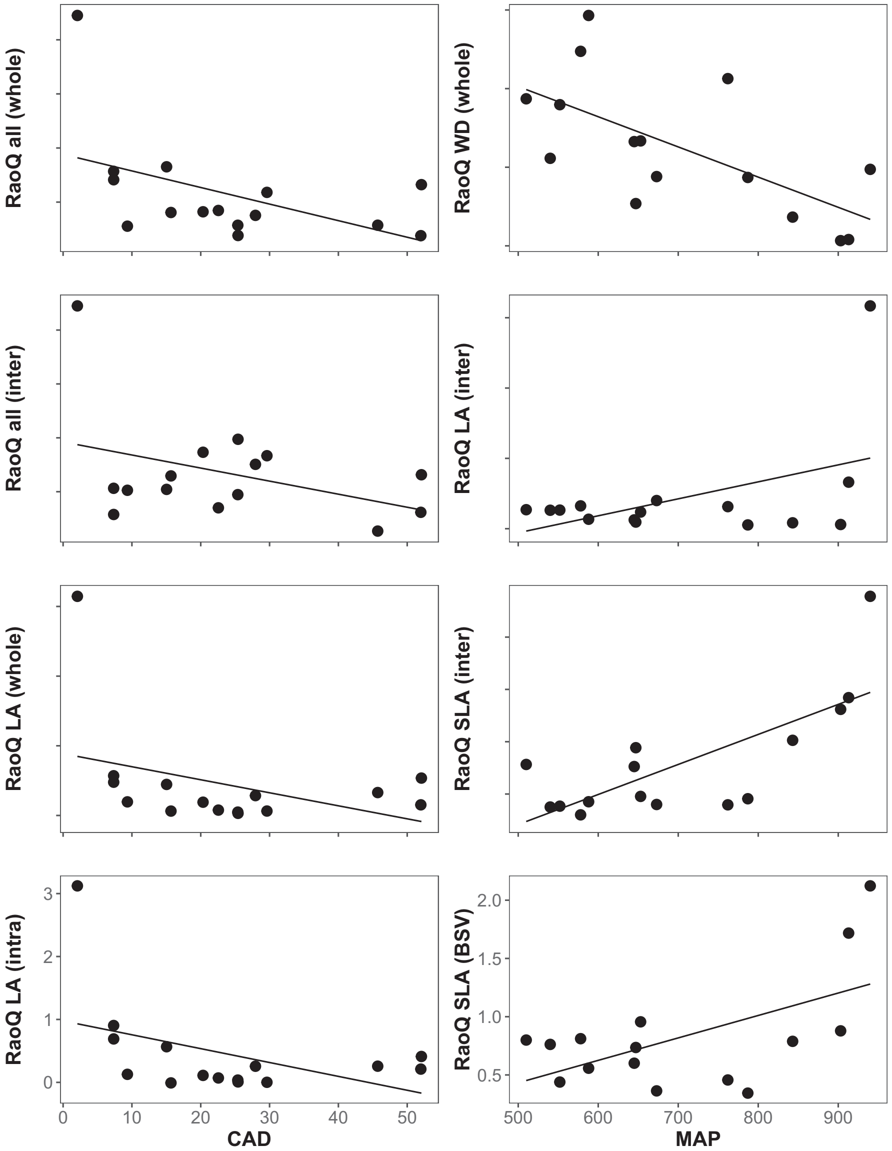

FIGURE 2 Significant relationships between environmental variables and functional trait diversity (RaoQ) considering the whole trait variability and inter- and intraspecific variability (inter and intra), as presented in Table 2. MAP, mean annual precipitation (mm); CAD, chronic anthropogenic disturbance (see Methods); WD, wood density (g/cm^3); LA, leaf area (cm^2); SLA, specific leaf area (cm^2/g)

organization. Internal filtering has been considered a measure of niche overlap among co-occurring species within local communities, while external filtering addresses niche overlap between communities, considering both individuals and species (Taudiere & Violle, 2016; Violle et al., 2012). Patterns of niche overlap (i.e., trait convergence or divergence) may be a result of environmental filtering or species interactions, such as competition and facilitation (Grime, 2006; Kraft et al., 2015; MacArthur & Levins, 1967; Mason et al., 2011; Schöb, Armas, & M., Guler, I. Prieto, and F. I. Pugnaire., 2013). The relation of precipitation and CAD with niche overlap among and within communities, respectively, is in accordance with Grime (2006), which suggests that productivity is the main β-filter while disturbance drives niche differentiation and species coexistence patterns at the local scale. Increased niche overlap with disturbance has also been observed in grasslands as a result of decreased biomass and thus reduced light competition (Mason et al., 2011). Anthropogenic disturbances are in fact expected to reduce biomass and alter microclimatic conditions, not only light availability but also decreasing soil and air moisture due to high insolation (Lebrija-Trejos et al., 2010; Ribeiro-Neto et al., 2016; Singh, 1998). In seasonally dry forests, light availability is not expected to be a limiting factor, but rather water availability largely shapes patterns of species distribution and community assembly (Allen et al., 2017; Grossiord et al., 2017; Maestre et al., 2016). Accordingly, the traits we found to be responsive to CAD were those related to both light capture and water conservation strategies (i.e., leaf area and specific leaf area; Westoby et al., 2002; Wright et al., 2017; Wright et al., 2001). On the other hand, precipitation has been recognized as a key driver of community-level patterns in SDTFs (Allen et al., 2017; Díaz & Cabido, 2001; Le Bagousse-Pinguet et al., 2017; Maestre et al., 2016), including in Caatinga dry forests, particularly through environmental filtering acting on species and trait distribution (Rito, Arroyo-Rodríguez, et al., 2017a; Sfair et al., 2018). Previous studies have in fact proposed that changes in precipitation may be more important than CAD (Rito, Arroyo-Rodríguez, et al., 2017a). Accordingly, we found that precipitation affected interspecific trait variation, trait diversity, and external filtering in our focal landscape.

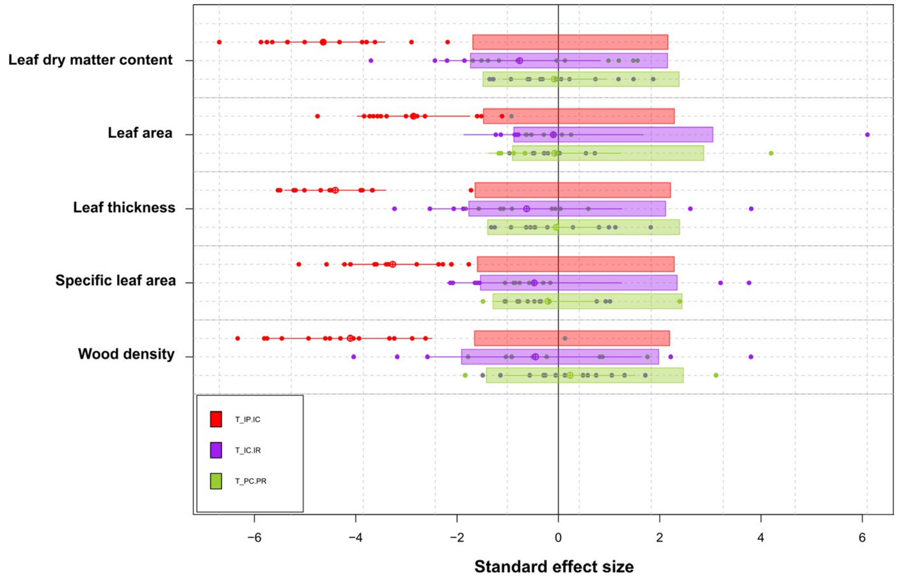

FIGURE 3 Standardized effect size (SES) of T-statistics for the five plant functional traits analyzed. For a given trait and a given metric, each colored dot represents the SES values for a given community ($n = 15$), which reflect the deviation in relation to what would be expected by chance. $T_{IP/IC}$: ratio of within-population variance to total within-community variance; $T_{IC/IR}$: community-wide variance relative to the total variance in the regional pool, assessed at the individual level; and $T_{PC/PR}$: community-wide variance relative to the total variance in the regional pool, assessed via population-level means. The crossed circles and the segments represent the mean and the standard deviation of the SES values for a given T-statistic and a given trait (i.e., mean and standard deviation of community values), respectively. For a given T-statistic, the mean of the SES (crossed circle) is significantly different from the null distribution if not embedded within the colored bar

Contrary to our expectations, precipitation and CAD did not affect several traits studied here. For example, CAD did not affect WD, LDMC, or leaf thickness, while precipitation also did not affect leaf thickness. This may be the result of two mechanisms: (1) negative covariation among inter- and intraspecific variations acting as a compensatory mechanism (Kichenin et al., 2013; Lepš et al., 2011); or (2) species bearing different strategies to cope with the same environmental constraints, such as reduced water availability (Borchert, 1994; Le Bagousse-Pinguet et al., 2017; Marks & Lechowicz, 2005). In Caatinga dry forests, some dominant species (e.g., *Jatropha* sp.) deal with reduced water availability by combining soft wood (i.e., high water storage) and acquisitive leaves, while others (e.g., *Croton* sp.) present hardwood (i.e., reduced cavitation risk) and more conservative leaves (Borchert, 1994; Hacke, Sperry, Pockman, Davis, & McCulloh, 2001). Thus, instead of any particular trait, stress tolerance is conferred by the combination of traits into particular life history strategies (e.g., drought-resistant and drought-avoidant; Pinho, Tabarelli, Engelbrecht, Sfair, & Melo, 2019), with different combinations able to deal with the same environmental constraints (Lebrija-Trejos et al., 2010; Muscarella & Uriarte, 2016; Rosado & de Mattos, 2017). This may also explain why the community-weighted mean traits (i.e., functional composition) did not change predictably in response to the gradients considered (results not shown).

These findings highlight trait variation as a key aspect of species assembly and community organization across environmental gradients, including those created by human-induced disturbances, such as the extraction of forest products. We stress the importance of intraspecific variability as a source of community-level trait variation in Caatinga dry forests, as documented elsewhere (Hulshof & Swenson, 2010), and which may be a common phenomenon among SDTFs globally. High intraspecific trait variability is a shared attribute among plant species that are successful in human-modified landscapes (Sfair et al., 2018). Therefore, intraspecific trait variability appears to be essential for species to occur across environmental and disturbance gradients by adapting to the local abiotic and biotic changes imposed by CAD. In fact, our trait sampling effort encompassed both common and rare species and both of these groups presented either low or high intraspecific variability (Table S2). Such variability can contribute to the local coexistence of individuals by decreasing the competition for scarce resources (Ackerly, 2003; Ashton, Miller, Bowman, & Suding, 2010; de Bello et al., 2011; Callaway, Pennings, & Richards, 2003), but also benefit from resources released by declining species, that is, compensatory dynamics (Lepš et al., 2011). On the other hand, the higher relative interspecific variation across communities in response to changes in precipitation levels suggests plant community structure is less resistant to these changes (Albert et al., 2011; Kichenin et al., 2013; Violle et al., 2012).

We assert that future climate change and increasing human pressure on vegetation (da Silva et al., 2017) will pose weaker negative effects, or even benefit those species bearing high intraspecific trait variability or ecological plasticity in detriment of specialists, as they can adjust their traits according to changing

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*[Correction added on November 20, 2019, after first online publication: Figure 3, has been changed to Figure 4 and new Figure 3 has been included."]

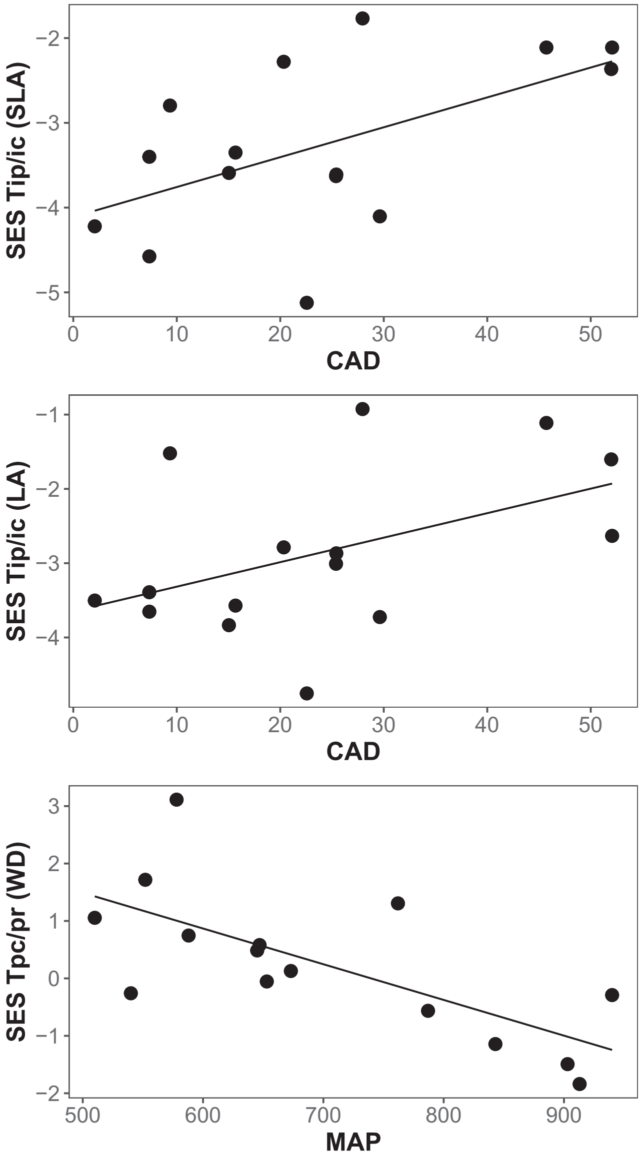

FIGURE 4 Significant relationships between the standard effect size (SES) of T-statistics relating internal and external filtering of plant traits within and across communities along gradients of mean annual precipitation (MAP) and chronic anthropogenic disturbance (CAD), in seasonally dry tropical forest patches (n = 15) in Caatinga, northeast Brazil. Results of regression models are shown in Table 3. $T_{IP/IC}$: ratio of within-population variance to total within-community variance; and $T_{PC/PR}$: community-wide variance relative to the total variance in the regional pool, assessed via population-level means. SLA, specific leaf area; LA, leaf area; WD, wood density.

TABLE 3 Results from multiple linear regression models applied to tree community functional attributes (standard effect sizes of T-statistics) and two predictor variables in dry forest patches (*n* = 15) in Caatinga, northeast Brazil. $T_{IP/IC}$: ratio of within-population (i.e., individuals from a species within a given community) variance to total within-community variance among individuals; $T_{IC/IR}$: community-wide variance relative to the total variance in the regional pool, assessed at the individual level; and $T_{PC/PR}$: community-wide variance relative to the total variance in the regional pool, assessed via species-level means. Significant parameter estimates are indicated with asterisks (**p* ≤ .05, ***p* ≤ .01). CAD, chronic anthropogenic disturbance

	Explanatory variables (estimate)		
T-statistics	Precipitation	CAD	Whole model R^2 (%)
Wood density			
$T_{IP/IC}$	−0.004	0.01	11.1
$T_{IC/IR}$	0.0002	0.04	9.4
$T_{PC/PR}$	**−0.006****	−0.01	**50.7***
Leaf area			
$T_{IP/IC}$	−0.002	**0.04***	31.6
$T_{IC/IR}$	−0.0009	−0.03	10.4
$T_{PC/PR}$	0.004	−0.03	28.0
Specific leaf area			
$T_{IP/IC}$	−0.002	**0.04***	**42.7***
$T_{IC/IR}$	−0.001	−0.03	14.0
$T_{PC/PR}$	0.002	0.02	25.2
Leaf dry matter content			
$T_{IP/IC}$	−0.001	0.01	5.9
$T_{IC/IR}$	0.001	−0.03	9.2
$T_{PC/PR}$	−0.003	−0.01	26.8
Leaf thickness			
$T_{IP/IC}$	−0.002	0.02	19.0
$T_{IC/IR}$	−0.002	0.004	7.0
$T_{PC/PR}$	−0.002	−0.009	11.1

conditions. The predicted increase in human pressure and aridity (PBMC, 2013) will trigger the functional reorganization of plant communities at multiple spatial scales by supporting the emergence of distorted functional communities, which in many situations are likely to be functionally impoverished and harbor low biodiversity (da Silva et al., 2017). By affecting traits related to carbon storage, nutrient cycling, and ecosystem productivity (e.g., wood density, SLA; Reich, 2014), communities are likely to affect the provision of ecological services that have been considered essential for local sustainability, such as the recovery of nutrient stocks for slash-and-burn agriculture.

Like other SDTFs, the Caatinga dry forest is not considered extremely rich in terms of woody plant species at the landscape scale as compared to humid forests. However, the Caatinga flora contains a considerable amount of both intra- and interspecific trait variation for traits directly linked to plant performance, such as WD and SLA. A substantial part of this variability (both inter- and intraspecific), however, is not randomly distributed across space as plants respond to changes in precipitation and CAD, and functional community organization is thus impacted at multiple spatial scales, that is, CAD and precipitation operating as key drivers. The results we present here have important applied implications—wide trait variation is expected to represent a key biological asset for the Caatinga resilience, which will become increasingly relevant as forests become exposed to further land use and climate change, that is, the conversion of old growth forests into human-modified landscapes. The generality of the patterns documented here needs further examination as they have both theoretical and applied implications relevant to understanding the resilience of seasonally dry tropical forests.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.jwstqjq4r (Zorger, Tabarelli, de Queiroz, Rosado, & Pinho, 22019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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