frontiers in Forests and Global Change

ORIGINAL RESEARCH
published: 19 November 2021
doi: 10.3389/ffgc.2021.717406

Linking Plant Functional Traits to Demography in a Fragmented Landscape

Rita de Cássia Quitete Portela, Sara Lucía Colmenares-Trejos and Eduardo Arcoverde de Mattos*

Department of Ecology and Graduate Program in Ecology, Federal University of Rio de Janeiro, Rio de Janeiro, Brazil

Habitat loss in highly deforested landscapes such as the Brazilian Atlantic Forest has been severely affecting the diversity and survival of palm species. As some species are more sensitive than others, trait responses to the environment, as well as environmental effects on fecundity, growth, and mortality rates, may affect species demography. Considering this context, we studied functional and demographic responses of three palm species (*Astrocaryum aculeatissimum*, *Euterpe edulis*, and *Geonoma schottiana*) to habitat loss in the Atlantic Forest in southeastern Brazil by measuring morpho-physiological traits related to plant growth and light acquisition for photosynthesis. We also tested the response of population fitness to fragment size. Plant survival and growth was subsequently monitored in 2006 and 2007, and population dynamics were summarized in pool matrices for large and small forest fragments in the monitoring periods comprehending one full year between 2005–2006 and 2006–2007. The asymptotic growth rate of populations (defined here as population fitness, λ) in five forest fragments was then calculated. Diameter of individuals of the demography plots (from year 2005 to 2007) was used to calculate the relative diameter growth rate. Later, in 2015, we measured a set of morpho-physiological functional traits in palms in the same plots used in the demographic studies. While *A. aculeatissimum* populations were stable in both monitoring periods in small and large fragments, *E. edulis* populations were predicted to decline due to intense predation by monkeys in the large fragment, but were stable in the smaller fragments, and *G. schottiana* populations were stable in the large fragments in both monitoring periods, but populations in the smaller fragments were predicted to decline in the second period, i.e., with lower fitness in these fragments. In addition, the functional traits analyzed showed that *G. schottiana* is a forest interior species associated with the shade/understory environment response. *E. edulis* was also affected by the size of the fragment, but due to a disruptive interaction with a predator and showed intermediate functional traits values. On the other hand, *A. aculeatissimum* thrived in areas with higher and lower incidence of light and was not demographically affected by forest remnant size. This suggests that *E. edulis* and *A. aculeatissimum* are habitat generalists. We concluded that differences in the ecophysiological performance

OPEN ACCESS

Edited by:
Gerardo Avalos, University of Costa Rica, Costa Rica

Reviewed by:
Daijun Liu, University of Birmingham, United Kingdom
Kelsey R. Carter, Los Alamos National Laboratory, United States
Ned Fetcher, Wilkes University, United States

****Correspondence:***
Rita de Cássia Quitete Portela
ritaportela@gmail.com

Specialty section:
This article was submitted to Forest Ecophysiology, a section of the journal Frontiers in Forests and Global Change

Received: *30 May 2021*
Accepted: *25 October 2021*
Published: *19 November 2021*

Citation:
Portela RCQ, Colmenares-Trejos SL and de Mattos EA (2021) Linking Plant Functional Traits to Demography in a Fragmented Landscape. Front. For. Glob. Change 4:717406. doi: 10.3389/ffgc.2021.717406

of palms due to distinct morpho-physiological functional traits related to leaf economic spectrum, such as LDMC or specific leaf area (SLA) and to photosynthetic responses to light environment as electron transport rate (ETR) and saturation irradiance (Ik) were linked to the demographic variation observed in forest remnants of different size.

Keywords: Atlantic Forest, conservation, demography, fragmentation, functional traits, palms

INTRODUCTION

Habitat fragmentation and habitat loss imply the ongoing partition of large areas into small and isolated patches or "islands" (Laurance et al., 2002; Liu et al., 2019), as well as changes in habitat configuration (Fahrig, 2003). These processes have profound effects on biodiversity (Fahrig, 2003; Haddad et al., 2015; Wilson et al., 2016). Fragmentation produces changes in population and community dynamics (Laurance et al., 2002; Haddad et al., 2015), however, the severity of impacts generated by fragmentation depends on factors such as fragment area, edge structure, matrix surrounding the fragment, distance, isolation, and habitat availability (Laurance et al., 2002; Fahrig, 2013; Wilson et al., 2016; Liu et al., 2019). Yet, the intensity of impact increases in smaller and more isolated fragments (Haddad et al., 2015; Liu et al., 2019). The response of species to fragmentation depends on life-history traits associated with dispersal, establishment, and persistence (Wilson et al., 2016; Zambrano et al., 2019) and are species-specific, depending on the ecological requirements of species (Ibáñez et al., 2014; Zambrano et al., 2019). Have been observed, however, that populations size of different species in forest remnants fluctuate and are less stable than those in forests that have not been fragmented (Laurance et al., 2002).

The ability of species to respond to changes in environmental conditions and resource availability are related to functional traits, which are defined as "measurable morphological, physiological or phenological features of species that impact their fitness *via* their effects on demographic features" (Violle et al., 2007). Functional traits also mediate the responses associated with fundamental processes such as species dispersal, establishment, and persistence (Ackerly and Cornwell, 2007; De Bello et al., 2013; Zambrano et al., 2019). The increase in species abundance with traits facilitating colonization and persistence, especially in isolated and/or smaller fragments, is a response that alters the growth and, eventually, the occurrence of some populations in the long term, changing the species composition and dynamics (Dupré and Ehrlén, 2002; May et al., 2013). Species with traits related to more conservative use of resources, such as low specific leaf area (SLA), high leaf dry matter content (LDMC), low leaf nitrogen content, and others are in the lower end of the leaf economic spectrum, showing often low growth rates and are more tolerant to environmental stresses. On the other hand, more acquisitive species are located at the opposite side of the leaf economic spectrum, showing higher growth rates and higher competitive ability in more productive environments (Wright et al., 2004; Messier et al., 2016). Leaf variation patterns are commonly associated with gradients of light, water, and nutrient availability. Plant size (height) is also a vital attribute to plant life cycles (Westoby et al., 2002). The relationship between functional traits related to leaf economics spectrum, and variation in plant life histories and plant demography was recently demonstrated, and may affect the ability of species to persist in fragmented landscapes (Adler et al., 2014; Rüder et al., 2018; Laughlin et al., 2020). In order to unravel the relationship between demography and functional traits, elasticity analysis may be used to investigate relative contributions to fitness components of survival, individual growth, and fecundity to population growth rates (Adler et al., 2014).

Previous studies in the Atlantic Forest in Brazil found that palms are sensitive to decreases in area and forest cover (Benchimol et al., 2016). Palm species dependent on the forest interior are more affected by habitat loss, while palm species that thrive in open areas become more abundant (Benchimol et al., 2016). Despite numerous studies on the effects of habitat loss and fragmentation, few have focused on the role of functional responses and population dynamics together in fragmentation scenarios. In this study, we aimed to verify whether a connection exists between functional traits and demography of different species in response to habitat size. We selected three palm species that occupy different forest *strata*: *Astrocaryum aculeatissimum*, *Euterpe edulis*, and *Geonoma schottiana*. These species were common in the fragments of different sizes selected for this study in the Atlantic Forest. We estimated population dynamics for each species in each of five fragments and measured seven key morphological functional traits. We also used rapid light curves (RLC) to measure the present state of light absorption in photosynthesis (Cavender-Bares and Bazzaz, 2008; Figueroa et al., 2013). We hypothesize that the understory species (*G. schottiana*) has traits related to shade habitats and respond negatively in terms of population demography to the loss of habitat. Additionally, species with traits more related to conservative use of resources will show higher elasticities to survival and will be more resistant to habitat loss.

MATERIALS AND METHODS

Study Sites

This study was carried out in five Atlantic Forest fragments, two of which are federal protected areas (hereafter "large fragments"): Poço das Antas Biological Reserve (∼3,500 ha) and União Biological Reserve (∼7,700 ha). The other three sites (hereafter "small fragments") are forest fragments located in private properties: Santa Helena (57 ha), Estreito (21 ha), and Afetiva-Jorge (19 ha). All sites are located in southeastern Brazil, in Rio de Janeiro state, in the municipalities of Rio das Ostras, Silva

Jardim, and Casimiro de Abreu. These fragments were part of a large, continuous expanse of forest until a century ago (Carvalho, 2005), when fragmentation began following the implementation of coffee production and other agricultural crops.

The habitat in all five sites is classified as Lowland Atlantic Rainforest ("Floresta Ombrófila Densa Submontana" *sensu* IBGE, 2012). All sites are surrounded by pasture, agricultural fields, and secondary forests. The climate in the area is classified as Walter and Lieth Equatorial type (Walter, 1971), with mean annual rainfall of ca. 2,100 mm (Souza and Martins, 2004). Although there is not a distinct dry season, rainfall from May to August is often lower.

Species Selected for the Study

Astrocaryum aculeatissimum (Schott) Burret is a monoecious, slow-growing palm that has single-stemmed (hereafter "solitary") or multi-stemmed habit. It is typically 4–8 m in height and 11–15 cm in diameter (Henderson et al., 1995; Lorenzi et al., 2004). It is endemic to the Atlantic Forest and occurs from the state of Bahia, in the northeast, to Santa Catarina, in the south (Henderson et al., 1995; Lorenzi et al., 2004). It is found primarily in the understory of lowland forests, occasionally on flooded sites and in the vegetation matrix surrounding forest fragments.

Euterpe edulis Mart. (i.e., *"palmito Juçara"*) is a monoecious, solitary, shade-tolerant palm. It is a slow-growing subcanopy palm that can reach 20 m in height and 10–15 cm in diameter. It occurs primarily in forests along the Atlantic coast of Brazil, but can be found inland as far as Argentina and Paraguay, in Seasonal Forests (Henderson et al., 1995). It occupies hill slopes and tops, and sites associated to seasonal flooding up to elevations of 1,000 m (Henderson et al., 1995; Silva-Matos and Watkinson, 1998). This species is harvested for heart-of-palm, one of the most abundant and valuable non-timber forest products in the Atlantic Forest (Fantini and Guries, 2007). It reaches maturity at 8 years of age, therefore harvesting should be done after that to allow the palm to reproduce (Gaiotto et al., 2003). However, intensive harvesting at any age has led to the decline of the species over much of the Atlantic Forest, so many of the surviving populations are small and fragmented (Galetti and Aleixo, 1998; Silva-Matos et al., 1999). Like all solitary palms, *E. edulis* has a single apical meristem, therefore, harvest the heart-of-palm causes the death of the genetic individual.

Geonoma schottiana Mart. (Ouricana) is a monoecious, solitary or rarely multi-stemmed, shade-tolerant, and slow-growing palm. It is typically 1–4 m in height and grows in the forest understory in lowland forests (Henderson et al., 1995; Lorenzi et al., 2004). It occurs in the Atlantic Forest and in forest formations in *Cerrado* (Henderson et al., 1995; Lorenzi et al., 2004). In the private property sites selected for this study, the leaves of *G. schottiana* are harvested for floral arrangements by cutting the leaves or the stem of the plant, which causes death.

Demographic Data

In each fragment, we censused palms in nine 30 m × 30 m plots distributed systematically in three blocks. Each block had three plots 50 m apart, while blocks were 100 m apart. One block was set up in the middle of each fragment and the other two blocks on opposite sides of the first block. In the protected areas, we used existing trails near the center of the fragments. All individuals for all sizes of the three palm species were numbered with an aluminum tag between June and September, 2005. Palm survival was subsequently monitored between June and September of 2006 and 2007. All new plants were also tagged. During each census, each plant was assigned to one of five development classes based on morphological and morphometric analysis: seedling, infant, juvenile, immature, and reproductive (**Table 1**; Portela et al., 2010).

Demographic Analysis

We developed summary matrices describing the dynamics of the populations in each fragment type (large and small) in each monitoring period (which comprised 1 year each, between 2005–2006 and 2006–2007) by pooling the data from the nine plots in each site type (large and small fragments) to create a "summary matrix." Summary matrices are the best means of synthesizing the demography of multiple populations because they account for the disproportionate weight that low plant numbers in some size classes in some locations can give to transition probabilities (Horvitz and Schemske, 1995). In our study, using pooled matrices was advantageous because it allowed

TABLE 1 | Characteristics, based on morphological and morphometrical analysis, of the five ontogenetic stages for *Astrocaryum aculeatissimum*, *Euterpe edulis*, and *Geonoma schottiana* in three small forest fragments and two large forest fragments in the Atlantic Rain Forest.

	Astrocaryum aculeatissimum	***Euterpe edulis***	***Geonoma schottiana***
Seedling	Bifid leaves	Palmate leaves	Bifid leaves
Infant	Bifid leaves, incompletely segmented ones or only incompletely segmented ones	Completely segmented leaves, but palmate ones can still be present	Bifid leaves or incompletely segmented ones or completely segmented ones, with diameter but stemless
Juvenile	First completely segmented leaf blades, but bifid leaves and incompletely segmented ones can be also present	Only completely segmented leaf blades, apparent stem with maximum diameter less than 52 mm	Bifid leaves or incompletely segmented ones or completely segmented ones, with apparent stem and diameter up to 30 mm
Immature	Completely segmented leaf blades and apparent stem but no signals of reproductive event	Completely segmented leaf blades, apparent stem with diameter bigger than 52 mm but no signals of reproductive event	Bifid leaves or incompletely segmented ones or completely segmented ones, with apparent stem and diameter bigger than 30 mm but no signals of reproductive event
Reproductive	Recognized by the production of flowers and fruits	Recognized by the production of flowers and fruits	Recognized by the production of flowers and fruits

us to estimate several vital rates not observed in some of the small forest fragments due to low plant density.

From 1 year to the next, plants may grow into the following development class (g = growth), remain in the same stage (s = stasis), shrink into a preceding one (r = regress), or die. For each matrix we used deterministic population matrix models, and we calculated the lower level vital rates (g, s, r, and fecundity), lower level vital rates elasticities and the asymptotic population growth rate (λ) (Caswell, 2001). The standard matrix population model will project population growth if the dominant eigenvalue (λ) of a matrix is >1.0 (implying no resource limitations or competition), or population decline if $\lambda < 1.0$ (Caswell, 2001). We concluded that estimates of λ were significantly different from 1.0 if the bias-corrected 95% confidence intervals (CI) failed to include 1.0. Confidence intervals were estimated by bootstrapping; the raw data (individuals) were resampled 2,000 times to obtain 2,000 transition matrices for which we estimated λ. We then used the distribution of these estimates of λ to calculate the upper and lower 95% CI using the procedure detailed in Stubben and Milligan (2007).

All analyses were carried out with the Popbio package (Stubben and Milligan, 2007) in R 2.15.1 software (R Development Core Team, 2015).

Relative Diameter Growth Rate

Diameter of individuals of the demography plots (from year 2005 to 2007) was used to calculate the relative diameter growth rate (RDGR). RDGR = lnDf − lnDi / Tf-Ti. Where Di is the initial diameter value (2005), Df is the final diameter value (2007) and Tf-Ti is the difference between final and initial measurement times, 2 years.

Plant Functional Traits Data

To measure functional traits, we selected randomly 15 plants per species within the nine demographic plots in each fragment, when available, totaling 45 individuals per species in the three small fragments and 30 in the two large ones. Leaflets from the middle part of a whole leaf, pertaining to the mid-crown of each plant, were collected for leaf trait measurements.

The traits measured in the field were height (H, cm), with a Nikon Forestry Pro Laser Rangefinder/Height Meter, basal stem diameter (BSD, mm) just above the roots with a caliper, leaf area (LA, cm^2) using a measuring tape and calculated from the area of the ellipse, and chlorophyll concentration in leaves using a non-destructive chlorophyll meter (soil-plant analysis development, Chlorophyll Meter SPAD- 502, Konica Minolta Sensing, Inc.).

For leaf-saturated weight and leaf thickness (TH, mm), small squares of pre-defined area were stored in Ziploc plastic bags with a humid cloth in the dark for 6 h, then weighed on a portable precision balance (Ohaus). Thickness was measured with a caliper (500-784 Mitutoyo IP67 Waterproof Electronic Caliper). The same leaf squares were dried in an oven for 72 h at 60°C and weighed again until constant dry mass values. Leaf saturated weight, dry weight and square area were used to calculate SLA ($m^2 \cdot kg^{-1}$) and LDMC ($mg \cdot g^{-1}$). Leaf veins were avoided in TH and SPAD readings.

We used RLC to determine the photosynthetic capacity of the different palm specimens in each forest fragment. RLC were measured using a PAM-2500 Portable Chlorophyll Fluorometer (Waltz). RLC provides key parameters such as α (alpha, electrons/photons), which refers to the initial slope of RLC related to the quantum efficiency of photosynthesis, maximum electron transport rate [ETRmax, μmol electrons/($m^2 \cdot s$)], and I_K [μmol photons/($m^2 \cdot s$)], which is the minimum saturating irradiance. The curve represents the relationship between ETR and irradiance (PAR: photosynthetic active radiation) emitted by the PAM fluorometer. The maximum quantum yield in limited light conditions is where alpha intersects the maximum ETR. The saturation irradiance (Ik) value indicates the point where the maximum ETR and alpha intersect, potentially representing the initial saturation point.

Analysis of Plant Functional Traits

As the data did not follow a normal distribution and due to small number of fragments in both category of size, we estimated the mean, size of standard error, standard deviation, and confidence intervals by applying the bootstrap method to each trait per species per fragment size, taking resamples 100,000 times with replacement from the original sample using the package boot in R software (R 3.1.3, R Development Core Team, 2015). We must point out that it is difficult to find well preserved fragments in the studied region. Because of that, fragments were not random but a fixed factor in our analysis.

RESULTS

Deterministic Asymptotic Growth Rate (λ)

Astrocaryum aculeatissimum populations were stable in both monitoring periods, as well as in the small and large fragments (**Table 2**). *E. edulis* populations declined at rates of 4.22 and 12.41% per year between 2005–2006 and 2006–2007, respectively, in large fragments. The 95% CI for these estimates were lower than 1.0 in both monitoring periods. In contrast, populations in the small fragments were stable throughout both periods. *G. schottiana* populations remained stable in the first period of the study in both fragment types, but then, only in the large fragment in the second period. In the second period, the population in the small fragments declined at a rate of 9.18%, with 95% CI for these estimates being lower than 1.0 in both periods.

Lower-Level Vital Rates

The survival rate of *A. aculeatissimum*, *E. edulis*, and *G. schottiana* was high in all development classes and exceeded 75% in post-seedling stages in the large and small fragments (**Table 3**). *A. aculeatissimum* and *E. edulis* had the highest seedling survival rates: 87.16 to 72.37%, whereas *G. schottiana* had the lowest: 43.82% in 2005–2006 and 22.51% in 2006–2007.

The growth of *A. aculeatissimum*, *E. edulis*, and *G. schottiana* in all stage classes did not vary between years or fragment size

(**Table 3**). However, the development of the seedling into the infant stage was slower in large fragments for *G. schottiana* and faster for *E. edulis* when compared with the small fragments, regardless of the monitoring period. The second-period growth of *G. schottiana* from juvenile to immature and the first-period growth of immature to reproductive were much faster in the large fragments compared with the small fragments, regardless of the period.

A small proportion of palms (less than 10%) receded to a previous stage class after a 1-year period (**Table 3**). In the case of *A. aculeatissimum*, 51.35 and 33.98% of juvenile plants receded to the infant stage in the second monitoring period in both small and large fragments, while 22.45% of *E. edulis* juveniles receded to the infant stage in the first monitoring period in large fragments. The negative growth of *G. schottiana* juveniles was much higher in small fragments in both transition years.

TABLE 2 | Deterministic asymptotic growth rate (λ) and 95% confidence intervals (95% CI) for *Astrocaryum aculeatissimum*, *Euterpe edulis*, and *Geonoma schottiana* in three small forest fragments and two large forest fragments in the Atlantic Rain Forest.

λ (95% CI)	Fragment size	*Astrocaryum aculeatissimum*	*Euterpe edulis*	*Geonoma schottiana*
2005–2006	Large	1.0000 (0.9848–1.0118)	0.9578 (0.9205–0.9994)	1.0050 (0.9821–1.0268)
	Small	1.0060 (0.9956–1.0141)	1.0033 (0.9385–1.0711)	0.9993 (0.9661–1.0238)
2006–2007	Large	0.9936 (0.9796–1.0010)	0.8759 (0.8231–0.9230)	0.9881 (0.9653–1.0078)
	Small	0.9977 (0.9863–1.0043)	1.0728 (0.9459–1.1377)	0.9082 (0.8261–0.9700)

If λ of a matrix is >1.0 the population is projected to grow, if λ = 1.0 the population is stable and if λ < 1.0 the population is projected to decline. Total sampling area in each forest fragment: 0.81 ha.

TABLE 3 | Lower-level vital rates for *Astrocaryum aculeatissimum*, *Euterpe edulis*, and *Geonoma schottiana* in three small and two large forest fragments in the Atlantic Rain Forest.

	Large fragments			Small fragments		
	Astrocaryum aculeatissimum	*Geonoma schottiana*	*Euterpe edulis*	*Astrocaryum aculeatissimum*	*Geonoma schottiana*	*Euterpe edulis*
s1 (2005–2006)	0.8716	0.3024	0.7533	0.7237	0.2251	0.6842
s1 (2006–2007)	0.9	0.3581	0.6767	0.7805	0.4382	0.8349
s2 (2005–2006)	0.991	0.8571	0.9455	0.9872	0.8585	0.8966
s2 (2006–2007)	0.9752	0.8843	0.9056	0.9519	0.8344	0.96
s3 (2005–2006)	0.9782	0.9024	0.9484	0.9852	0.9643	0.918
s3 (2006–2007)	0.9955	0.9667	0.9156	0.9923	0.8478	0.9434
s4 (2005–2006)	0.9877	0.9206	0.8476	1	0.8367	0.9873
s4 (2006–2007)	0.9867	0.8889	0.7717	0.9896	0.8654	0.96
s5 (2005–2006)	0.9857	0.9646	0.9265	1	0.9851	1
s5 (2006–2007)	0.9932	0.9478	0.8	0.9947	0.8261	1
Fecundity (2005–2006)	0.7214	4.5756	0.4412	0.2019	4.3433	7.5455
Fecundity (2006–2007)	0.3767	5.7855	0.8714	0.262	6.058	15.3571
g1 (2005–2006)	0.1579	0.0594	0.1858	0.2	0.1154	0.0385
g1 (2006–2007)	0.1893	0.0583	0.2778	0.1563	0.1275	0.033
g2 (2005–2006)	0.0117	0.2986	0.2846	0.0104	0.2102	0.1923
g2 (2006–2007)	0.0109	0.2701	0.4171	0.0322	0.3175	0.4583
g3 (2005–2006)	0.0045	0.1892	0.1633	0.0302	0.1481	0.1071
g3 (2006–2007)	0.0023	0.1379	0.156	0.0194	0.0769	0.12
g4 (2005–2006)	0.075	0.1483	0.037	0.1023	0.0732	0.0248
g4 (2006–2007)	0.1216	0.075	0.0178	0.1474	0.0222	0.0333
r1 (2005–2006)	0.0104	0.0208	0.0423	0.0052	0.017	0.0385
r1 (2006–2007)	0.0121	0.0093	0.0095	0	0	0
r2 (2005–2006)	0.0401	0.0541	0.2245	0.0244	0.1481	0.0714
r2 (2006–2007)	0.5135	0.0862	0.0355	0.3398	0.2051	0
r3 (2005–2006)	–	0.0138	0.0265	–	0.0488	0.0083
r3 (2006–2007)	–	0.025	0.0178	–	0.022	0

Total sampling area in each forest fragment: 0.81 ha. s1, seedling survival; g1, growth of seedling to infant; s2, infant survival; r1, negative growth of infant; g2, growth of infant to juvenile; s3, juvenile survival; r2, negative growth of juvenile; g3, growth of juvenile to immature; s4, immature survival; r3, negative growth of immature; g4, growth of immature to reproductive; s5, survival of reproductive; f5, fecundity, the ratio of the number of new seedlings observed in t + 1 over the number of reproductives individuals in t.

Euterpe edulis was the palm of highest fecundity in small fragments in both monitoring periods. *G. schottiana* fecundity was higher, regardless of fragment size and period, compared with the other two species, except with *E. edulis* in small fragments. *E. edulis* had a much lower fecundity rate in large fragments in both monitoring periods (**Table 3**). For the three species and for the two kinds of fragments, the fecundity rate was higher in the second monitoring period for all three species in all fragment sizes, with the exception of *A. aculeatissimum* in large fragments in the second monitoring period.

Lower-Level Vital Rates Elasticities

For both transition years, elasticity patterns for the three palm species were very similar to each other and for the two kinds of fragments. The highest elasticity values (higher than 0.40) were for survival, especially for the later ontogenetic stages: immature and reproductive (**Table 4**). Values for growth, regressions and fecundity were generally low. The highest vital rates elasticities for *A. aculeatissimum* were similar between both transitions years and kind of fragment, with the highest elasticities representing survival of reproductive. For *G. schottiana* in the second transition year in the small fragments, the elasticity for the reproductive survival was lower when compared with the big fragment and previous year. The highest vital rates elasticities for *E. edulis* were similar between the two kinds of fragments, but different between years, the elasticities representing survival of reproductive were lower in the second transition year. For the three palms, the survival of reproductives was the most important lower level vital rate for λ and should be the primary targets of management efforts.

Relative Diameter Growth Rate

The three species showed a diameter growth gradient, in the following sequence from the least to the largest: *A. aculeatissimum*, *E. edulis*, and *G. schottiana* (**Figure 1**). Immature and reproductive individuals of *A. aculeatissimum* presented a very low RDGR in both fragment types. Immature individuals of *E. edulis* presented a higher RDGR in large

TABLE 4 | Elasticity of lower-level vital rates for *Astrocaryum aculeatissimum*, *Euterpe edulis*, and *Geonoma schottiana* in three small and two large forest fragments in the Atlantic Rain Forest.

	Large fragments			Small fragments		
	Astrocaryum aculeatissimum	***Geonoma schottiana***	***Euterpe edulis***	***Astrocaryum aculeatissimum***	***Geonoma schottiana***	***Euterpe edulis***
s1 (2005–2006)	0.0313	0.0424	0.0597	0.0161	0.0156	0.0580
s1 (2006–2007)	0.0001	0.0390	0.0666	0.0082	0.0517	0.1419
s2 (2005–2006)	0.3460	0.0001	0.1089	0.1525	0.0001	0.0708
s2 (2006–2007)	0.0200	0.0001	0.0940	0.0578	0.1366	0.0714
s3 (2005–2006)	0.1363	0.0351	0.0777	0.0913	0.0314	0.0572
s3 (2006–2007)	0.0013	0.0882	0.273	0.0124	0.102	0.1254
s4 (2005–2006)	0.0347	0.1155	0.1338	0.0591	0.0517	0.2593
s4 (2006–2007)	0.0038	0.1507	0.2283	0.0181	0.3783	0.2426
s5 (2005–2006)	**0.4452**	**0.7242**	**0.5988**	**0.6741**	**0.8422**	**0.5335**
s5 (2006–2007)	**0.9717**	**0.6134**	0.3083	**0.9006**	0.3012	0.3820
Fecundity (2005–2006)	0.0065	0.0307	0.0202	0.0065	0.0125	0.0212
Fecundity (2006–2007)	0.0005	0.0261	0.0293	0.0028	0.0299	0.0376
g1 (2005–2006)	0.0083	0.0306	0.0217	0.0069	0.0125	0.0213
g1 (2006–2007)	0.0000	0.0260	0.0294	0.0028	0.0300	0.0376
g2 (2005–2006)	0.0089	0.0000	0.0339	0.0054	0.0000	0.0232
g2 (2006–2007)	0.0006	0.0000	0.0376	0.0044	0.0509	0.0412
g3 (2005–2006)	0.0065	0.0099	0.0146	0.0065	0.0070	0.0131
g3 (2006–2007)	0.0005	0.0154	0.0317	0.0028	0.0148	0.0304
g4 (2005–2006)	0.0030	0.0259	0.0202	0.0065	0.0125	0.0212
g4 (2006–2007)	0.0005	0.0261	0.0292	0.0028	0.0300	0.0376
r1 (2005–2006)	0.0018	0.0000	0.0013	0.0003	0.0000	0.0001
r1 (2006–2007)	0.0001	0.0000	0.0002	0.0000	0.000	0.000
r2 (2005–2006)	0.0024	0.0011	0.0750	0.0006	0.0024	0.0020
r2 (2006–2007)	0.0002	0.0048	0.0089	0.0016	0,0000	0.000
r3 (2005–2006)	–	0.0007	0.0026	–	0.0001	0.0008
r3 (2006–2007)	–	0.0023	0.005	–	0.0037	0.0000

Total sampling area in each forest fragment: 0.81 ha. s1, seedling survival; g1, growth of seedling to infant; s2, infant survival; r1, negative growth of infant; g2, growth of infant to juvenile; s3, juvenile survival; r2, negative growth of juvenile; g3, growth of juvenile to immature; s4, immature survival; r3, negative growth of immature; g4, growth of immature to reproductive; s5, survival of reproductive; f5, fecundity, the ratio of the number of new seedlings observed in t + 1 over the number of reproductives individuals in t. Bold values represent the higher elasticities.

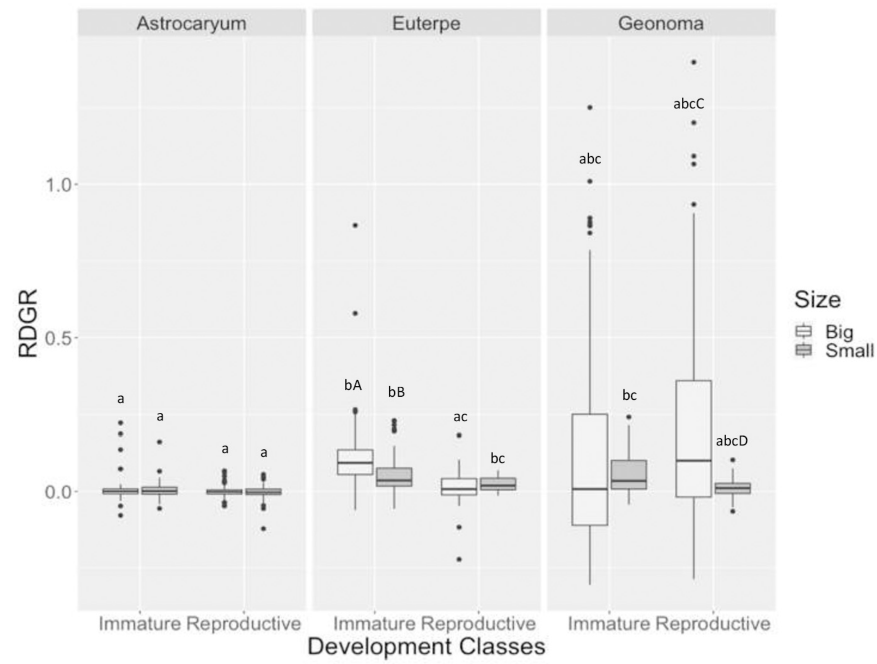

FIGURE 1 | Relative diameter growth rate (RDGR) of individuals of the demography plots (from year 2005 to 2007). The bootstrap confidence intervals were calculated for mean difference, lowercase letters indicate differences in the mean value of the attribute between species, and capital letters indicate differences between fragments.

fragments compared with individuals in small fragments. Reproductive individuals of *G. schottiana* presented a higher RDGR in large fragments compared with individuals in small fragments, but the RDGR of immature individuals was not different between the two types of fragments.

Functional Traits

The bootstrap confidence intervals were calculated for mean difference (**Table 5**). Bootstrap and confidence limits for H suggested no differences in the mean H between fragment sizes, but it was between species. *A. aculeatissimum* and *E. edulis* were taller, reaching the canopy strata in some areas, while *G. schottiana* was the smallest, growing in the understory (**Figure 2A**). *E. edulis* BSD was larger in the large fragments, while *G. schottiana* showed the lower values (**Figure 2B**). Morphological leaf traits differed between species (**Figures 2C–F**). *A. aculeatissimum* showed the highest LA, TH, LDMC, and lower SLA, whereas *G. schottiana* showed the inverse results. Leaf thickness (TH, mm) was the only trait that was lower in small fragments in *G. schottiana*. Physiological traits related to the photosynthetic response to light showed different trends among species and fragments (**Figures 2G–J**). Maximum electron transport rate (ETRmax, μmol electrons $m^{-2}s^{-1}$) was lower in *G. schottiana*, but did not differ between fragment size (**Figure 2G**). Minimum Ik [μmol photons/(m^{2}*s)] did not differ between fragments, but it was lower in *G. schottiana* (**Figure 2H**). The quantum efficiency of photosynthesis (α, electrons/photons) was similar between species and fragments (**Figure 2I**). SPAD values were similar between species and fragment size (**Figure 2J**).

DISCUSSION

The connections between functional traits and demography are not easily demonstrated (Yang et al., 2018). The connections become even more challenging when individuals of different species are subjected to distinct environmental conditions, as those found in fragments of different sizes (Zambrano et al., 2019). We observed, however, that three palm species occurring in the Atlantic Rain Forest differed regarding functional traits related to leaf economic spectrum and also showed differential responses to population growth rates when occurring in fragments of different sizes. As expected, *G. schottiana*, the only understory species showed morpho-physiological functional traits related to more shady environments, such as lower LA, TH, LDMC, ETR and Ik, and higher SLA. *E. edulis*, despite been the tallest species showed often intermediary functional trait values, such as LA, TH, and SLA. In contrast, *A. aculeatissimum* showed traits more related to a conservative use of resources, very low growth rates, and showed population stability in time and by fragment size. Despite all species showed elasticity values more strongly related to survival, *G. schottiana* and *E. edulis* showed declines in population growth rates in small and large fragments, respectively. *G. schottiana*, however, also showed lower vital rates and elasticity for the reproductive survival associated to small fragments and in most cases only in the second

TABLE 5 | The bootstrap confidence intervals for mean of: relative diameter growth rate (RDGR), height (H, cm), basal stem diameter (BSD, mm), leaf area (LA, cm^2), leaf thickness (TH, mm), and leaf dry matter content (LDMC, $mg \cdot g^{-1}$), specific leaf area (SLA, $m^2 \cdot kg^{-1}$), parameter α (alpha, electrons/photons), maximum electron transport rate [ETRmax, μmol electrons/($m^2 \cdot s$)], I_K, [μmol photons/($m^2 \cdot s$)], and chlorophyll concentration (SPAD).

Size	Species	Class	RDGR mean	5%	95%
Big	*G. schottiana*	Immature	0.1161	0.0688	0.1652
Big	*E. edulis*	Immature	0.1080	0.0967	0.1205
Big	*A. acculeatissimum*	Immature	0.0092	0.0006	0.0190
Big	*G. schottiana*	Reproductive	0.1977	0.1603	0.2362
Big	*E. edulis*	Reproductive	0.0129	−0.0005	0.0258
Big	*A. acculeatissimum*	Reproductive	−0.0004	−0.0026	0.0018
Small	*G. schottiana*	Immature	0.0628	0.0446	0.0818
Small	*E. edulis*	Immature	0.0513	0.0436	0.0595
Small	*A. acculeatissimum*	Immature	0.0060	−0.0005	0.0132
Small	*G. schottiana*	Reproductive	0.0118	0.0047	0.0189
Small	*E. edulis*	Reproductive	0.0256	0.0166	0.0349
Small	*A. acculeatissimum*	Reproductive	−0.0030	−0.0056	−0.0006

Size	Species	Trait	Mean	IC 5%	IC 95%
Big	*A. acculeatissimum*	α	0.292	0.276	0.307
Big	*A. acculeatissimum*	DAS	97.781	93.899	101.785
Big	*A. acculeatissimum*	ETR	150.728	137.162	163.595
Big	*A. acculeatissimum*	H	3.658	3.276	4.065
Big	*A. acculeatissimum*	Ik	523.628	463.672	583.613
Big	*A. acculeatissimum*	LA	5.669	4.959	6.350
Big	*A. acculeatissimum*	LDMC	485.345	451.465	524.637
Big	*A. acculeatissimum*	SLA	6.000	5.556	6.476
Big	*A. acculeatissimum*	SPAD	65.231	61.797	68.392
Big	*A. acculeatissimum*	TH	0.308	0.293	0.323
Big	*E. edulis*	α	0.320	0.297	0.343
Big	*E. edulis*	DAS	125.430	117.957	133.065
Big	*E. edulis*	ETR	137.050	124.320	149.350
Big	*E. edulis*	H	7.253	6.203	8.353
Big	*E. edulis*	Ik	442.385	384.790	501.065
Big	*E. edulis*	LA	1.875	1.609	2.123
Big	*E. edulis*	LDMC	435.231	420.168	450.304
Big	*E. edulis*	SLA	9.769	9.126	10.420
Big	*E. edulis*	SPAD	60.930	58.160	63.575
Big	*E. edulis*	TH	0.181	0.169	0.193
Big	*G. schottiana*	α	0.284	0.266	0.302
Big	*G. schottiana*	DAS	55.731	51.506	59.878
Big	*G. schottiana*	ETR	90.769	84.670	96.573
Big	*G. schottiana*	H	1.133	0.934	1.329
Big	*G. schottiana*	Ik	332.100	296.955	368.078
Big	*G. schottiana*	LA	0.455	0.340	0.575
Big	*G. schottiana*	LDMC	364.400	356.282	372.734
Big	*G. schottiana*	SLA	15.541	14.833	16.279
Big	*G. schottiana*	SPAD	55.282	52.245	58.150
Big	*G. schottiana*	TH	0.139	0.132	0.146
Small	*A. acculeatissimum*	α	0.254	0.234	0.273
Small	*A. acculeatissimaum*	DAS	97.574	92.808	102.043
Small	*A. acculeatissimum*	ETR	132.576	115.421	150.298
Small	*A. acculeatissimum*	H	3.814	3.410	4.257
Small	*A. acculeatissimum*	Ik	524.292	456.271	595.173
Small	*A. acculeatissimum*	LA	6.211	5.426	6.883
Small	*A. acculeatissimum*	LDMC	476.150	463.176	489.790

(Continued)

TABLE 5 | (Continued)

Size	Species	Trait	Mean	IC 5%	IC 95%
Small	*A. acculeatissimum*	SLA	5.685	5.399	5.970
Small	*A. acculeatissimum*	SPAD	68.624	62.367	72.514
Small	*A. acculeatissimum*	TH	0.310	0.295	0.326
Small	*E. edulis*	α	0.289	0.270	0.312
Small	*E. edulis*	DAS	101.581	95.835	107.268
Small	*E. edulis*	ETR	136.678	126.840	146.868
Small	*E. edulis*	H	7.943	7.487	8.360
Small	*E. edulis*	Ik	488.497	445.123	531.977
Small	*E. edulis*	LA	1.328	1.224	1.436
Small	*E. edulis*	LDMC	443.242	433.599	451.969
Small	*E. edulis*	SLA	10.768	10.013	11.536
Small	*E. edulis*	SPAD	65.137	63.020	67.177
Small	*E. edulis*	TH	0.146	0.137	0.155
Small	*G. schottiana*	α	0.299	0.289	0.309
Small	*G. schottiana*	DAS	58.197	54.824	61.578
Small	*G. schottiana*	ETR	97.079	89.972	104.267
Small	*G. schottiana*	H	1.674	1.433	1.928
Small	*G. schottiana*	Ik	324.993	295.936	354.248
Small	*G. schottiana*	LA	0.766	0.674	0.859
Small	*G. schottiana*	LDMC	378.126	364.205	393.915
Small	*G. schottiana*	SLA	15.892	15.059	16.749
Small	*G. schottiana*	SPAD	53.786	48.903	58.014
Small	*G. schottiana*	TH	0.118	0.112	0.124

period of study. This indicates that this species might be the most negatively affected by fragmentation when in conjunction with drought years.

According to the scientific literature, the three palms analyzed in our study are considered shade-tolerant species (Arroyo-Rodríguez et al., 2007; Gatti et al., 2011), capable of regenerating in the shaded understory of mature forests (Tabarelli et al., 1999). However, species varied in a continuum along the leaf economic spectrum with probable consequences to the observed responses to fragment size. It is important to note, that the causes for population declines to fragmentation may differ between *E. edulis* and *G. schottiana*. Different from *G. schottiana*, *E. edulis* population was decreasing in the large fragments in both monitoring periods. This was caused by heart-of-palm consumption by a hyper-abundant monkey population (*Sapajus nigritus*) in these areas. This dramatic population decline was detected in a 10-year plant demographic study in the same area (Portela and Dirzo, 2020). Apart from this disruptive interaction, this palm species seem to have higher capacity to overcome the challenges of high light availability or fluctuating light conditions (Schumann et al., 2017; Li et al., 2019), such as would occur in smaller fragments with more open canopy, sunflecks, or tree-fall gaps. Besides the differences in leaf functional traits, the three studied species presents higher values of sensibility that is characteristic of long-lived and slow-grow species. Species considered to be long-lived and slow-grow commonly have a greater influence of individuals from late (reproductive) classes on λ, as they have a higher survival rate within the population. In short-lived fast-grow species, individuals from early classes (seedling) tend to have the greatest influence on λ, precisely due to the high survival and growth rates of these individuals (Franco and Silvertown, 2004).

A substantial loss of palm stems has been reported in the scientific literature in response to reduced forest cover on a landscape scale, following a non-linear pattern decline, which suggests that Arecaceae is very sensitive to deforestation and habitat loss (Benchimol et al., 2016). The response of palms to reduced forest cover was positive for open-area species and negative for forest-interior species. Some genera of palm species, like *Geonoma* and *Bactris*, are already known for reduced population growth in altered environments, and categorized as forest-interior species (Chazdon, 1985; Svenning, 2001; Benchimol et al., 2016). Benchimol et al. (2016) stated that the entire *Geonoma* genus represents conspicuous elements of Atlantic Forests, found in closed and less disturbed forests. Their assessment may be used as indicator of local levels of forest degradation, particularly related to the structural shrinkage of native forests and increasing levels of canopy openness. Chazdon (1985) shows that lower biomass costs of light interception in adult *Geonoma cuneata* from a well preserved tropical premontane wet forest enable this species to exploit successfully the most deeply shaded microsites in the rain forest understory. Low light levels required to saturate photosynthesis by means of low Ik, together with leaf traits related to low leaf construction costs, such as lower values of LA, LDMC, and higher SLA are crucial for *G. schottiana* be able to deal with the light environment of the forest understory (Poorter and Bongers, 2006; Poorter, 2009). In addition, the low photosynthetic potential evidenced by low ETR values may extend the payback time of the investment in leaf construction. In contrast, adult *E. edulis* palms showed a generalist response in light behavior (Benchimol et al., 2016) and was the species with intermediary functional trait values, but young individuals had low potential for growth and survival in forests with greater canopy openness and light transmission (Gatti et al., 2011; Cerqueira et al., 2021). Therefore, small forest fragments have more open canopy and seem to be unfavorable for the establishment of typical shade-tolerant species as *G. schottiana*, and even for those with great plasticity

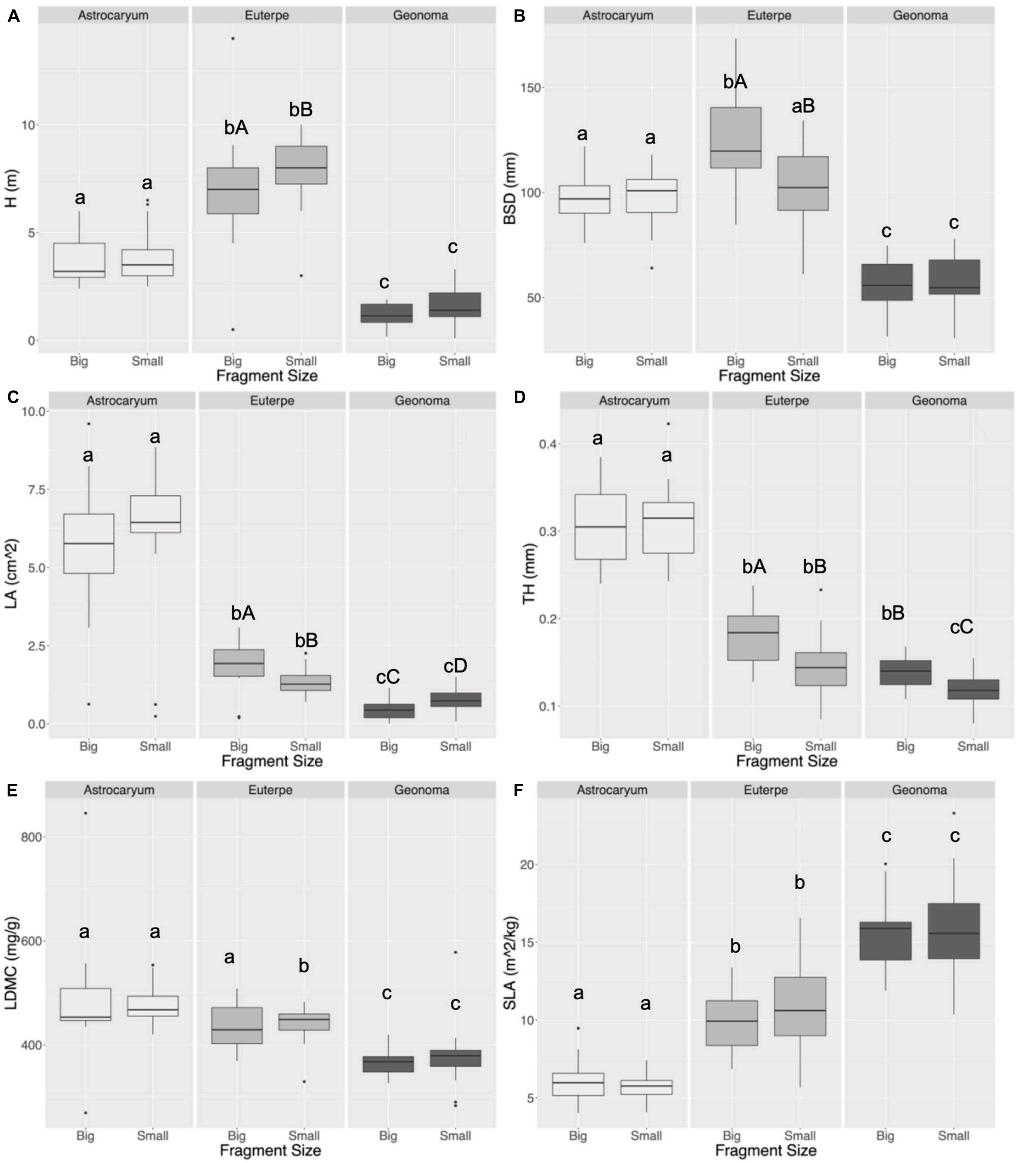

FIGURE 2 | (Continued)

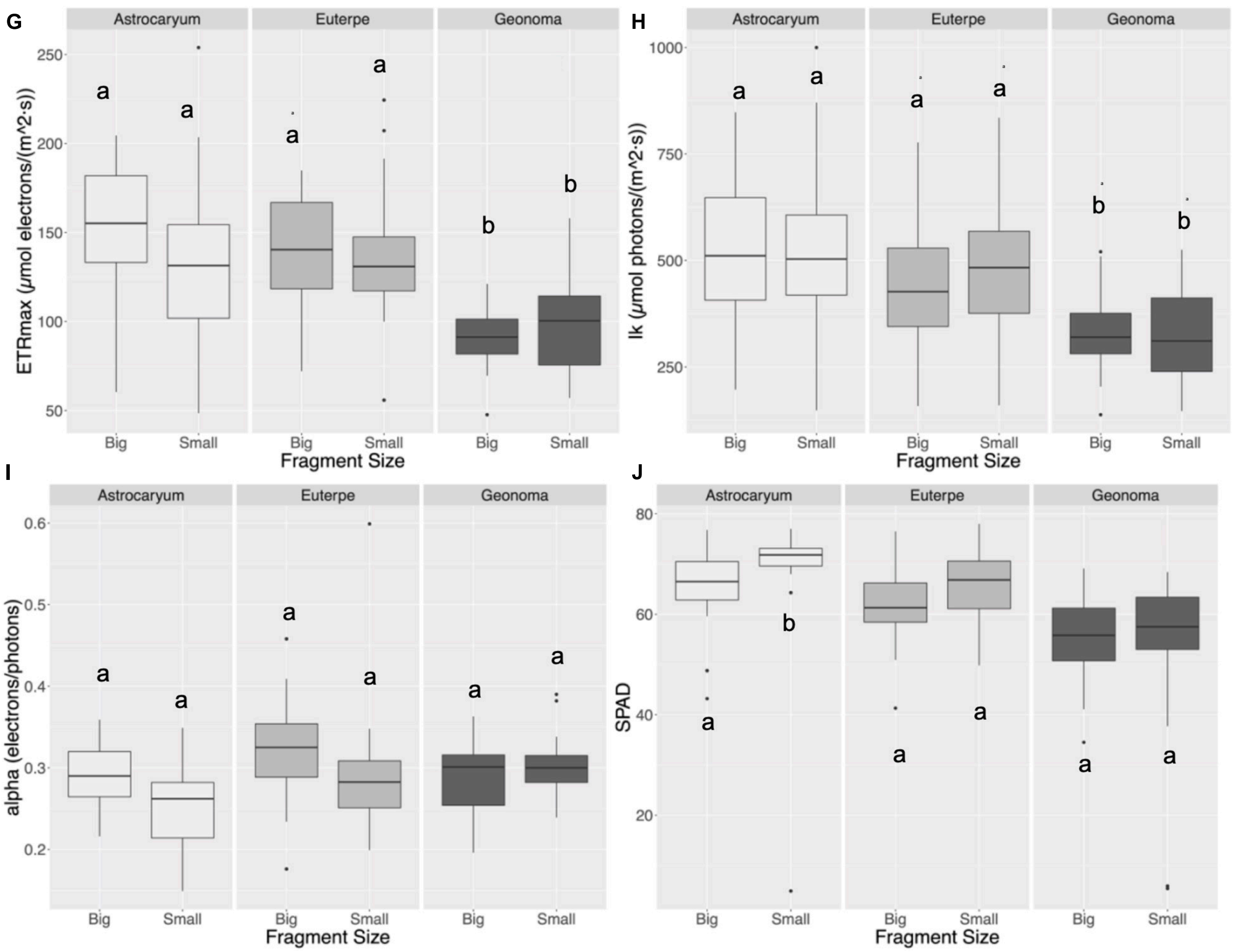

FIGURE 2 | Functional traits measured for each palm species in large and small fragments: height (H, cm – **A**), basal stem diameter (BSD, mm – **B**), leaf area (LA, cm^2 – **C**), leaf thickness (TH, mm – **D**), and leaf dry matter content (LDMC, $mg{\cdot}g^{-1}$ – **E**), specific leaf area (SLA, $m^2{\cdot}kg^{-1}$ – **F**). We used rapid light curves (RLC) to measure the present state of photosynthesis using a PAM-2500 Portable Chlorophyll Fluorometer (Waltz). RLC provide the key parameter α (alpha, electrons/photons – **I**), which represents the initial slope of RLC related to the quantum efficiency of photosynthesis, maximum electron transport rate [ETRmax, μmol electrons/($m^2{\cdot}s$) – **G**], and I_K, [μmol photons/($m^2{\cdot}s$) – **H**], which refers to the minimum saturating irradiance and chlorophyll concentration (SPAD – **J**). The bootstrap confidence intervals were calculated for mean difference, lowercase letters indicate differences in the mean value of the attribute between species, and capital letters indicate differences between fragments.

and wide geographical distribution as *E. edulis*. This trend has potentially severe ecological and ecosystem consequences (Cerqueira et al., 2021).

As aforementioned, *G. schottiana* was more affected demographically by habitat reduction than the other two palms in our study. Seedling survival was much lower compared with the other two species, and negative growth of juveniles was much higher in small fragments in both monitoring periods. The same intense negative growth was observed in small fragments for *Heliconia acuminata*, a perennial herb native to central Amazonia (Bruna and Oli, 2005). The population of *G. schottiana* in small fragments was decreasing in size in the second monitoring period, a trend that seemed to be directly related to a reduction in rainfall, which amounted to 3,472 mm in 2005, 2,664 mm in 2006, and 2,271 mm in 2007. The effects of rainfall reductions could be more pronounced in small fragments because it tends to be drier due to edge effects (Laurance et al., 2002). As Braz et al. (2016) stated that *Geonoma* seeds are sensitive to water scarcity, this might explain the lower seedling survival rate. However, in a climate change scenario, *Geonoma* may not be endangered in small forest fragments, as an increase in precipitation and temperature is predicted for southeastern Brazil over the coming decades (Vale et al., 2021), along with a probable decrease in the duration of dry spells (Nunes et al., 2018). However, uncertainty on the occurrence of extreme rainfall events may not be ruled out (Zilli et al., 2017).

It seems evident that forest-interior species such as *G. schottiana* are more affected by habitat loss and forest fragmentation. In contrast, *E. edulis*, an endangered species, and *A. aculeatissimum*, an endemic species of the Atlantic Forest, may be favored by their higher capacity to use higher light intensities due to their higher ETR and Ik, which may explain the occurrence of persistent populations (stable lambda) in small forest fragments. The size of the fragments analyzed in our study represents the size of the majority of fragments in the Atlantic Forest (more than 80% of the fragments are <50 ha; Ribeiro et al., 2009). Souza and Prevedello (2020) studied the density and demography of *E. edulis* and found that protected areas may be crucial for the long-term conservation of overexploited plants. Mendes and Portela (2020) presented empirical data on the importance of small populations in very small forest fragments, even with few adults/ha. Demographic data collected over 15 years (2005–2019) from three small Atlantic Rainforest fragments showed that all *E. edulis* populations were demographically viable. Volenec and Dobson (2020) synthesized results of existing empirical studies on the contribution of individual small reserves to biodiversity conservation across taxa and ecosystems. They found that small reserves and fragments may provide a significant contribution to maintain matrix quality in the landscape, as they can harbor significant portions of regional biodiversity. As mentioned, small fragments represent the majority of Atlantic Forest habitat left, and may be essential to maintain viable populations in areas of high human disturbance. Small populations scattered in a highly fragmented landscape might constitute a metapopulation that can help maintain viable genetic populations, therefore deserving attention and conservation efforts.

CONCLUSION

Differences in ecophysiological performance due to distinct morpho-physiological functional traits related to leaf economic spectrum, such as LDMC or SLA and to photosynthetic responses to light environment as ETR and Ik were linked to the demographic variation of palms in forest remnants with different characteristics. *G. schottiana* was demographically affected by habitat reduction (lower fitness in small fragments). Given the species morphological and physiological traits, it should be classified as a low disturbance forest interior species. *E. edulis* was also affected by the size of the fragment, but due to a disruptive interaction with a predator and showed intermediate functional traits values. On the other hand, *A. aculeatissimum* were not demographically affected by forest remnant size, which is probably due to higher photosynthetic capacity as well as other morphological characteristics related to a conservative use of resources in addition to the capacity for shade tolerance. We highlight the importance of considering small Atlantic Forest fragments in private properties for biodiversity conservation efforts, as they contribute to the maintenance of populations with different morpho-physiological functional traits and demographic behavior on a landscape scale. Conserving these small habitats is possible to conserve different life-histories, even for close related species.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

RP, SC-T, and EM conceived this study, collected the data, and wrote the manuscript. RP and SC-T analyzed the data. All authors contributed to the article and approved the submitted version.

FUNDING

Financial support was provided by FAPESP (Proc. No. 2005/60788-4) and CAPES fellowship to RP and SC-T.

ACKNOWLEDGMENTS

We thank Eraldo dos Santos Almeida, Adilson Pintor, and Antonio Tavares de Oliveira for help in the field. We are grateful to ICMBIO for permission to work in their protected areas and to private landowners for permission to work in the fragments. We also would like to thanks the reviewers comments that improved the manuscript.

REFERENCES

Ackerly, D. D., and Cornwell, W. K. (2007). A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecol. Lett.* 10, 135–145. doi: 10.1111/j.1461-0248.2006.01006.x

Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S., Ray-mukherjee, J., Mbeau-Ache, C., et al. (2014). Functional traits explain variation in plant life history strategies. *Proc. Natl. Acad. Sci. U.S.A.* 111, 740–745. doi: 10.1073/pnas.1410430111

Arroyo-Rodríguez, V., Aguirre, A., Benítez-Malvido, J., and Mandujano, S. (2007). Impact of rain forest fragmentation on the population size of a structurally important palm species: *Astrocaryum mexicanum* at Los Tuxtlas, Mexico. *Biol. Conserv.* 138, 198–206. doi: 10.1016/j.biocon.2007.04.016

Benchimol, M., Talora, D. C., Mariano-Neto, E., Oliveira, T. L. S., Leal, A., Mielke, M. S., et al. (2016). Losing our palms: the influence of landscape-scale deforestation on *Arecaceae* diversity in the Atlantic forest. *For. Ecol. Manag.* 384, 314–322. doi: 10.1016/j.foreco.2016.11.014

Braz, M. I. G., Moura, R. M., Portela, R. C. Q., and de Mattos, E. A. (2016). Ample germination ability under wide-ranging environmental conditions in a common understory tropical palm. *Plant Species Biol.* 31, 211–218. doi: 10.1111/1442-1984.12104

Bruna, E. M., and Oli, M. K. (2005). Demographic effects of habitat fragmentation on a tropical herb: life-table response experiments. *Ecology* 86, 1816–1824. doi: 10.1890/04-1716

Caswell, H. (2001). *Matrix Population Model: Construction, Analysis and Interpretation*, 2nd Edn. Sunderland, MA: Sinauer Associates, 722.

Carvalho, F. A. (2005). *Efeitos da Fragmentação Florestal na Florística e Estrutura da Mata Atlântica Submontana de Região de Imbaú, Município de Silva Jardim, RJ.* Ph.D. thesis. Campos dos Goytacazes, BR: Universidade Estadual no Norte Fluminense Darcy Ribeiro. doi: 10.1590/S0102-33062006000300022

Cavender-Bares, J. A., and Bazzaz, F. (2008). "From leaves to ecosystems: using chlorophyll fluorescence to assess photosynthesis and plant function in ecological studies," in *Chlorophyll a Fluorescence. Advances in Photosynthesis and Respiration*, Vol. 19, eds G. Papageorgiou and C. Govindjee (Dordrecht: Springer), 737–755. doi: 10.1007/978-1-4020-3218-9_29

Cerqueira, A. F., Rocha-Santos, L., Benchimol, M., and Mielke, M. S. (2021). Habitat loss and canopy openness mediate leaf trait plasticity of an endangered palm in the Brazilian Atlantic Forest. *Oecologia* 196, 619–631. doi: 10.1007/s00442-021-04879-x

Chazdon, R. L. (1985). Leaf display, canopy structure, and light interception of two understory palm species. *Am. J. Bot.* 72, 1493–1502. doi: 10.2307/2443299

De Bello, F., Vandewalle, M., Reitalu, T., Lepš, J., Prentice, H. C., Lavorel, S., et al. (2013). Evidence for scale- and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. *J. Ecol.* 101, 1237–1244. doi: 10.1111/1365-2745.12139

Dupré, C., and Ehrlén, J. (2002). Habitat configuration, species traits and plant distributions. *J. Ecol.* 90, 796–805. doi: 10.1046/j.1365-2745.2002.00717.x

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34, 487–515. doi: 10.1146/annurev.ecolsys.34.011802.132419

Fahrig, L. (2013). Rethinking patch size and isolation effects: the habitat amount hypothesis. *J. Biogeogr.* 40, 1649–1663. doi: 10.1111/jbi.12130

Fantini, A. C., and Guries, R. (2007). Forest structure and productivity of palmiteiro (Euterpe edulis Martius) in the Brazilian Mata Atlântica. *For. Ecol. Manag.* 242, 185–194.

Figueroa, F. L., Jerez, C. G., and Korbee, N. (2013). Use of in vivo chlorophyll fluorescence to estimate photosynthetic activity and biomass productivity in microalgae grown in different culture systems. *Lat. Am. J. Aquat. Res* 41, 801–819. doi: 10.3856/vol41-issue5-fulltext-1

Franco, M., and Silvertown, J. (2004). A comparative demography of plants based upon elasticities of vital rates. *Ecology* 85, 531–538. doi: 10.1890/02-0651

Galetti, M., and Aleixo, A. (1998). Effects of palm heart harvesting on avian frugivores in the Atlantic rain forest of Brazil. *J. Appl. Ecol.* 35, 286–293.

Gaiotto, F. A., Grattapaglia, D., and Vencovsky, R. (2003). Genetic structure, mating system and long-distance gene flow in *Euterpe edulis* mart. *J. Hered.* 94, 399–406. doi: 10.1093/jhered/esg087

Gatti, M. G., Campanello, P. I., and Goldstein, G. (2011). Growth and leaf production in the tropical palm *Euterpe edulis*: light conditions versus developmental constraints. *Flora Morphol. Distrib. Funct. Ecol. Plants* 206, 742–748. doi: 10.1016/j.flora.2011.04.004

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., et al. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1:e1500052. doi: 10.1126/sciadv.1500052

Henderson, A., Galeano, G., and Bernal, R. (1995). *Field Guide to the Palms of the Americas*. Princeton, NJ: Princeton University Press.

Horvitz, C. C., and Schemske, D. W. (1995). Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. *Ecol. Monogr.* 65:155. doi: 10.2307/2937136

Ibáñez, I., Katz, D. S. W., Peltier, D., Wolf, S. M., and Connor Barrie, B. T. (2014). Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess-multiresponse dynamics. *J. Ecol.* 102, 882–895. doi: 10.1111/1365-2745.12223

IBGE (2012). *Manual de Classificação da Vegetação Brasileira. Coordenação de Recursos Naturais e Estudos Ambientais. Série Secundária: Manuais técnicos em geociências*. Brasil: IBGE.

Laughlin, D. C., Gremer, J. R., Adler, P. B., Mitchell, R. M., and Moore, M. M. (2020). The net effect of functional traits on fitness. *Trends Ecol. Evol.* 35, 1037–1047. doi: 10.1016/j.tree.2020.07.010

Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., et al. (2002). Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conserv. Biol.* 16, 605–618. doi: 10.1046/j.1523-1739.2002.01025.x

Li, Z. R., Wakao, S., Fischer, B. B., and Niyogi, K. K. (2019). Sensing and responding to excess light. *Annu. Rev. Plant Biol.* 60, 239–260. doi: 10.1146/annurev.arplant.58.032806.103844

Liu, J., Coomes, D. A., Gibson, L., Hu, G., Liu, J., Luo, Y., et al. (2019). Forest fragmentation in China and its effect on biodiversity. *Biol. Rev.* 94, 1636–1657. doi: 10.1111/brv.12519

Lorenzi, H., Souza, H. M., Medeiros-Costa, J. T., Cerqueira, L. S. C., and Ferreira, E. (2004). *Palmeiras Brasileiras e Exóticas Cultivadas*. Nova Odessa: Plantarum.

May, F., Giladi, I., Ristow, M., Ziv, Y., and Jeltsch, F. (2013). Plant functional traits and community assembly along interacting gradients of productivity and fragmentation. *Perspect. Plant Ecol. Evol. Syst.* 15, 304–318. doi: 10.1016/j.ppees.2013.08.002

Mendes, E. T. B., and Portela, R. C. Q. (2020). Comments on "the importance of protected areas for overexploited plants: evidence from a biodiversity hotspot". souza and prevedello 2020. *Biol. Conserv.* 243:108482. doi: 10.1016/j.biocon.2020.108617

Messier, J., McGill, B. J., Enquist, B. J., and Lechowicz, M. J. (2016). Trait variation and integration across scales: Is the leaf economic spectrum present at local scales? *Ecography* 13, 685–697. doi: 10.1111/ecog.02006

Nunes, L. H., Greco, R., and Marengo, J. A. (2018). *Climate Change in Santos Brazil: Projections, Impacts and Adaptation Options*. Berlin: Springer. doi: 10.1007/978-3-319-96535-2

Poorter, L. (2009). Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests. *New Phytol.* 181, 890–900. doi: 10.1111/j.1469-8137.2008.02715.x

Poorter, L., and Bongers, F. (2006). Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* 87, 1733–1743. doi: 10.1890/0012-9658(2006)87[1733:LTAGPO]2.0.CO;2

Portela, R. C. Q., Bruna, E. M., and Santos, F. A. M. (2010). Demography of palm species in Brazil's Atlantic forest: a comparison of harvested and unharvested species using matrix models. *Biodivers. Conserv.* 19, 2389–2403. doi: 10.1007/s10531-010-9846-5

Portela, R. C. Q., and Dirzo, R. (2020). Forest fragmentation and defaunation drive an unusual ecological cascade: predation release, monkey population outburst and plant demographic collapse. *Biol. Conserv.* 252:108852. doi: 10.1016/j.biocon.2020.108852

R Development Core Team (2015). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., and Hirota, M. M. (2009). The Brazilian Atlantic forest: how much is left, and how is the remaining forest dis- tributed? Implications for conservation. *Biol. Conserv.* 142, 1141–1153. doi: 10.1016/j.biocon.2009.02.021

Rüder, N., Comita, L. S., Condit, R., Purves, D., Rosenbaum, B., Visser, M. D., et al. (2018). Beyond the fast-slow continuum: demographic dimensions structuring a tropical tree community. *Ecol. Lett.* 21, 1075–1084. doi: 10.1111/ele.12974

Schumann, T., Paul, S., Melzer, M., Dörmann, P., and Jahns, P. (2017). Plant growth under natural light conditions provides highly flexible short-term acclimation properties toward high light stress. *Front. Plant Sci.* 8:681. doi: 10.3389/fpls.2017.00681

Silva-Matos, D. M., Freckleton, R. P., and Watkinson, A. R. (1999). The role of density dependence in the population dynamics of a tropical palm. *Ecology* 80, 2635–2650. doi: 10.1111/nph.15107

Silva-Matos, D. M., and Watkinson, A. R. (1998). The fecundity, seed and seedling ecology of the edible palm *Euterpe edulis* in south-eastern Brazil. *Biotropica* 30, 595–603. doi: 10.1111/j.1744-7429.1998.tb00099.x

Souza, A. C., and Prevedello, J. A. (2020). The importance of protected areas for overexploited plants: evidence from a biodiversity hotspot. *Biol. Conserv.* 243:108482. doi: 10.1016/j.biocon.2020.108482

Souza, A. F., and Martins, F. R. (2004). Population structure and dynamics of a neotropical palm in fire-impacted fragments of the Brazilian Atlantic Forest. *Biodivers. Conserv.* 13, 1611–1632. doi: 10.1023/B:BIOC.0000029326.44647.7f

Stubben, C. J., and Milligan, B. G. (2007). Estimating and analyzing demographic models using the popbio package in R. *J. Stat. Softw.* 22, 1–23. doi: 10.18637/jss.v022.i11

Svenning, J.-C. (2001). On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (Arecaceae). *Bot. Rev.* 67, 1–53. doi: 10.1007/BF02857848

Tabarelli, M., Mantovani, W., and Peres, C. A. (1999). Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biol. Conserv.* 91, 119–127. doi: 10.1016/S0006-3207(99)00085-3

Vale, M. M., Arias, P. A., Ortega, G., Cardoso, M., Oliveira, B. F. A., Loyola, R., et al. (2021). "Climate change and biodiversity in the Atlantic Forest: best climatic models, predicted changes and impacts, and adaptation options," in *The Atlantic Forest: History, Biodiversity, Threats and Opportunities of the Mega-Diverse Forest*, eds M. C. M. Marques and C. E. V. Grelle (Cham: Springer), 253-267. doi: 10.1007/978-3-030-55322-7_12

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., et al. (2007). Let the concept of trait be functional! *Oikos* 116, 882–892. doi: 10.1111/j.2007.0030-1299.15559.x

Volenec, Z. M., and Dobson, A. P. (2020). Conservation value of small reserves. *Conserv. Biol.* 34, 66–79. doi: 10.1111/cobi.13308

Walter, H. (1971). *Ecology of Tropical and Subtropical Vegetation*. Edinburgh: Oliver and Boyd.

Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., and Wright, I. J. (2002). Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* 33, 125–159. doi: 10.1146/annurev.ecolsys.33.010802.150452

Wilson, M. C., Chen, X. Y., Corlett, R. T., Didham, R. K., Ding, P., Holt, R. D., et al. (2016). Habitat fragmentation and biodiversity conservation: key findings and future challenges. *Landsc. Ecol.* 31, 219–227. doi: 10.1007/s10980-015-0312-3

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., et al. (2004). The worldwide leaf economics spectrum. *Nature* 428, 821–827. doi: 10.1038/nature02403

Yang, J., Cao, M., and Swenson, N. G. (2018). Why functional traits do not predict tree demographic rates. *Trends Ecol. Evol.* 33, 326–336.

Zambrano, J., Garzon-Lopez, C. X., Yeager, L., Fortunel, C., Cordeiro, N. J., and Beckman, N. G. (2019). The effects of habitat loss and fragmentation on plant functional traits and functional diversity: what do we know so far? *Oecologia* 191, 505–518. doi: 10.1007/s00442-019-04505-x

Zilli, M. T., Carvalho, L. M. V., Liebmann, B., and Dias, M. A. S. (2017). A comprehensive analysis of trends in extreme precipitation over southeastern coast Brazil. *Int. J. Climatol.* 37, 2269–2279. doi: 10.1002/joc.4840

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.