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## Is there variation in ten woody species reproductive phenology within the Atlantic Forest biodiversity hotspot?

Vanessa Danielle Magalhães <sup>a</sup>, Renato A. Ferreira de Lima <sup>b</sup> and Klécia Gili Massi <sup>c</sup>

<sup>a</sup>Centro de Tecnologia das Radiações, Instituto de Pesquisas Energéticas e Nucleares, Lineu Prestes, Butantã, São Paulo, Brazil;

<sup>b</sup>Departamento de Ciências Biológicas, ESALQ, Universidade de São Paulo, Piracicaba, Brazil; <sup>c</sup>Departamento de Engenharia Ambiental, Instituto de Ciência e Tecnologia, Universidade Estadual “Júlio de Mesquita Filho”, São José dos Campos, Brazil

### ABSTRACT

Understanding reproductive phenology in tropical and subtropical forests is challenging. Thus, there are scarce large-scale phenological studies for those forests. Digitized herbarium collections can provide valuable information for understanding biological rhythms, e.g. timing of reproduction. Our aim was to verify the geographical variability of flowering and fruiting patterns and the effects of local climate on the reproductive phenology of woody species in the Atlantic Forest biodiversity hotspot. We used herbarium records compiled from the Global Biodiversity Information Facility – GBIF, speciesLink, JABOT, and the “Portal de Datos de Biodiversidad Argentina” as a main source of data to assess differences in reproductive phenology for 10 species with wide geographical distribution in the Atlantic Forest. Contrary to our expectations, we observed a non-seasonal reproductive phenology of all species and relations with temperature in the northern forests and to precipitation in the southern forests. When considered individually, there was no obvious relationship between phenophases and climatic factors. We expected that species occurring in a broad geographic distribution would change their biological rhythms related to local environmental factors, but it is likely that widely distributed species are abundant exactly because they are less dependent on biophysical characteristics of the environment. This is the first study comparing species located in the northern and southern regions of the Atlantic Forest using herbarium data, highlighting its importance to understand large scale ecological rhythms in tropical biomes.

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scale phenology; tropical  
rainforest



### Introduction


Phenology can be defined as the study of timing of recurring biological events, including its biotic and abiotic drivers (Howe and Smallwood 1982). Studies on reproductive phenology are mainly based on data from local, short-term studies, generally spanning between one and three years long (Fava et al. 2019). There is a lack of long-term, large-scale phenological studies, particularly for tropical and subtropical forests. The use of digitized herbarium data has great potential to expand phenological research for tropical plants (Davis et al. 2022). In Brazil, Fava et al. (2019) is an example of such an approach for the Brazilian Savanna.

In the Brazilian Atlantic Forest, many biogeographical studies revealed spatial variations in plant species distribution (Neto et al. 2015; Bacci et al. 2020; Peres et al. 2020), but phenological studies on a broad geographical scale are scarce (Zalamea et al. 2011). Filling this gap could help to improve large-scale distribution models of tropical woody species, to understand phenological sensitivity to climate change and to support the potential use of non-timber forest products, such as the production of seeds and fruits.

Biological collections, such as herbaria, are essential for studying biodiversity (Graham et al. 2004; Lima et al. 2021), representing the main source of plant species records currently available. Many herbaria have electronic databases available online, and these records have been widely used for macroecology, biogeography and conservation (Graham et al. 2004; Dauby et al. 2017; Lima et al. 2020; Davis et al. 2022). However, the herbarium data also have an untapped potential to provide more information beyond species occurrences, including valuable information on plant species phenology that can be used to assess species reproductive patterns at large geographical scales (Borchert 1996; Zalamea et al. 2011; Mendoza et al. 2017; Meineke et al. 2018; Fava et al. 2019; Lima et al. 2021). Different from temperate regions, where there are studies using phenological data from digitized herbarium, similar analyses have still to be performed for tropical regions (Davis et al. 2022). Two recent studies have focused only on species in the Brazilian Cerrado (Fava et al. 2019; Lima et al. 2021) and in the Atlantic Forest (Lima et al. 2021).

Species occurring in broad geographic distribution might change their ecological processes and biological

**CONTACT** Vanessa Danielle Magalhães  [van.biologa@gmail.com](mailto:van.biologa@gmail.com)  Centro de Tecnologia das Radiações, Instituto de Pesquisas Energéticas e Nucleares, - Avenida Professor Lineu Prestes, 2242, Butantã, São Paulo, Brazil - 05508-000

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rhythms related to local environmental factors, such as temperature and precipitation (Begon et al. 2006). Some studies on the timing of plant reproduction in Brazilian ecosystems have found this timing to be phylogenetically conserved (Davies et al. 2013; Staggemeier et al. 2015; Brito et al. 2017; Oliveira et al. 2022). i.e. species living in sites with different environments exhibit the same phenological patterns. Although information on phenological changes related to climate variations for isolated or for a few species is available in tropical ecosystems (Fava et al. 2019; Lima et al. 2021; Pedroso et al. 2021), analyses using multiple species at large spatial scales are rare, thus highlighting the importance of this study. Studies comparing the phenology of different forest successional stages and of restored sites in the Atlantic Forest, which are related to alterations in environmental factors, showed that forest stages present remarkably similar patterns of phenology (Cruz-Neto et al. 2018; Cardoso et al. 2019).

To improve our understanding of plant species phenological dynamics in the Atlantic Forest biodiversity hotspot, we used herbarium collections to examine broad scale phenological patterns, focusing on woody species of the Atlantic Forest. Our aim was to examine the geographical variability of flowering and fruiting and to test the effects of local climate on reproductive phenology between species occurring in the Northeastern and South-Southeastern regions of the Atlantic Forest. Since there is a north/south split in the Atlantic Forest flora (Neto et al. 2015; Bacci et al. 2020) we expected variability in reproductive phenology between these regions, due to their climatic differences (Alvares et al. 2013).

## Materials and methods

### Study site

The Atlantic Forest biome, a biodiversity hotspot (Myers et al. 2000), originally covered an area equivalent to 1,315,460 km<sup>2</sup> mainly along the Brazilian coast (IBGE 2012), including parts of Paraguay and Argentina. Due to intense deforestation and human disturbance that mostly occurred in the first half of the nineteenth century (Dean 1996), only about 13% of Atlantic Forest native vegetation cover remains in Brazil (Fundação SOS Mata Atlântica/INPE 2018). Nature reserves protect only 9% of the remaining forest (Ribeiro et al. 2009). This forest is home to about 5% of the world flora and 2% of the endemic vascular plants (Stehmann et al. 2009), and in Brazil is divided, by the Conde Gap located at 11° 48' S and 37° 37' W, into the Northeastern and Southeastern floristic regions (Neto et al. 2015). The Atlantic Forest biome has many different plant physiognomies, including

evergreen and seasonal forests, mangroves, and highland grasslands (mma.gov.br), which may be related to different regional environmental parameters, such as soil types, altitude, salinity, among others.

### Herbarium records

As a starting point, we used the same herbarium dataset used by Lima et al. (2020), which corresponded to millions of herbarium records for the Atlantic Forest woody flora, obtained from the Global Biodiversity Information Facility (GBIF.org GBIF Occurrence Download 2019), speciesLink (<https://specieslink.net>), JABOT (<http://jabot.jbrj.gov.br>), and the “Portal de Datos de Biodiversidad Argentina” (<https://datos.sndb.mincyt.gob.ar>). These records were confirmed by specialists, cleaned and validated as described in Lima et al. (2020), which included the removal of duplicated specimens across herbaria, invalid geographical coordinates, duplicated geographical coordinates and spatial outliers within species. These procedures were implemented using the workflow and tools which are currently available in the “plantR” R package (Lima et al. 2021).

We filtered this initial dataset of records by selecting only those containing in the Darwin Core fields “occurrenceRemarks” or “notes” the words “flower” or “fruit” - or their variations, e.g. inflorescence and infructescence, both in English and in Portuguese/Spanish. This filtering aimed to select only those records where the collector described the presence of flowers or fruits. Next, we performed a second filter to retain only those records with at least the information on the collection year and month. Finally, we selected only species that had more than 10 records with flowers and fruits in each of the Northeast and South-Southeast regions of the Atlantic Forest, which is the suggested minimum number of records for tropical woody species according to Fournier (1974). The selection of species with more than 10 records reduces the chances of miscalculating the phenological timing of species, which include different developmental stages, such as green to ripe fruits.

Ten species passed these three filters of all records available for the Atlantic Forest woody flora (Table 1). For all records of these species (a total of 2077 valid records), we retained the information on the date of collection (day, month, and year), the phenological phase (flower or fruit), and the validated geographical coordinates. Records refer to 127 years of plant collections (from 1892 to 2019) and spread out through Brazil (as we see in Supplementary Material 1).

**Table 1.** List of studied species, life-forms and number of observations of flowering (FL) and fruiting (FR) in the Atlantic Forest in northeast (N) and south-southeast (S), Brazil (total of 2077 valid records).

Family	Species	Life-form	FL in N	FR in N	FL in S	FR in S
Fabaceae	<i>Andira fraxinifolia</i> Benth	Tree	42	52	65	54
	<i>Chamaecrista ensiformis</i> (Vell.) H.S.Irwin & Barneby	Tree/Shrub	44	24	18	14
	<i>Inga laurina</i> (Sw.) Willd.	Tree	62	51	35	19
	<i>Pterocarpus rohrii</i> Vahl	Tree	14	10	26	12
Malpighiaceae	<i>Byrsonima sericea</i> DC.	Tree	155	105	29	17
Meliaceae	<i>Guarea guidonia</i> (L.) Sleumer	Tree	25	39	17	28
Myrtaceae	<i>Myrcia splendens</i> (Sw.) DC.	Tree	173	170	169	100
	<i>Myrcia tomentosa</i> (Aubl.) DC.	Tree	35	37	26	25
Rutaceae	<i>Psidium guineense</i> Sw.	Shrub	48	58	26	18
	<i>Esenbeckia grandiflora</i> Mart.	Shrub	24	64	33	114

### Climatic data

We extracted mean monthly temperature and precipitation data based on the validated geographical coordinates of each species recorded from maps provided by Alvares et al. (2013, 2015), both at ~100 m resolution, and then we calculated an average value for each region (Northeastern and South-Southeastern). These two climate variables are taken as the best ones to predict phenological variations (e.g. Araye et al. 2022). Temperature in the Northeast and South-Southeast regions had similar seasonality (warmer summers: from December to March and colder winters: June to August), but with higher temperatures in the Northeast region (Figure 1). Precipitation in the South-Southeast region was more seasonal (wetter period from October to March and drier from May to September) than in the Northeast region (which was more homogeneously distributed throughout the year) (Figure 1).

### Data analyses

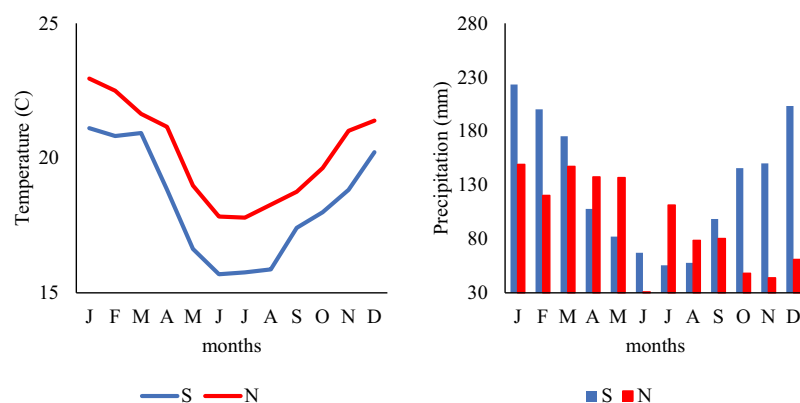
To test for flowering and fruiting seasonality, i.e. non-random distribution of the phenophases throughout the year, we applied Hermans–Rassons test. The flowering and fruiting patterns of the Atlantic Forest in the Northeast and South-Southeast regions were compared by performing a two-sample Watson–Williams

test (W), which analyzed whether species exhibited similar seasonality in both regions. Relationships (not causes) between the proportion of flowering and fruiting registers and the monthly average temperature and monthly total precipitation were calculated using multiple linear regression equations between phenological records and monthly average temperature and monthly total precipitation for species individually and for all species together. All data analyses were conducted using the StatCirc package in R software (R Development Core Team 2019).

### Results

Overall, we found that flowering and fruiting of all species combined were non-seasonal (Table 2 and Supplementary Material 2). Flowering and fruiting of species in the Northeast region did not relate to precipitation, but they were related to monthly temperature (Supplementary Material 3). On the contrary, flowering and fruiting of species in the South-Southeast region of the Atlantic Forest were related to precipitation, while fruiting was also related to temperature and precipitation (Supplementary Material 3).

When we considered species individually, we found that for most species reproductive timing was non-seasonal in both regions of the Atlantic Forest for 17 of 40 (42.5%) of the evaluated phenophases (Table 2 and



**Figure 1.** Mean monthly temperature (left, in Celsius degrees) and annual precipitation (right, in mm) along the year in the Atlantic Forest in northeast (N, red) and south-southeast (S, blue), Brazil. Mean monthly temperature and precipitation refers to average values for each species and region (depending on the number of observations).

**Table 2.** Hermans-rassons-test (T) and P-value (P) for flowering (FL) and fruiting (FR) seasonality of studied species in the Atlantic Forest in northeast (N) and south-southeast (S), Brazil (total of 2077 valid records). Significant relationships ( $p < 0.05$ ) are indicated in bold.

Family	Species	FL in N	FR in N	FL in S	FR in S
-	All	$T = 4.265, p = 0.253$	$T = 2.873, p = 0.554$	$T = 4.263, p = 0.250$	$T = 3.173, p = 0.478$
Fabaceae	<i>Andira fraxinifolia</i>	$T = 2.560, p = 0.647$	$T = 4.254, p = 0.255$	$T = 6.698, \mathbf{P = 0.050}$	$T = 4.808, p = 0.184$
	<i>Chamaecrista ensiformis</i>	$T = 4.643, p = 0.202$	$T = 20.178, \mathbf{P < 0.001}$	$T = 8.407, \mathbf{P = 0.014}$	$T = 10.931, \mathbf{P = 0.002}$
	<i>Inga laurina</i>	$T = 0.897, p = 0.172$	$T = 5.182, p = 0.138$	$T = 4.952, p = 0.162$	$T = 7.074, \mathbf{P = 0.039}$
	<i>Pterocarpus rohrii</i>	$T = 8.723, \mathbf{P = 0.012}$	$T = 9.683, \mathbf{P = 0.005}$	$T = 5.632, p = 0.101$	$T = 12.398, \mathbf{P < 0.001}$
Malpighiaceae	<i>Byrsonima sericea</i>	$T = 2.974, p = 0.516$	$T = 1.802, p = 0.851$	$T = 9.003, \mathbf{P = 0.010}$	$T = 14.487, p < 0.001$
Meliaceae	<i>Guarea guidonia</i>	$T = 4.954, p = 0.167$	$T = 4.531, p = 0.205$	$T = 18.541, \mathbf{P < 0.001}$	$T = 3.893, p = 0.319$
	<i>Myrcia splendens</i>	$T = 2.790, p = 0.578$	$T = 5.052, p = 0.154$	$T = 3.835, p = 0.328$	$T = 2.036, p = 0.791$
Myrtaceae	<i>Myrcia tomentosa</i>	$T = 12.688, \mathbf{P < 0.001}$	$T = 9.624, \mathbf{P = 0.006}$	$T = 20.909, \mathbf{P < 0.001}$	$T = 6.896, \mathbf{P = 0.046}$
	<i>Psidium guineense</i>	$T = 3.864, p = 0.312$	$T = 5.917, p = 0.086$	$T = 6.254, p = 0.070$	$T = 8.433, \mathbf{P = 0.014}$
Rutaceae	<i>Esenbeckia grandiflora</i>	$T = 12.500, \mathbf{P < 0.001}$	$T = 5.007, p = 0.162$	$T = 13.742, \mathbf{P < 0.001}$	$T = 1.957, p = 0.804$

Supplementary Material 2). Despite that, six species had seasonal flowering (*A. fraxinifolia*, *B. sericea*, *C. ensiformis*, *E. grandiflora*, *G. guidonia*, *M. tomentosa*) and five had seasonal fruiting (*C. ensiformis*, *B. sericea*, *I. laurina*, *M. tomentosa*, *P. guineense* and *P. rohrii*) in the forests of South-Southeast region. Only the flowering of *E. grandiflora*, *M. tomentosa* and *P. rohrii* and fruiting of *C. ensiformis*, *M. tomentosa* and *P. rohrii* were seasonal in Northeast Atlantic Forests.

The flowering and fruiting timing for most species was similar in the South-Southeast and Northeast regions of the Atlantic Forest for 14 of 20 (70%) of the evaluated phenophases (Table 3 and Supplementary Material 2). The main exceptions were flowering of *B. sericea* and *M. tomentosa* (earlier in the south for both species) and fruiting of *C. ensiformis*, *I. laurina*, *B. sericea* and *P. guineense*, (earlier and/or longer in the south for all species) which had different timings between regions (Table 3 and Supplementary Material 2).

In the Northeast region, seven species had at least one of their phenophases influenced by temperature, while in the South-Southeast there were six species. As for precipitation, five and six species in the Northeast and South-Southeast regions, respectively, showed at least one phenophase influenced by it (Supplementary Material 3). Seven species were affected by temperature in the Northeast region, and in two species both phenophases were influenced, totaling nine phenophases. *Inga laurina* was a species with reproductive phenophases more related to climate. Flowering and fruiting of three species (*Guarea guidonia* and *Pterocarpus rohrii*) did not correlate with any climatic parameters. Flowering of *Chamaecrista ensiformis* and *Inga laurina* and fruiting of *Myrcia splendens* and *Myrcia tomentosa* were affected by temperature both in the Northeast and South-Southeast regions of the Atlantic Forest. Finally, the flowering of *Esenbeckia grandiflora* was associated with precipitation both in the north and south latitudes (Supplementary Material 3).

**Table 3.** Watson-test (W) and P-value (P) for flowering and fruiting of studied species compared between the Atlantic Forest in northeast and South-Southeast, Brazil (total of 2077 valid records). Significant relationships ( $p < 0.05$ ) are indicated in bold.

Species	Flowering	Fruiting
All	$W = 0.127, p > 0.10$	$W = 0.068, p > 0.10$
<i>Andira fraxinifolia</i>	$W = 0.088, p > 0.10$	$W = 0.136, p > 0.10$
<i>Chamaecrista ensiformis</i>	$W = 0.138, p > 0.10$	$W = 0.338, \mathbf{P < 0.01}$
<i>Inga laurina</i>	$W = 0.138, p > 0.10$	$W = 0.201, \mathbf{P < 0.05}$
<i>Pterocarpus rohrii</i>	$W = 0.062, p > 0.10$	$W = 0.127, p > 0.10$
<i>Byrsonima sericea</i>	$W = 0.194, \mathbf{P < 0.05}$	$W = 0.340, \mathbf{P < 0.01}$
<i>Guarea guidonia</i>	$W = 0.142, p > 0.10$	$W = 0.072, p > 0.10$
<i>Myrcia splendens</i>	$W = 0.067, p > 0.10$	$W = 0.097, p > 0.10$
<i>Myrcia tomentosa</i>	$W = 0.235, \mathbf{P < 0.05}$	$W = 0.111, p > 0.10$
<i>Psidium guineense</i>	$W = 0.081, p > 0.10$	$W = 0.392, \mathbf{P < 0.001}$
<i>Esenbeckia grandiflora</i>	$W = 0.124, p > 0.10$	$W = 0.096, p > 0.10$

## Discussion

This study aimed at verifying the geographical variability and the effects of climatic drivers on the reproductive phenology (flowering and fruiting) of 10 widely distributed woody species in the Atlantic Forest. According to Gallinat et al. (2021), the understanding of regional and global-scale phenology has been largely limited, but a new generation of analytical tools and data sources, such as digitized herbarium records, permits investigating patterns and drivers of phenology across large spatial scales, an emerging field called macrophenology. This is the first study of reproductive macrophenology using herbarium data of woody species in the Atlantic Forest, highlighting its importance to understand large scale ecological rhythms in tropical biomes.

When all species were considered together, we observed a non-seasonal reproductive phenology and relations with temperature in the northern forests and to precipitation in the southern forests. When considered individually, there was no obvious relationship between phenophases and climatic factors. However, more phenophases were seasonal in the south than in the north, and that could be explained by the stronger climatic variation observed in the south compared to the north. In another study, flowering and fruiting of four tropical Melastomataceae species occurring in the Atlantic Forest did relate to precipitation and temperature, showing influences of local conditions (Lima et al. 2021).

We expected differences in reproductive phenology of individual species between the Northeast and South-Southeast regions, related to the climate differences between these regions. However, we found that the majority of the woody species studied here did not have a seasonal pattern of flowering and fruiting, i.e. most reproduced during the whole year. Tropical rainforest species have diversified phenological patterns, and one of these known patterns is non-seasonal (Morellato et al. 2013; Staggemeier et al. 2020). The absence of seasonality might be attributed, among other things, to climate homogeneity (Rathcke and Lacey 1985). In the Atlantic Biome, precipitation and temperature are very variable among regions, but our results did not show these variables to be influential on broad-scale phenology, likely because our data reflect average values from records along the gradient.

As a consequence of non-seasonality, if a plant flowers and/or fruits along the year in different sites, then the comparison among them would not show variations. This reproductive similarity, which we observed for most of the studied woody species occurring in the Northeast and South-Southeast regions of the Atlantic Forest, might be genetically conserved. There is evidence for genetic conservatism in traits linked to phenology (Davis et al. 2022). One could argue that within

the Atlantic Forest environmental differentiations are not significant, yet reflecting on similar reproductive timing patterns. However, other studies performed in different Brazilian biomes subjected to distinct climate conditions, showed a similar phenological behavior (Goulart et al. 2005). In addition, climate diagrams of studied Northeast and South-Southeast Atlantic Forest indicate that rainfall is more homogeneously distributed in the Northeast forests than in the South-Southeast ones. In addition, a few species did show variations in reproductive phenology between Northeast and South-Southeast regions, and we observed a time lag (an earlier and sometimes longer flowering and fruiting in the south), possibly attributed to other biotic and abiotic variables.

We expected that this climate variation between regions, especially related to rainfall, would influence the flowering and fruiting of the studied woody species, which we did not verify. Again, as a consequence of non-seasonality, if a plant presents a given phenophase along the year in different sites, then the relation with environmental factors would be non-significant. Despite of that, there were species that exhibited some correlations between phenology and climate (for example *Inga laurina*) and these species should be evaluated in large-scale studies in field conditions. We expected that species occurring in a broad geographic distribution would change their biological rhythms related to local environmental factors, but it is likely that widely distributed species, such as the ones used in this study, are abundant exactly because they are less dependent on biophysical characteristics.

Herbarium collections are still rarely applied in broad scale tropical phenology studies (Fava et al. 2019; Du et al. 2020; Oliveira et al. 2022), however they are an important source of information to investigate the relationships between geographical variation and reproduction of plants (as such as citizen science data), and they might suggest new possibilities to explore tropical phenology. According to Davis et al. (2022) these data are not only lacking for individual species at a single place and time but there are few long term spatially or temporally extensive phenological data from any tropical location. Despite the hundreds of thousands herbarium records initially inspected in this study, we could not include more species in the analyses because of the difficulty in finding enough records with all information needed for the different regions of the Atlantic Forest.

Despite the small number of species passing the methodology filters for addressing responses at the biome scale, reproductive phenology data for tropical forest species are scarce, making this study relevant. In addition, the selected species were present in Northeast and South-Southeast forests (covering more than 1.500.000 km<sup>2</sup>), such a broad geographical range is not commonly found in phenological studies.

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## Disclosure statement

No potential conflict of interest was reported by the author(s).

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## Notes on contributors

**Renato A. Ferreira de Lima** PhD in Ecology, Professor at University of São Paulo, working with plant ecology.

**Klécia Gili Massi** PhD in Ecology, Professor at São Paulo State University, working with restoration and conservation.

**Vanessa Danielle Magalhães** PhD student at University of São Paulo, working with plant extracts with biological effects for the development of biomaterials.

## ORCID

Vanessa Danielle Magalhães  <http://orcid.org/0000-0002-7006-3563>

Renato A. Ferreira de Lima  <http://orcid.org/0000-0002-1048-0138>

Klécia Gili Massi  <http://orcid.org/0000-0003-1823-7965>

## Author contributions

VDM, RAFL and KGM conceived and designed the analysis; RAFL collected data; VDM and KGM performed the analysis; VDM, RAFL and KGM wrote and reviewed the paper.

## Data availability statement

The data that support the findings of this study are available from the corresponding author, VDM, upon reasonable request.

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