

UNIVERSIDADE FEDERAL DE SÃO CARLOS

Pedro Mauricio Pedroso

SECAS CAUSAM MUDANÇAS NA FENOLOGIA REPRODUTIVA DE *SYAGRUS ROMANZOFFIANA*, MAS NÃO ALTERAM A PREDAÇÃO DE SUAS SEMENTES

Sorocaba,

2021

UNIVERSIDADE FEDERAL DE SÃO CARLOS

Pedro Mauricio Pedroso

SECAS CAUSAM MUDANÇAS NA FENOLOGIA REPRODUTIVA *DE SYAGRUS ROMANZOFFIANA*, MAS NÃO ALTERAM A PREDUÇÃO DE SUAS SEMENTES

Trabalho de Conclusão de Curso para obtenção
do título de Bacharel em Ciências Biológicas.

Orientação: Prof. Dr. Alexander V. Christianini

Financiamento: PIBIC/CNPq

Sorocaba,

2021

Pedroso, Pedro M.

Secas causam mudanças na fenologia reprodutiva de *Syagrus romanzoffiana*, mas não alteram a predação de suas sementes / Pedro M. Pedroso -- 2021.
38f.

TCC (Graduação) - Universidade Federal de São Carlos,
campus Sorocaba, Sorocaba

Orientador (a): Alexander V. Christianini

Banca Examinadora: João Augusto Piratelli, Paulo
Henrique Santos A. Camargo

Bibliografia

1. Fenologia reprodutiva. 2. Secas. 3. Predação de
sementes. I. Pedroso, Pedro M.. II. Título.

Ficha catalográfica desenvolvida pela Secretaria Geral de Informática
(SIn)

DADOS FORNECIDOS PELO AUTOR

Bibliotecário responsável: Maria Aparecida de Lourdes Mariano -
CRB/8 6979

Folha de aprovação

Pedro Mauricio Pedroso

"Secas causam mudanças na fenologia reprodutiva de *Syagrus romanzoffiana*, mas não alteram a predação de suas sementes"

Trabalho de Conclusão de Curso

Universidade Federal de São Carlos – Campus Sorocaba

Sorocaba, 17 de Junho de 2021.



Orientador

Prof. Dr. Alexander Vicente Christianini



Membro 1

Prof. Dr. João Augusto Piratelli



Membro 2

Dr. Paulo Henrique Santos A. Camargo

DEDICATÓRIA

Este trabalho é dedicado a Elisabete Mara Pedroso, minha mãe, que desde sempre me deu suporte e apoio através de muito esforço, trabalho e amor.

AGRADECIMENTO

Meu principal agradecimento é ao meu orientador, Alexander V. Christianini, pelas ideias que me cativaram, ajuda em campo e na elaboração e revisão de trabalhos e por todo o acompanhamento desde o início. À Vanessa Mariano pela ajuda em campo e correções em diversos textos. A todos meus colegas de laboratório e amigos que me ajudaram durante as coletas de dados e idas a campo. E ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) pelas bolsas de Iniciação Científica.

RESUMO

PEDROSO, Pedro Mauricio. Secas causam mudanças na fenologia reprodutiva de *Syagrus romanzoffiana*, mas não alteram a predação de suas sementes. 2021. Trabalho de Conclusão de Curso – Universidade Federal de São Carlos, *campus* Sorocaba, Sorocaba, 2021.

A Mata Atlântica é um *hotspot* para biodiversidade e atualmente ocupa uma pequena fração de sua área original. Além dos efeitos de borda causados pela fragmentação do habitat, suas espécies vegetais e animais enfrentam ainda os efeitos das mudanças climáticas. Tais mudanças podem afetar variantes do clima e ocasionar eventos extremos com maior frequência, como as secas. Plantas e animais respondem às variáveis abióticas e tais respostas são importantes para compreender os efeitos das mudanças do clima sob os organismos e em suas interações. As palmeiras são um importante elemento dentro da Mata Atlântica, principalmente porque produzem frutos durante a estação seca do ano quando há menor oferta de recursos para os animais frugívoros. As interações planta-animal podem ser benéficas para as plantas, como a dispersão de sementes, ou negativas, como na predação de sementes. Assim, compreender os fatores que impactam de alguma forma a reprodução de plantas que fornecem recursos para outros organismos é essencial, uma vez que mudanças em características reprodutivas de um organismo podem ser refletidas para outras espécies, como seus predadores. Neste trabalho avaliamos se as secas alteram a fenologia reprodutiva de *Syagrus romanzoffiana*, uma espécie-chave na Mata Atlântica, e se as possíveis alterações têm consequências em cascata para os animais que consomem suas sementes. Os resultados principais indicam que as secas aumentam a quantidade de cachos de frutos imaturos, mas reduz o número de cachos de flores e frutos maduros. As secas também podem atrasar ou adiantar a época de ocorrência destas estruturas. No entanto, tais mudanças não refletem em diferenças nas taxas de predação de *Syagrus romanzoffiana*, cujo principal predador (besouro) não é saciado pelo aumento da produção de sementes, ao contrário do predador vertebrado, os esquilos. Assim, apesar das alterações causadas pela seca na fenologia reprodutiva de *S. romanzoffiana* não são refletidas em seus predadores de sementes.

Palavras-chave: Mata Atlântica. Alterações Climáticas. Seca. ENSO. Saciação do predador. *Syagrus romanzoffiana*.

ABSTRACT

The Atlantic Forest is a biodiversity hotspot and currently occupies a small fraction of its original area. In addition to the edge effects caused by habitat fragmentation, its plant and animal species also face the effects of climate change. Such changes can affect climate variations and cause more frequent extreme events, such as droughts. Plants and animals respond to abiotic variables and such responses are important to understand the effects of climate change on organisms and their interactions. Palm trees are an important element within the Atlantic Forest, mainly because they produce fruit during the dry season of the year when there is less supply of resources for fruit-eating animals. Plant-animal interactions can be beneficial to plants, such as seed dispersal, or negative, such as seed predation. Thus, understanding the factors that somehow impact the reproduction of plants that provide resources for other organisms is essential, since changes in reproductive characteristics of an organism can be reflected for other species, such as its predators. In this work we evaluated whether droughts alter the reproductive phenology of *Syagrus romanzoffiana*, a key species in the Atlantic Forest, and whether the possible alterations have cascading consequences for animals that consume its seeds. The main results indicate that drought increases the number of bunches of immature fruits, but reduces the number of bunches of flowers and ripe fruits. Droughts can also delay or advance the time of occurrence of these structures. However, such changes do not reflect differences in predation rates of *Syagrus romanzoffiana*, whose main predator (beetle) is not satiated by increased seed production, unlike the vertebrate predator, squirrels. Thus, despite the changes caused by drought in the reproductive phenology of *S. romanzoffiana*, seed predators are not affected.

Keywords: Atlantic Forest. Climate change. Drought. ENSO. predator satiation. *Syagrus romanzoffiana*.

LISTA DE FIGURAS

| | |
|--|----|
| Figura 1 – Indivíduo adulto de <i>Syagrus romanzoffiana</i> | 11 |
| Figura 2 – Number of reproductive structures..... | 19 |
| Figura 3 – Temporal distribution of reproductive structures..... | 20 |
| Figura 4 – Distribution of the frequency of reproductive structures..... | 21 |
| Figura 5 – Predation of <i>Syagrus romanzoffiana</i> seeds..... | 24 |
| Figura 6 – Predator satiation | 26 |

SUMÁRIO

| | |
|--|----|
| 1 INTRODUÇÃO | 11 |
| 2 ARTIGO | 13 |
| 2.1 introduction..... | 14 |
| 2.3 material and methods..... | 16 |
| 2.3.1 Study site | 16 |
| 2.3.2 Study species | 16 |
| 2.3.3 Reproductive phenology..... | 17 |
| 2.3.4 Seed predation | 18 |
| 2.3.5 Data analysis..... | 18 |
| 2.4 Results | 20 |
| 2.4.1 Plant phenology | 20 |
| 2.4.2 Phenology and climatic variables | 22 |
| 2.4.3 Seed predation and predator satiation..... | 25 |
| 2.5 Discussion..... | 27 |
| 2.6 Conclusions | 30 |
| 2.7 References | 31 |
| 3 CONSIDERAÇÕES FINAIS | 36 |
| 4 REFERÊNCIAS | 37 |

1 INTRODUÇÃO

A Mata Atlântica brasileira, considerada um dos *hotspots* globais de biodiversidade (Myers *et al.* 2000), hoje ocupa cerca de 28% de seu 1 milhão de km² original, composto principalmente por fragmentos desconectados de vegetação secundária (Rezende *et al.* 2018). Palmeiras são constituintes típicos da vegetação da Mata Atlântica, onde ocorrem cerca de 45 espécies de palmeiras, muitas delas endêmicas (veja Galetti *et al.* 2006). No entanto, várias dessas palmeiras na Mata Atlântica sofreram os efeitos da fragmentação da floresta, corte seletivo e perda de dispersores de sementes (Galetti e Aleixo 1998, Galetti *et al.* 2006).

Estas plantas são sugeridas como espécies-chave na manutenção da fauna de vertebrados frugívoros pela presença de seus frutos em períodos de escassez de outros recursos e são consumidos por uma grande variedade de animais (Galetti e Aleixo, 1998). Entre essas espécies estão besouros e esquilos (*Guerlinguetus*), predadores de sementes que parecem aumentar em abundância em áreas fragmentadas (Wright, 2003).

Como entre 70% e 90% das espécies de árvores e arbustos tropicais frequentemente dependem de animais para dispersar suas sementes e a maioria dessas espécies não se reproduzem vegetativamente (Jordano, 2000), a importância das interações planta-animal para a regeneração das espécies vegetais é clara. Por outro lado, certas interações com animais também podem ser negativas para o valor adaptativo das plantas, como no caso da predação de sementes. De acordo com a frequência e intensidade dessas interações, os animais herbívoros podem comprometer a regeneração das plantas (Hulme, 1998).

Devido à dependência dos seres vivos em relação ao ambiente abiótico e biótico, suas respostas às variáveis climáticas são importantes para entender os efeitos das mudanças climáticas na biologia e ecologia desses organismos (Morelato *et al.* 2016). Os efeitos das mudanças climáticas que estão em curso têm influência sob fatores climáticos e é esperado que eventos extremos como secas e inundações se tornem mais comuns (IPCC, 2019). Além disso, os efeitos de borda em fragmentos de florestas tropicais causam mudanças na temperatura, luz, umidade, densidade das plantas, entre outros aspectos (Murcia, 1995). Assim, alterações nestes componentes abióticos podem ser refletidos em mudanças na fenologia de espécies vegetais (Morelato *et al.* 2016).

Modificações nos fatores abióticos têm o potencial de alterar, restringir ou mesmo inibir o desenvolvimento de plantas, como a palmeira *Syagrus romanzoffiana*, uma palmeira considerada um importante recurso na Mata Atlântica devido a suas interações com diversos

organismos no bioma (Bernacci *et al.* 2008; Mendes *et al.* 2015). Pouco se sabe sobre a capacidade de regeneração e persistência dessas plantas em áreas fragmentadas e que estão sob os efeitos das mudanças climáticas. Assim, o objetivo deste trabalho foi retratar a fenologia reprodutiva de *Syagrus romanzoffiana* e tentar estimar os possíveis efeitos das mudanças climáticas em sua reprodução e na predação de suas sementes ao se comparar estas variáveis entre anos sujeitos a secas ou não.



Figura 1. Indivíduo adulto de *Syagrus romanzoffiana*. Localizado no *campus* Sorocaba da Universidade Federal de São Carlos.

2 ARTIGO

SECAS CAUSAM MUDANÇAS NA FENOLOGIA REPRODUTIVA DE *SYAGRUS ROMANZOFFIANA*, MAS NÃO ALTERAM A PREDAÇÃO DE SUAS SEMENTES

DROUGHT CHANGES FRUITING PHENOLOGY, BUT DOES NOT AFFECT SEED PREDATION OF A KEYSTONE PALM

Resumo

Modelos de mudanças climáticas preveem um aumento na frequência, intensidade e duração de eventos climáticos extremos, como o El Niño (ENSO), que provocam secas severas no sudeste do Brasil. Essas mudanças podem influenciar a fenologia reprodutiva de plantas, com potenciais consequências posteriores para a regeneração das espécies. No entanto, as respostas das plantas às secas e as consequências em cascata para os animais ainda são mal descritas para as espécies tropicais. Aqui foi avaliado se a fenologia e a predação de sementes de uma espécie-chave (*Syagrus romanzoffiana*) são influenciadas por secas na Mata Atlântica no sudeste do Brasil. Registramos a fenologia reprodutiva e a predação de sementes da palmeira em fragmentos florestais por 4 anos, parte deles impactados por fortes secas do ENSO. Os padrões de floração e frutificação foram correlacionados com as variáveis climáticas, especialmente temperatura e precipitação. O número de cachos com flores ou frutos maduros diminuiu nos períodos de seca. A seca também alterou os padrões sazonais da fenologia reprodutiva quando comparada com os períodos regulares de chuva, antecipando o surgimento das flores e retardando a ocorrência de frutos verdes. A saciedade do predador foi observada para roedores, mas não para besouros. Nossos resultados indicam que a seca afeta a fenologia reprodutiva dessa palmeira, mas não há efeitos em cascata claros sobre a predação de sementes.

Palavras-chave: Mata Atlântica. Palmeira. Alterações Climáticas. ENSO. Saciação do predador.

Abstract

Climate change models predict an increase in frequency, intensity, and duration of extreme climatic events, such as El Niño Southern Oscillation (ENSO) that provoke severe droughts in southeastern Brazil. These changes can influence plant reproductive phenology, with potential delayed consequences for plant regeneration. However, plant responses to droughts, and the cascading consequences for animals, are still poorly described for tropical species. Here we evaluated whether phenology and seed predation of a keystone palm (*Syagrus romanzoffiana*) are influenced by droughts in the Atlantic Forest in southeastern Brazil. We recorded the reproductive phenology and seed predation of the palm in forest fragments for 4 years, part of them impacted by severe droughts from ENSO. Flowering and fruiting patterns were correlated with climatic variables, especially temperature and precipitation. The number of bunches with flowers or ripe fruits decreased in periods of drought. Drought also changed the seasonal patterns of reproductive phenology when compared with regular rainfall periods, anticipating flower set and delaying unripe fruit occurrence. Predator satiation was observed for rodents, but not for weevils. Our results indicate that drought affects reproductive phenology of this keystone palm, but there are no clear cascading effects on seed predation.

Keywords: Atlantic Forest. Palm-tree. Climate change. Drought. ENSO. predator satiation.

2.1 INTRODUCTION

Climate change will probably lead to an increased duration, frequency, and intensity of extreme events, such as droughts, floods, and storms (IPCC, 2019). Climate change could lead to an extension of the dry season in some tropical areas, and consequently to the shortening of the wet season with implications for plant phenology (Morellato *et al.* 2016). There is an expectancy of increases in the frequency of El Niño Southern Oscillation (ENSO), which has important implications for the climate in certain areas of the tropics (Yeh *et al.* 2009). Species phenology, i.e., the periodic events in the life of living beings and their correlations with climate variations, has been considered an important tool to interpret the effects of climate change on animals and plants, as well as in predictive models of future scenarios with higher temperatures (Memmott *et al.* 2007; Parmesan, 2006). However, information about tropical and subtropical plant phenology and studies investigating changes in plant phenology due to climate change,

and their consequences for animals that interact with these species, are still rare (Mendoza *et al.* 2017; Morellato *et al.* 2016; Hegland *et al.* 2009; Memmott *et al.* 2007).

It is common that the availability of fleshy fruits decreases in the dry season in the Atlantic forest (Genini *et al.* 2009; Morellato *et al.* 2000). Severe droughts in Central America caused by ENSO can decrease fruit availability to vertebrates and leading to an increased mortality of frugivores (Wright *et al.* 1999). Scarcity of food resources may turn frugivores that feed on fruit pulp and behave as seed dispersers into seed predators, leading to a disruption of mutualistic interactions (Jorge and Howe, 2009). The impacts of climate change on long-term species persistence will probably depend on how the species will manage such changes, as well as the effects on interspecific interactions (Morellato *et al.* 2016; Bogdziewicz *et al.* 2020). For example, an increase in temperature caused by climate change induces greater regularity in seed production of the mast seeding *Fagus sylvatica* over the years in Europe, which could be interpreted as beneficial to plant recruitment (Bogdziewicz *et al.* 2020). However, the regular supply of *F. sylvatica* seed resources year after year increased rodent abundance permanently, resulting in much higher and regular seed predation rates, which is capable to limit plant recruitment (Bogdziewicz *et al.* 2020). The once successful predator satiation strategy of *F. sylvatica* is no longer working in a scenario of climate change (Bogdziewicz *et al.* 2020).

Palms are considered keystone species to frugivores due to a high fruit production that supports a broad range of animals that consume their fruits and seeds (e.g., frugivorous vertebrates) specially in periods of fruit scarcity (Genini *et al.* 2009; Terborgh, 1986). In the Atlantic Forest, the palm *Syagrus romanzoffiana* provides fruits for at least 60 vertebrate species from different taxonomic groups, as well as weevils whose larvae develop inside seeds (Mendes *et al.* 2015). This palm produces fruits during all year and is crucial for the local fauna, especially during the dry season (Mendes *et al.* 2015; Genini *et al.* 2009). Understanding the responses of the phenology of *S. romanzoffiana* to climate change can help us to predict potential implications for many interacting species. Thus, the main aims of this paper were: (i) to investigate the response of *Syagrus romanzoffiana* reproductive phenology to changes in climatic variables, including periods of drought; (ii) to assess the effect of drought on seed predation rates and test if a higher seed production leads to satiation of seed predators.

2.3 MATERIAL AND METHODS

2.3.1 Study site

This study was conducted in 4 remnants of Atlantic Forest (0.22, 1.46, 4.1 and 9.72 ha) located at Federal University of São Carlos (UFSCar) in Sorocaba, southeastern Brazil (47°31'28" E; 23°34'53" S). Average annual temperature is 20.8 °C and the average annual rainfall is 1356 mm (INMET, 2020), with its rainy season from October to March with 166.20 ± 55.85 mm mean precipitation and mean temperature of $23.3^\circ \pm 1^\circ \text{C}$, the dry season is from April to September, with 59.53 ± 16.90 mm mean precipitation and $18.72 \pm 1.72^\circ \text{C}$ (INMET, 2020). Vegetation is characterized as Seasonal Semideciduous Forest, where part of the trees defoliates during the dry season, in secondary successional stage, with Myrtaceae and Fabaceae being the most common tree families (Corrêa *et al.* 2014; Kortz *et al.* 2014). The remnants are surrounded by pastures dominated by alien African grasses, *Brachiaria decumbens* Stapf and *Melinis minutifolia* P. Beauv. Due to their small size, the forest fragments are certainly subjected to edge effects. These remnants are representative of most Atlantic forest fragments, which are usually irregularly shaped and smaller than 50 ha (Ribeiro *et al.* 2009).

There is a scarcity of large bodied birds and mammals in the study sites. Some species that potentially interact with *Syagrus romanzoffiana* are occasionally spotted in the area, such as brown brocket deer *Mazama gouazoubira*, crab-eating fox *Cerdocyon thous*, pampas fox *Lycalopex gymnocercus* and argentine black and white tegu *Salvator merianae*, as well as birds such as rusty-margined guan *Penelope superciliaris* and the white-eyed parakeet *Psittacara leucophthalmus*. Squirrels (*Guerlinguetus brasiliensis*) are commonly seen in the area, and frequently prey on the seeds of *S. romanzoffiana*, being also able to disperse some of these seeds (Da Silva *et al.* 2011).

2.3.2 Study species

Syagrus romanzoffiana (Cham.) Glassman (Arecaceae) is a single trunk palm that reaches between 8 and 20 m high and up to 64 cm basal diameter (Bernacci *et al.* 2007). The species has a wide distribution in Brazil, occurring in the Atlantic Forest and portions of the Cerrado savanna (Leitman *et al.* 2012). The ripe fruit is an orange-colored drupe, measuring from 18 to 26 mm long, with a fibrous mesocarp, rigid endocarp and containing one seed (Goudel *et al.* 2013). A palm may produce several reproductive bunches a year, each bunch

bearing on average ca. 800 fruits (Galetti *et al.* 1992). Fruits are available throughout the year, with peak production during the rainy season (Freire *et al.* 2013, but see below).

The fruits and seeds of this species are consumed by insects and small to large vertebrates (Mendes *et al.* 2015), such as ring-tailed coati *Nasua nasua* and South America tapir *Tapirus terrestris* (Varela and Bucher, 2006). However, some species are able to penetrate the thick endocarp and consume its endosperm, making seed germination unfeasible. Its main predators at the site are rodents (*Guerlinguetus brasiliensis*, Sciuridae) and weevils (mainly *Revena rubiginosa*, Curculionidae; Mariano and Christianini, 2016), with the latter using the seed endosperm for larval development (Galetti *et al.* 1992; Da Silva *et al.* 2012).

2.3.3 Reproductive phenology

To evaluate the reproductive phenology of *S. romanzoffiana*, we marked 16 adults in the forest fragments (DBH = 29.17 ± 5.97 cm, height = 7.53 ± 1.31 m; mean \pm SD). All plants were at least 20 meters away from the nearest conspecific adult. Between August 2017 to December 2019, we recorded the presence and the number of bunches with inflorescences (including floral buds), unripe fruits and ripe fruits. In addition, we considered phenology data from the same plants recorded during September 2010 to September 2011 (Mariano and Christianini, 2016) and between July 2015 and September 2016. To avoid bias in the analysis due to different sampling periods in each year, we used the same periods of time (starting in September and ending in August of the following year) for the intervals of 2010-2011, 2015-2016, 2017-2018 and 2018-2019, totaling 57 months of sampling. Climate data were extracted from the Meteorological Database for Education and Research (BDMEP) of the Brazilian National Institute of Meteorology (INMET) measured at the Sorocaba - SP station (approximately 20 km away from the study site). To obtain the monthly number of days with rainfall, we selected data for minimum precipitation obtained from the Rainfall Climate Hazards Group IR Precipitation with Stations (CHIRPS; ClimateSERV, 2020). Temperature and precipitation data were then correlated with the following phenological variables: (a), number of palms with reproductive bunches; and (b) number of reproductive bunches per palm.

To distinguish periods of regular rainfall precipitation from those experiencing droughts, we considered the monthly average precipitation from 2000 to 2019 (107.69 ± 5.69 mm, mean \pm SE) as the historical average. If the precipitation in a sampling period (2010-2011, 2015-2016, 2017-2018 and 2018-2019) was above the historical average, we considered the

period as regular (wet), and if below the average, as dry. Regular rainfall periods were 2010-2011 (117.42 ± 4.65 mm monthly rainfall) and 2015-2016 (134.91 ± 3.11 mm) and the dry periods were 2017-2018 (80.92 ± 3.16 mm) and 2018-2019 (84.42 ± 2.82 mm).

2.3.4 Seed predation

To evaluate the amount of seed predation and the impact by different agents, we estimated the sources of *S. romanzoffiana* seed predation by inspecting seeds fallen beneath palm canopy. We established a 0.5 x 1 m plot beneath the canopy of five palm trees in July 2011, July 2015, August 2017 and August 2019. We sampled all seeds in the surface of each plot. The source of predation was attributed to a particular agent according to distinctive marks left on the seed endocarp. For example, triangular openings indicated predation by the squirrel *Guerlinguetus brasiliensis*, while circular holes are typical of the emergence of an adult weevil that destroy seed during larvae stage (Bordignon *et al.* 1996; Alves-Costa and Knogge, 2005). Seeds were further classified as: preyed on by other rodents, when the openings on the endocarp were different from those reported by Bordignon *et al.* (1996); intact, when they showed no signs of predation or apparent damage; rotten when the seed broke after applying pressure with the fingers; aborted, when the fruit was less than half the size of ripe fruits. This last “aborted” category was only included in the classification of seeds in 2017 and the seeds classified in this category were not collected in previous years. In total, we inspected 8,267 seeds over the years.

2.3.5 Data analysis

To analyze seasonality on reproductive phenology, we used circular statistics using the “circular” package (Agostinelli and Lund, 2017) in R (R Development Core Team, 2014). The frequencies of flowers and fruit bunches were grouped into months, separated by 30° from each other, with January being the month represented by 0°. To investigate whether the flowering and fruiting phenology of the palm is seasonal, we used the circular statistics using the Rao spacing test. To test whether the flowering and fruiting season differed between dry and regular periods, we used the non-parametric Watson-Wheeler test. The average period of flower and fruit occurrence were identified using the circular average, given in radians, and converted into degrees to associate it with the corresponding month. To investigate possible relationships between climate variables and flowering and fruiting of *S. romanzoffiana*, we built multiple linear models. We separately used the number of flowers and fruits bunches and the number of

individuals showing some reproductive bunch as dependent variables. Average, minimum and maximum monthly temperature, monthly daylight hours, monthly precipitation, number of rainy days during the month, monthly rainfall 1-year before, precipitation of the previous 6 months (ca. the time needed from emission of a bunch to fruit maturation) and rainfall of the previous month, were used as explanatory variables. First, correlation tests were performed between all the explanatory variables and in cases where two of these variables had a high correlation (> 0.70), one was eliminated at random from the model. From the complete models, variables without significant correlations ($p > 0.05$) were excluded one by one until only significant variables remained in the model, using the “bbmle” package (Bolker, 2020) in R (R Development Core Team, 2014).

To test if seed predation varied over time and the influence of drought and predation agents, we performed two separate analyses. First, we compared seed predation by different predation agents and periods (both fixed), ignoring the differentiation between drought and regular periods. A separate analysis incorporating the differentiation between drought and regular rainfall periods as another factor (instead of year) was performed. For both analyses we used generalized linear mixed models (GLMM) using the maximum likelihood method, with the number of seeds preyed on (converted to log) as response variable, palm tree as a random effect factor and predation agent and period (year or drought status) as fixed effect factors.

To test whether the number of bunches produced by individuals and the population differed between the regular and dry periods, we used ANOVA. To test the predator's satiation hypothesis, we used linear regressions and paired t-test of the number of seeds preyed on against the number of seeds sampled beneath palms (an estimate of palm seed crop). The number of seeds preyed on by weevils or squirrels, as well as the total number of sampled seeds (i.e. estimated crop size), were log-transformed ($\log + 1$) to perform a log-log regression following the function $\log(y + 1) = a + b \cdot \log(x + 1)$, where x is the total number of seeds sampled per palm and y the number of seeds preyed on by weevils or squirrels; b is the slope of the line representing the proportion of seeds preyed on versus the total number of seeds and a is the constant. Predator satiation occurs if the proportion of preyed seeds decreases with an increase in the total amount of seeds, i.e., when $b < 1$. If $b = 1$, seed predation is proportional to seed production, whereas if $b > 1$, the proportion of seeds preyed on increases with increasing seed production (Harms *et al.* 2000). The observed seed predation was compared with expected values if the proportion of seeds preyed on would be a simple function of the number of seeds produced (i.e. if $b = 1$) using a paired t-test.

2.4 RESULTS

2.4.1 Plant phenology

Flowering was not evenly distributed throughout the year for periods of drought ($U = 309.873$, $p < 0.001$) and regular rainfall ($U = 327.270$, $p < 0.001$). However, there was a difference in flower seasonality between drought and regular rainfall periods ($W = 24.05$, $df = 2$, $p < 0.001$): during periods of drought, the average month of flower occurrence was January ($\bar{\alpha} = 24.77^\circ \pm 62.88^\circ$; mean angle \pm SD), while in periods of regular rainfall, the average vector for flower production was May ($\bar{\alpha} = 135.29^\circ \pm 76.64^\circ$). The number of bunches with flowers was higher in the regular rainfall periods ($F_{1,38} = 6.07$, $p = 0.018$, Fig. 2).

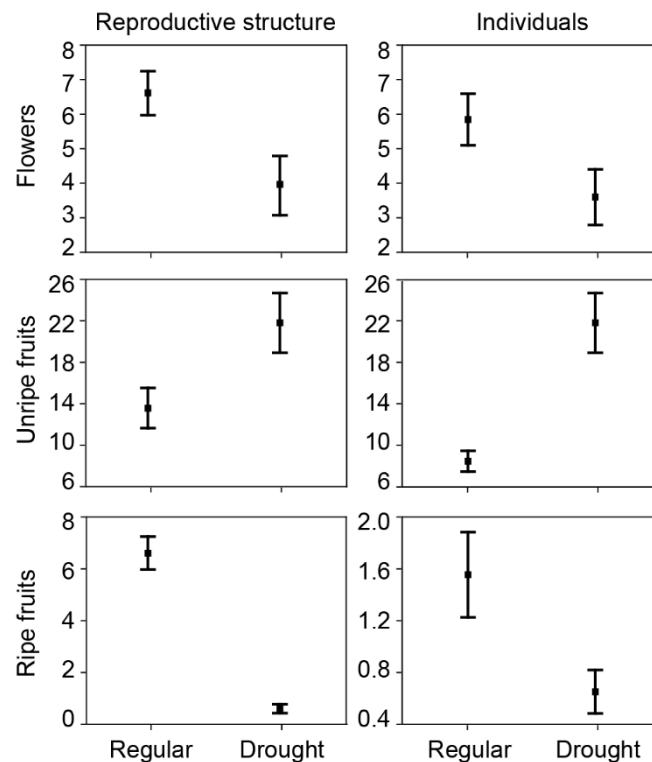


Figure 2. Differences in the number of individuals of *Syagrus romanzoffiana* showing some reproductive structure (left) and number of bunches (right) during droughts and regular rainfall. Vertical bars represent 95% CI. $N = 57$ months.

March was the average month for unripe fruit production during drought ($\bar{a} = 66.91^\circ \pm 57.85^\circ$), whereas in regular rainfall periods the average vector was January ($\bar{a} = 27.96^\circ \pm 69.27^\circ$), confirming a change in seasonality also for unripe fruit bunches ($W = 30,339$, $df = 2$, $p < 0.001$). However, droughts presented a higher number of bunches with unripe fruits, when compared to periods of regular rainfall ($F_{1,38} = 5.57$, $p = 0.023$). The monthly distribution of unripe bunches was not homogeneous during drought ($U = 350.09$, $p < 0.001$) or regular rainfall periods ($U = 344.12$, $p < 0.001$, Fig. 3).

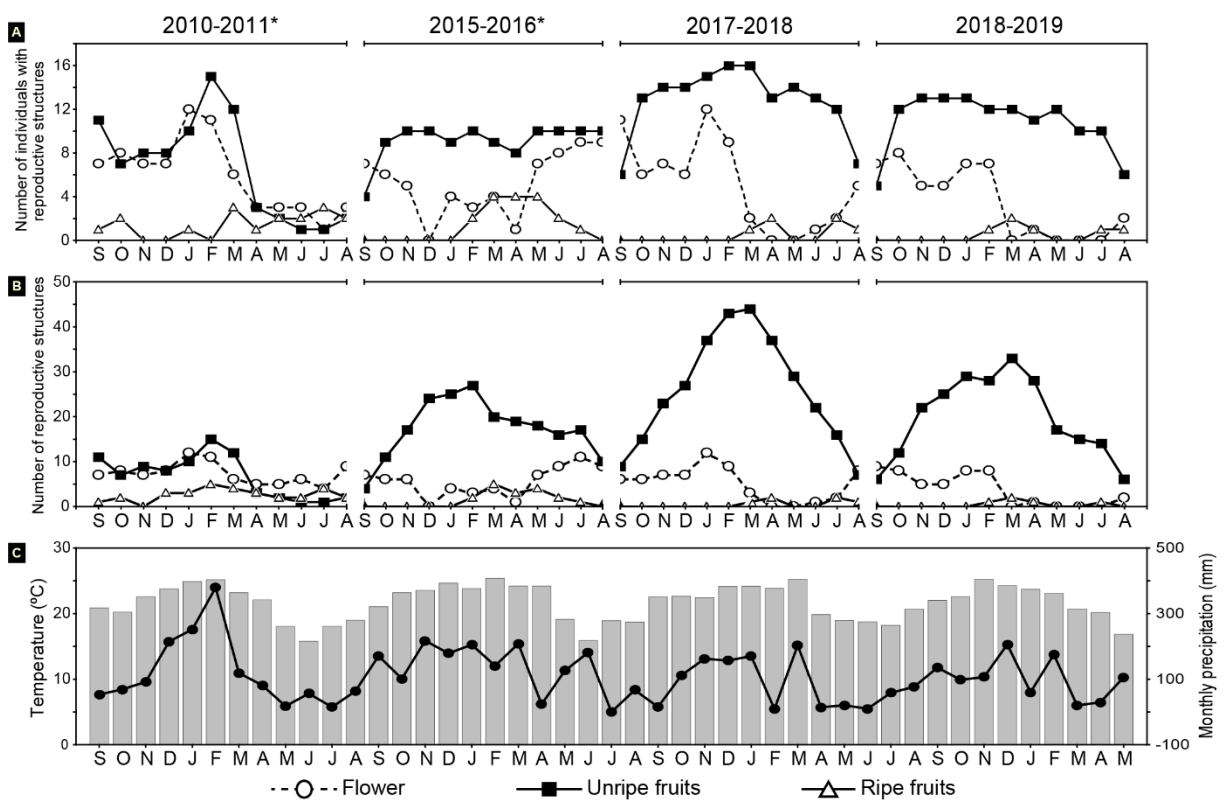


Figure 3. Temporal distribution of reproductive structures in 16 *S. romanzoffiana* palms and variation in rainfall and temperature in southeastern Brazil (September 2010 to May 2019). Number of individuals carrying bunches (A); total number of flowers (dashed line with empty circles), unripe fruits (solid line with black squares) and ripe fruits (solid line with empty triangles) (B); average temperatures in °C (gray bars) and accumulated monthly precipitation in mm (solid line with black circles) (C). * Periods of regular rainfall.

There was no difference in ripe fruit seasonality between regular and dry periods ($W = 0.092$, $df = 2$, $p = 0.95$). The peak of ripe fruits, on average, occurred in April in drought conditions ($\bar{a} = 112.91^\circ \pm 61.27^\circ$) and March for regular rainfall periods ($\bar{a} = 89.11^\circ \pm 53.79^\circ$).

However, the number of ripe bunches was higher for periods with regular precipitation ($F_{1,38} = 12,464$, $p = 0.001$, Fig. 4). Fruits were not homogeneously distributed throughout the year during drought ($U = 180$, $p < 0.05$) and regular rainfall periods ($U = 291.43$, $p < 0.001$).

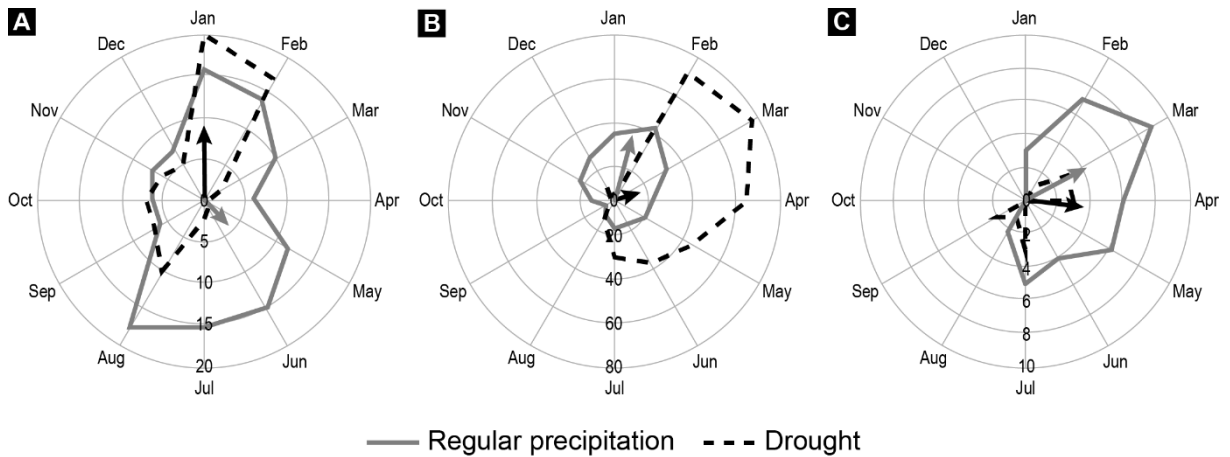


Figure 4. Distribution of the frequency of reproductive structures of *S. romanzoffiana* individuals associated with the months of the year ($n = 57$) in small fragments of Atlantic Forest in southeastern Brazil. A) Frequency of flowers (bunches with flower buds and flowers combined). B) Unripe fruits. C) Ripe fruits. Solid lines indicate the flowers and fruits frequency in periods with regular rainfall. Dashed lines indicate the frequency of reproductive structures in droughts. The black arrow refers to the average vector (\bar{a}) for dry periods and the gray arrow refers to regular periods.

2.4.2 Phenology and climatic variables

The proportion of individuals with flowers in the population responded positively to the precipitation of the previous year ($F_{1,1} = 4.09$, $p = 0.048$) and current year ($F_{1,1} = 4,859$, $p = 0.031$). The number of bunches with flowers was positively related to the precipitation of the current year ($t = 2.240$, $p = 0.029$).

The number of palm trees with unripe fruits was influenced by the number of rainy days in the month ($F_{1,1} = 20.783$, $p < 0.001$). The number of unripe fruits bunches was influenced by the average maximum temperatures ($F_{1,1} = 6,018$, $p = 0.012$) and also by the number of rainy days in the month ($F_{1,1} = 8,788$, $p = 0.005$).

The number of individuals with ripe fruits was correlated with the average temperature ($F_{1,1} = 4.736$, $p = 0.035$, Tab. 1), average maximum temperature ($F_{1,1} = 6.307$, $p = 0.016$) and monthly daylight hours ($F_{1,1} = 5.996$, $p = 0.018$). The number of ripe fruit bunches was

correlated with the rainfall of the previous month ($F_{1,1} = 8.609$, $p = 0.005$), current rainfall ($F_{1,1} = 7.629$, $p = 0.008$), average maximum temperature ($F_{1,1} = 8.065$, $p = 0.006$) and monthly daylight hours $F_{1,1} = 7.027$, $p = 0.011$, Table 1).

Table 1. Results of linear models of the effect of climatic variables on the number of individuals in the population showing bunches of flowers or fruits (on the left) and number of reproductive structures (on the right). Only variables retained in the models are shown.

| Dependent Variables | Independent Variables | Individuals | | | | | | Reproductive structures | | | | | |
|---------------------|--------------------------|-------------|---------|--------|--------|-----|------|-------------------------|---------|--------|--------|-----|------|
| | | Sum of sq. | F-value | RSS | AIC | D.F | p | Sum of sq. | F-value | RSS | AIC | D.F | p |
| Flowers | | | | | | | | | | | | | |
| | Previous 1-year rainfall | 38.13 | 4.09 | 541.49 | 132.32 | 1 | 0.05 | | | | | | |
| | Current Rain | 45.30 | 4.86 | 548.66 | 133.07 | 1 | 0.03 | 50,808 | 50,196 | 607,51 | 136.88 | 1 | 0.03 |
| Unripe fruits | | | | | | | | | | | | | |
| | Rainy days in the month | 258.92 | 20.78 | 944.14 | 162.01 | 1 | 0.00 | 675.22 | 8.79 | 4593 | 243.95 | 1 | 0.01 |
| | Average Max. Temp. | | | | | | | 462.38 | 6.02 | 4381 | 241.39 | 1 | 0.02 |
| Ripe fruits | | | | | | | | | | | | | |
| | Average Temp. | 6.07 | 4.74 | 63.7 | 18.86 | 1 | 0.03 | | | | | | |
| | Average Max. Temp. | 8.08 | 6.31 | 65.72 | 20.38 | 1 | 0.02 | 13.88 | 8.06 | 89.62 | 37.58 | 1 | 0.01 |
| | Daylight hours | 7.68 | 6.00 | 54.32 | 20.08 | 1 | 0.02 | 12.10 | 7.03 | 87.83 | 36.60 | 1 | 0.01 |
| | Previous month rainfall | | | | | | | 14.82 | 8.61 | 90.56 | 38.09 | 1 | 0.01 |
| | Current Rain | | | | | | | 13.13 | 7.63 | 88.87 | 37.17 | 1 | 0.01 |

2.4.3 Seed predation and predator satiation

Seed predation by weevils corresponded to $30\% \pm 9\%$ (mean \pm SD, Fig. 4) of the seeds produced per plant per year. Squirrels destroyed $21\% \pm 12\%$ of the seeds. No seeds were preyed on by both agents (squirrels plus weevils). Predation by other rodents was recorded for $7\% \pm 9\%$ of the seeds per palm. Rotten seeds accounted for $7\% \pm 8\%$ and aborted seeds $15\% \pm 25\%$. Intact seeds represented $20\% \pm 12\%$ of the sampled seeds.

Seed predation rates did not differ between years ($t = -1.410$, $df = 1$, $p = 0.393$), but there was a difference between predation agent ($t = -3.619$, $df = 13$, $p = 0.003$) and in the interaction between predator and year ($t = 3.616$, $df = 13$, $p = 0.003$). When analyzing the effect of drought on seed predation, there was no significant difference on predation rates between drought and regular periods ($t = 0.635$, $df = 20$, $p = 0.532$). Predation agent ($t = 0.481$, $df = 20$, $p = 0.635$) and the interaction between predation agent and drought ($t = -1.598$, $df = 20$, $p = 0.125$) also did not differ between regular rainfall and drought periods. Therefore, drought does not seem to affect seed predation rates, as well as seed predation by different agents (Fig. 5).

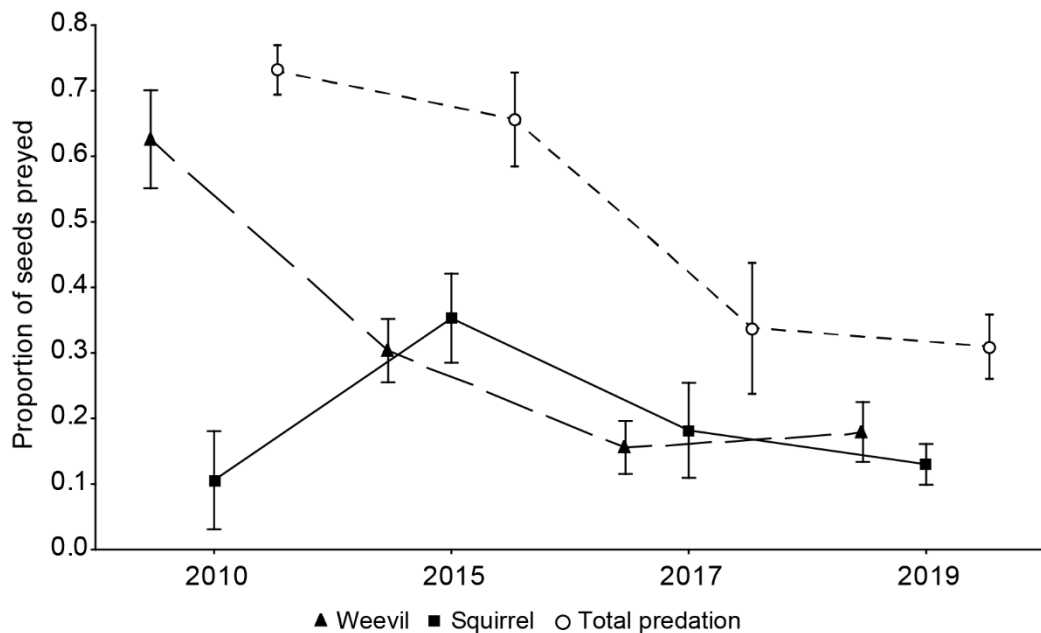


Figure 5. Predation of *Syagrus romanzoffiana* seeds by weevils and squirrels over time and the sum of predation by weevils and squirrels (total predation). Black triangles and long dashed line represent seed predation by weevils (*Revena rubiginosa*); black squares and continuous lines represent predation by squirrels (*Guerlinguetus brasiliensis*) and empty circles with short dashed lines represent total predation. Vertical bars represent 95% CI.

Table 2. *Syagrus romanzoffiana* seed predation by weevils and rodents in small Atlantic Forest during 2011, 2015, 2017 and 2019.

| Sources of mortality | 2011 | 2015 | 2017 | 2019 |
|-----------------------------|-------------|-------------|-------------|-------------|
| Preyed on by weevils | | | | |
| Mean | 0.626 | 0.222 | 0.156 | 0.179 |
| Standard deviation | 0.167 | 0.090 | 0.090 | 0.102 |
| Preyed on by squirrels | | | | |
| Mean | 0.106 | 0.447 | 0.182 | 0.130 |
| Standard deviation | 0.167 | 0.260 | 0.162 | 0.070 |
| Preyed on by other rodents | | | | |
| Mean | 0.031 | 0.000 | 0.009 | 0.140 |
| Standard deviation | 0.033 | 0.000 | 0.006 | 0.092 |
| Rotten | | | | |
| Mean | 0.110 | 0.000 | 0.078 | 0.167 |
| Standard deviation | 0.083 | 0.000 | 0.040 | 0.086 |
| Intact | | | | |
| Mean | 0.122 | 0.332 | 0.069 | 0.128 |
| Standard deviation | 0.048 | 0.251 | 0.064 | 0.161 |
| Aborted | | | | |
| Mean | | | 0.506 | 0.254 |
| Standard deviation | | | 0.256 | 0.187 |

The influence of palm crop size on seed predation differed for weevils and squirrels (Fig. 5). Seed predation by weevils was related to seed production per palm ($y = -1.324 + 1.264x$, $r^2 = 0.56$, $t = 4.79$, $df = 18$, $p < 0.001$), increasing in palms with higher seed production (paired-t test: $t = 5.546$, $df = 19$, $p < 0.001$). Seed predation by squirrels was also influenced by seed production ($y = -0.549 + 0.833x$, $r^2 = 0.21$, $t = 2.20$, $p = 0.040$), but increases in predation did not follow the slope of increase in crop size (paired-t = -2.753 , $df = 19$, $p = 0.012$). Therefore, predator satiation seems to work for squirrels, but not for weevils (Fig. 6).

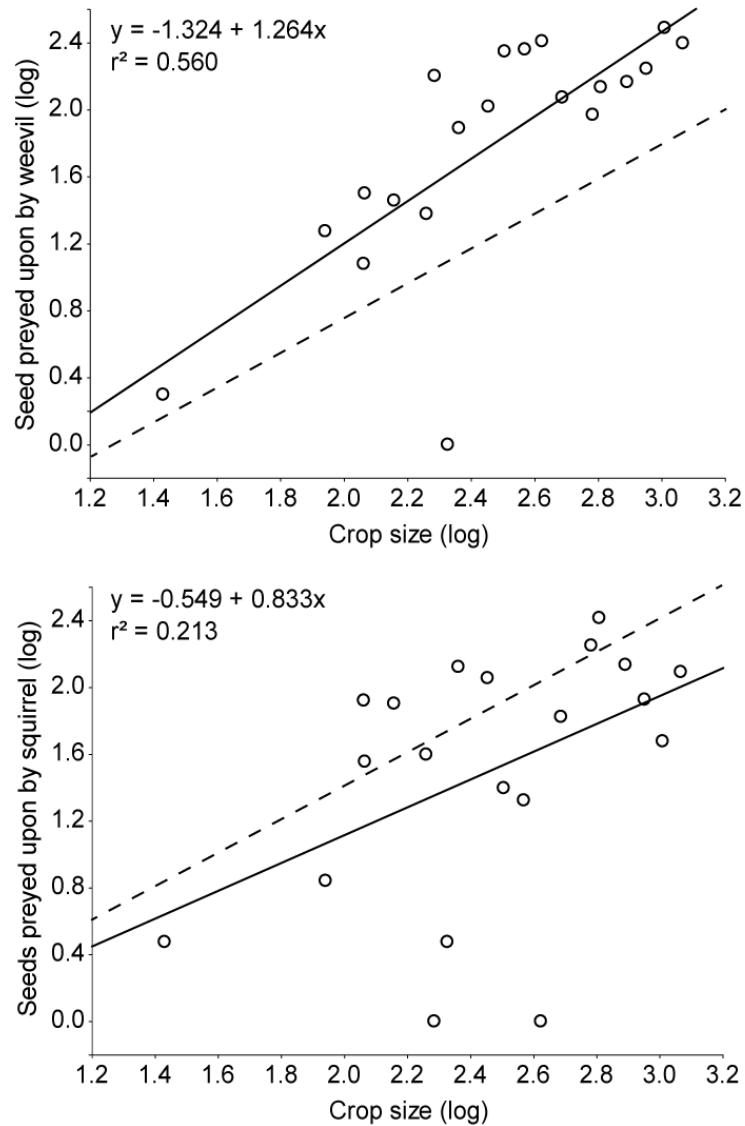


Figure 6. *Syagrus romanzoffiana* seeds preyed on by weevils (above) and squirrels (below) in relation to the number of seeds collected annually under the canopy of 5 palm trees in an area of 0.5 m² for 4 years (2010, 2016, 2017 and 2019). Dashed line represents the expected seed predation if it is exactly proportional to seed production.

2.5 DISCUSSION

Our analyses suggest that periods of drought can present a negative impact on *S. romanzoffiana* flower and ripe fruit production, as well as changes in the palm reproductive phenology seasonal patterns. However, contrary to expectations, bunches with unripe fruit are more common during periods of drought. Despite the impact of different seed predators (i.e., weevil or squirrel), which varies temporally, there was no significant difference in *S. romanzoffiana* seed predation between dry and regular rainfall periods. The persistent fruit production indicates that these fruits might be important resources for the maintenance of the

local fauna, especially in winter, when the community experiences a lower availability of fruits and seeds (Genini *et al.* 2009). However, since *S. romanzoffiana* phenology responds to climatic variables, the long-term persistence of this palm's resources, and its effects on other species, become uncertain when considering climate change scenarios.

We found that droughts induce changes in seasonality and the number of bunches with flowers in *S. romanzoffiana*. Under regular rainfall conditions, flowering peaks occur in the dry season, but during periods subject to drought, flowering is anticipated by about 4 months. In addition, fewer flower bunches are produced during periods of drought. Flowering anticipation is often a response to water stress in plants (Kazan and Lyons, 2016). This anticipation may also lead to a decrease in reproductive success if it produces a mismatch between the timing of flower production and pollinator activity (Parmesan, 2006). The most frequent pollinators of palms are beetles and bees with a wide variation in the mechanisms of such interaction. Some pollinating beetles can also act like predators of reproductive tissues and use developing fruits for oviposition (de Medeiros *et al.* 2019) and its importance as pollinators can be considerable, especially in less healthy environments (Barfod *et al.* 2011). There is no detailed data for pollination of this palm, which makes it difficult to link the impacts of changes in palm phenology with pollinators. Anyway, frugivorous and granivorous animals that depend on *S. romanzoffiana* unripe and ripe fruits and also seeds may face the effects on changes in seasonality in food resources due to the effects of droughts on palm phenology and production of reproductive bunches (Wright *et al.* 1999).

Contrary to expectations, drought increases the production of bunches of *S. romanzoffiana* with unripe fruits, but at the same time reduces the number of bunches with ripe fruits. This palm can tolerate treefall gaps, forest edges and small forest fragments, where there is greater light availability, lower humidity and higher temperatures, indicating that the species is tolerant to great microclimatic variations (Matos and Alves, 2008). Droughts can increase fruiting in some plants from tropical regions, as has already been seen in periods of moderate droughts induced by ENSO (El Niño Southern Oscillation), which decreases rainfall while increases average temperatures (Detto *et al.* 2018). Furthermore, during droughts, flowers life span can be shorter, thus, resulting in a faster transition to unripe fruits (within a month). Consequently, due to the periodicity of data collection, unripe fruit bunches are more observed than flowers (author's personal observation). Higher temperatures can anticipate fruit ripening of cultivated and wild species (Menzel *et al.* 2006). For *S. romanzoffiana*, production of bunches with ripe fruits increases with high monthly temperatures and monthly daylight hours.

In addition, the number of ripe bunches is reduced during droughts, which might be influenced by a decrease in soil water availability (Vogado, *et al.* 2020). Thus, it is of great relevance to understand how plant populations and communities will respond to drought events, and their potential cascading effects on other trophic levels (Morellato *et al.* 2016).

Changes in the seasonality of palm phenology can have positive or negative effects on frugivorous seed dispersers and seed predators (Memmott *et al.* 2007; Post *et al.* 2008). Our results indicate that seed predation rates are not consistently affected by droughts. However, the relative importance of each predation agent, i.e., seed predation by weevils or squirrels, varies between periods, indicating that different predatory agents might respond differently to climate variables. Weevils are not satiated by an increased seed production, unlike squirrels. Since the weevil *Revena rubiginosa* larvae depend on *S. romanzoffiana* seeds to complete the life cycle, during years of small crops the weevils' population may be reduced (Alves-Costa and Knogge, 2005). Thus, during the next breeding event there will be fewer adult weevils and a lower rate of seed predation, allowing squirrels to explore more *S. romanzoffiana* seeds in these years following low crop sizes. On the other hand, during years of large crop sizes, weevils would be able to prey on more palm seeds, reducing the number of seeds available to squirrels. Squirrels can also exploit other food sources in their diet (Miranda, 2005). Hence, the interannual variation in seed damage made by a specific predator agent is compensated, at least partially, by the other predator, and the total rate of seed predation remains reasonably constant over time. In this way, the increase in predation by an agent does not result in greater total predation, but in a reduction in predation by other predators (see also Wright, 2003).

Variation on fruit and seed sizes between years or following droughts, and its consequences on resource availability, were not considered here, but may also have affected our results (Moegenburg, 1996). As droughts anticipate the flowering of *S. romanzoffiana*, the ripening of the fruits, which requires around 5 to 6 months (author's personal observation), occurs during the driest season of the year, in contrast to the periods of regular rainfall, when the greatest presence of ripe fruits occurs during the rainy season. During the dry season there is usually less fleshy fruit available at plant community level (Genini *et al.* 2009) and it is likely to expect a further reduction in resources during periods of droughts. Thus, ripe fruits, which have a different chemical composition from unripe fruits (such as a higher amount of lipids, Barbi *et al.* 2020), can be more attractive to animals in periods of famine (Wright *et al.* 1999). The decrease in records of bunches with ripe fruits may be a consequence of a faster consumption of the fruits available during periods of fruit scarcity (i.e., during droughts). Given

the time interval of our observations (once a month) we cannot properly evaluate this possibility. However, unripe palm fruits seem to be targeted by squirrels specially during periods of drought (author's personal observation). A decrease in records of bunches with ripe fruits during droughts may also be the result of a higher rate of failure (e.g. abortion) during seed development. However, great variations in the numbers of seeds aborted were also observed between years of regular rainfall (Table 2).

Successful plant recruitment, specially of large-seeded species, often relies on seed numbers and adequate conditions for establishment (Moles and Westoby, 2002). When considering the predicted increases in the frequency, intensity and duration of droughts, already observed Brazil and other tropical regions (Spinoni *et al.* 2019), the long-term maintenance of *S. romanzoffiana* in remnants of Atlantic forest may be uncertain. Although changes in palm phenology not seem to affect the amount of seeds losses to predators, future studies should evaluate the impact of climate change on further recruitment stages, such as the likelihood of palm seed germination, seedling survival and recruitment. Given the importance of this palm for the animal community, a decrease in recruitment of this palm may compromise the maintenance of the frugivore community and the interactions they maintain in the long term.

2.6 CONCLUSIONS

Droughts displace the temporal pattern of flower and fruit production in the palm *Syagrus romanzoffiana* and seems to change the reproductive output, reducing the quantity of bunches with flowers and ripe fruits of this palm in Atlantic Forest fragments in southeastern Brazil. These changes are likely to impact animals that rely on fruits and seeds, but we detected no effect of drought on the amount of seed losses to squirrels and weevils. The relative importance of different seed predation agents varies over time irrespective of drought. Therefore, despite the effects of drought on reproductive phenology, we detected no cascading effects on seed predation of this palm.

2.7 REFERENCES

- Agostinelli, C., Lund, U. 2017. R package 'circular': Circular Statistics (version 0.4-93). URL <https://r-forge.r-project.org/projects/circular/>
- Alves-Costa, C.P., Knogge, C., 2005. Larval competition in weevils *Revena rubiginosa* (Coleoptera: Curculionidae) preying on seeds of the palm *Syagrus romanzoffiana* (Arecaceae). *Naturwissenschaften* 92, 265–268. <https://doi.org/10.1007/s00114-005-0620-6>
- Barbi, R.F.T., Hornung, P.S., Ávila, S., Alves, F.E.S.B, Beta, T. Ribani, R.H., 2020. Ripe and unripe inajá (*Maximilia maripa*) fruit: a new high source of added value bioactive compounds. *Food Chemistry* 331, 127333. <https://doi.org/10.1016/j.foodchem.2020.127333>
- Barfod, A.S., Hagen, M., Borchsenius, F., 2011. Twenty-five years of progress in understanding pollination mechanisms in palms (Arecaceae). *Ann. Bot.* 108, 1503–1516. <https://doi.org/10.1093/aob/mcr192>
- Bolker, B., R Development Core Team., 2020. *bbmle: Tools for General Maximum Likelihood Estimation*. R package version 1.0.23.1. <https://CRAN.R-project.org/package=bbmle> (accessed 08.10.2020)
- Bernacci, L.C., Martins, F.R., Santos, F.A.M., 2007. Estrutura de estádios ontogenéticos em população nativa da palmeira *Syagrus romanzoffiana* (Cham.) Glassman (Arecaceae). *Acta Botanica Brasilica* 22, 119-130.
- Bogdziewicz, M., Kelly, D., Thomas, P.A., Lageard, J.G.A., Hacket-Pain, A., 2020. Climate warming disrupts mast seeding and its fitness benefits in European beech. *Nature Plants* 6, 88-94. <https://doi.org/10.1038/s41477-020-0592-8>
- Bordignon, M., Margarido, T.C.C., Lange, R.R., 1996. Formas de abertura dos frutos de *Syagrus romanzoffiana* (Chamisso) Glassman efetuadas por *Sciurus Ingrams Thomas* (Rodentia, Sciuridae). *Revista Brasileira de Zoologia* 13, 821-828. <https://doi.org/10.1590/S0101-81751996000400002>
- ClimateSERV. Rainfall Climate Hazards Group IR Precipitation with Stations., 2020. <https://climateserv.servirglobal.net/> (accessed 06.10.2020)
- Corrêa, L.S., Cardoso-Leite, E., Castello, A.C.D., Coelho, S., Kortz, A.R., Villela, F.N.J., Koch, I., 2014. Estrutura, composição florística e caracterização sucessional em remanescente de floresta estacional semidecidual no sudeste do Brasil. *Rev. Arvore* 38, 799–809. <https://doi.org/10.1590/S0100-67622014000500004>

- da Silva, F.R., Begnini, R.M., Lopes, B.C., Castellani, T.T., 2012. Temporal Variation in Seed Predation by Insects in a Population of *Syagrus romanzoffiana* (Arecaceae) in Santa Catarina Island, SC, Brazil. *Neotrop. Entomol.* 41, 17–21. <https://doi.org/10.1007/s13744-011-0002-z>
- da Silva, F.R., Begnini, R.M., Lopes, B.C., Castellani, T.T., 2011. Seed dispersal and predation in the palm *Syagrus romanzoffiana* on two islands with different faunal richness, Southern Brazil. *Stud. Neotrop. Fauna Environ.* 46, 163–171. <https://doi.org/10.1080/01650521.2011.617065>
- de Medeiros, B.A.S., Núñez-Avellaneda, L.A., Hernandez, A.M., Farrell, B.D. 2019. Flower visitors of the licuri palm (*Syagrus coronata*): brood pollinators coexist with a diverse community of antagonists and mutualists. *Biological Journal of the Linnean Society* 126, 666–687. <https://doi.org/10.1093/biolinnean/blz008>
- Detto, M., Wright, S.J., Calderón, O., Muller-Landau, H.C., 2018. Resource acquisition and reproductive strategies of tropical forest in response to the El Niño-Southern Oscillation. *Nat. Commun.* 9, 1–8. <https://doi.org/10.1038/s41467-018-03306-9>
- Fleming, T.H., Breitwisch, R., Whitesides, G., 1987. Patterns of tropical vertebrate frugivore diversity. *Ann. Rev. of Eco. and Syst.* 18, 91–109. <https://doi.org/10.1146/annurev.es.18.110187.000515>
- Freire, C.C., Closel, M.B., E.H. e F.N.R., 2013. Reproductive Phenology, Seed Dispersal and Seed Predation in *Syagrus romanzoffiana* in a Highly Fragmented Landscape. *Annales Botanici Fennici* 50, 220–228. <https://doi.org/10.5735/086.050.0403>
- Galetti, M., Paschoal, M., Fernando, F., Pedroni, P., 1992. Predation on palm nuts (*Syagrus romanzoffiana*) by squirrels (*Sciurus ingrami*) in south-east Brazil. *J. Trop. Ecol.* 8, 121–123. <https://doi.org/10.1017/S0266467400006210>
- Genini, J., Galetti, M., Morellato, L.P.C., 2009. Fruiting phenology of palms and trees in an Atlantic rainforest land-bridge island. *Flora Morphol. Distrib. Funct. Ecol. Plants* 204, 131–145. <https://doi.org/10.1016/j.flora.2008.01.002>
- Goudel, F., Shibata, M., Coelho, C.M.M., Miller, P.R.M., 2013. Fruit biometry and seed germination of *Syagrus romanzoffiana* (Cham.) Glassm. *Acta Botanica Brasilica* 27, 147–154. <http://dx.doi.org/10.1590/S0102-33062013000100015>
- Grimm, A.M., Ferraz, S.E.T., Gomes, J. 1998. Precipitation Anomalies in Southern Brazil Associated with El Niño and La Niña Events. *Journal of Climate* 11, 2863–2880. [https://doi.org/10.1175/1520-0442\(1998\)011<2863:PAISBA>2.0.CO;2](https://doi.org/10.1175/1520-0442(1998)011<2863:PAISBA>2.0.CO;2)

- Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.L., Totland, Ø. 2009. How does climate warming affect plant-pollinator interactions?. *Ecology Letters* 12, 184-195. <https://doi.org/10.1111/j.1461-0248.2008.01269.x>
- Instituto Nacional de Meteorologia INMET. Normais climatológicas do Brasil. URL <https://portal.inmet.gov.br/normais> (accessed 06.10.2020).
- IPCC, 2019. Land–climate interactions. In: *Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems*. <https://www.ipcc.ch/srccl/> (accessed 08.02.2020)
- Jorge, M.L.S.P., Howe, H.F., 2009. Can forest fragmentation disrupt a conditional mutualism? A case from central Amazon. *Oecologia* 161, 709–718. <https://www.doi.org/10.1007/s00442-009-1417-7>
- Kazan, K., Lyons, R., 2016. The link between flowering time and stress tolerance. *J. Exp. Bot.* 67, 47–60. <https://doi.org/10.1093/jxb/erv441>
- Kortz, A.R., Coelho, S., Castello, A.C.D., Leite, E.C. 2014. Wood vegetation in Atlantic rain forest remnants in Sorocaba (São Paulo, Brazil). *Check List*. 10, 344-354. <https://doi.org/10.15560/10.2.344>
- Leitman, P., Henderson, A., Noblick, L. *Arecaceae in Lista de Espécies da Flora do Brasil, Jardim Botânico do Rio de Janeiro.*, 2012. URL <http://floradobrasil.jbrj.gov.br/2012/> (accessed 08.01/.2020)
- Mariano, V., Christianini, A. V., 2016. Reproductive phenology, seed removal and early regeneration in relation to distance from parental plants of a native palm in small Atlantic forest fragments. *Acta Bot. Brasilica* 30, 176–182. <https://doi.org/10.1590/0102-33062015abb0302>
- Matos, D.M.S., Alves, L.F., 2008. Palm species distribution and soil moisture in a swampy area of the Atlantic Forest, south-eastern Brazil. *Ecotropica* 14, 69-74.
- Memmott, J., Craze, P.G., Waser, N.M., Price, M. V., 2007. Global warming and the disruption of plant-pollinator interactions. *Ecol. Lett.* 10, 710–717. <https://doi.org/10.1111/j.1461-0248.2007.01061.x>
- Mendes, C.P., Ribeiro, M.C., Galetti, M., 2015. Patch size, shape and edge distance influence seed predation on a palm species in the Atlantic forest. *Ecography* 39, 465-475. <https://doi.org/10.1111/ecog.01592>

- Mendoza, I., Peres, C.A., Morellato, L.P., 2017. Continental-scale patterns and climatic drivers of fruiting phenology: A quantitative Neotropical review. *Global and Planetary Change*. 148, 227-241. <https://doi.org/10.1016/j.gloplacha.2016.12.001>
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.E., Zach, S., Zust, A., 2006. European phenological response to climate change matches the warming pattern. *Glob. Chang. Biol.* 12, 1969–1976. <https://doi.org/10.1111/j.1365-2486.2006.01193.x>
- Miranda, J.M.D., 2005. Dieta de *Sciurus ingrami* Thomas (Rodentia, Sciuridae) em um remanescente de Floresta com Araucária, Paraná, Brasil. *Rev. Bras. Zool.* 22, 1141–1145. <https://doi.org/10.1590/s0101-81752005000400047>
- Moegenburg, S. M., 1996. Sabal palmetto seed size: causes of variation, choices of predators, and consequences for seedlings. *Oecologia* 106, 539-543. <https://doi.org/10.1007/bf00329713>
- Moles, A. T., Westoby, M. 2002. Seed addition experiments are more likely to increase recruitment in larger-seeded species. *Oikos* 99, 241-248.
- Morellato, L.P.C., Talora, D.C., Takahasi, A., Bencke, C.C., Romera, V.B.P. 2000. Phenology of Atlantic Rain Forest Trees: A Comparative Study. *Biotropica* 32, 811-823. [https://doi.org/10.1646/0006-3606\(2000\)032\[0811:POARFT\]2.0.CO;2](https://doi.org/10.1646/0006-3606(2000)032[0811:POARFT]2.0.CO;2)
- Morellato, L.P.C., Alberton, B., Alvarado, S.T., Borges, B., Buisson, E., Camargo, M.G.G., Cancian, L.F., Carstensen, D.W., Escobar, D.F.E., Leite, P.T.P., Mendoza, I., Rocha, N.M.W.B., Soares, N.C., Silva, T.S.F., Staggemeier, V.G., Streher, A.S., Vargas, B.C., Peres, C.A., 2016. Linking plant phenology to conservation biology. *Biol. Conserv.* 195, 60–72. <https://doi.org/10.1016/j.biocon.2015.12.033>
- Parmesan, C., 2006. Ecological and Evolutionary Responses to Recent Climate Change. *Annu. Rev. Ecol. Evol. Syst.* 37, 637–669. <https://doi.org/10.2307/annurev.ecolsys.37.091305.30000024>
- Post, E., Pedersen, C., Wilmers, C.C., Forchhammer, M.C., 2008. Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. *Proc. R. Soc. B Biol. Sci.* 275, 2005–2013. <https://doi.org/10.1098/rspb.2008.0463>
- R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing. <http://www.r-project.org/> (accessed 02.01.2020)

- Ribeiro, M. C., Metzger, J.P., Martensen, A. C., Ponzoni, F.J., Hirota, M.M. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* 142, 1141-1153.
<https://doi.org/10.1016/j.biocon.2009.02.021>
- Spinoni, J., Barbosa, P., De Jager, A., McCormick, N., Naumann, G., Vogt, J.V., Magni, D., Masante, D., Mazzeschi, M., 2019. A new global database of meteorological drought events from 1951 to 2016. *Journal of Hydrology: Regional Studies* 22, 100593.
<https://doi.org/10.1016/j.ejrh.2019.100593>
- Terborgh, J. 1986. Keystone plant resources in the tropical forest. In: Soule M. (ed.) *Conservation biology: the science of scarcity and diversity*. Sunderland, Sinauer Associates. 330-344
- Thuiller, W., 2004. Patterns and uncertainties of species' range shifts under climate change. *Glob. Chang. Biol.* 10, 2020–2027. <https://doi.org/10.1111/j.1365-2486.2004.00859.x>
- Varela, O., Bucher, E.H., 2006. Passage time, viability, and germination of seeds ingested by foxes. *Journal of Arid Environments* 67, 566–578. <https://doi.org/10.1016/j.jaridenv.2006.03.013>
- Van der Putten, W.H., Macel, M., Visser, M.E., 2010. Predicting species distribution and abundance responses to climate change: Why it is essential to include biotic interactions across trophic levels. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 2025–2034. <https://doi.org/10.1098/rstb.2010.0037>
- Vogado, N.O., Liddell, M. J., Laurance, S.G.W., Campbell, M.J., Chessman, A. W., Engert, J.E., Palma, A.C., Ishida, F.Y., Cernusak, L.A. 2020. The effects of an experimental drought on the ecophysiology and fruiting phenology of a tropical rainforest palm. *J. of Plant Ecology* 13, 744-753. <https://doi.org/10.1093/jpe/rtaa069>
- Wilson, R. J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R., Monserrat, V.J., 2005. Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters* 8, 1138-1146. <https://doi.org/10.1111/j.1461-0248.2005.00824.x>
- Wright, S.J., 2003. The myriad effects of hunting for vertebrates and plants in tropical forests. *Perspect. Plant Ecol. Evol. Syst.* 6, 73–86.
- Wright, S.J., Carrasco, C., Calderon, O., Paton, S., 1999. The El Niño Southern Oscillation, Variable Fruit Production, and Famine in a Tropical Forest. *Ecology* 80, 1632.
<https://doi.org/10.2307/176552>
- Yeh, S.W., Kug, J.S., Dewwite, B., Kwon, M.H., Kirtman, B.P., Jin, F.F. 2009. El Niño in a changing climate. *Nature* 461, 511-514. <https://doi.org/10.1038/nature08316>

3 CONSIDERAÇÕES FINAIS

As secas são capazes de alterar a sazonalidade da fenologia reprodutiva de *Syagrus romanzoffiana*, bem como influenciar na quantidade de cachos produzidos, tanto reduzindo a quantidade de cachos maduros, como aumentando o número de cachos com frutos imaturos, mas tais alterações não repercutem na quantidade de sementes que são predadas por besouros ou esquilos no local de estudo. No entanto, a predação de sementes de *S. romanzoffiana* varia de acordo com o tipo de agente e com o ano em análise. Os resultados sugerem que as mudanças climáticas afetem mais a reprodução das palmeiras do que a quantidade de sementes que perdem para predadores no local de estudo. A continuação da coleta de dados ao longo dos anos é importante para ampliar a resolução destes resultados e nos permitir ter maior entendimento sobre os fatores importantes para a reprodução da espécie e possíveis efeitos em outros níveis tróficos, bem como para analisar outros aspectos da biologia da espécie, como sua dinâmica populacional.

4 REFERÊNCIAS

- BERNACCI, L.C., MARTINS, F.R., SANTOS, F.A.M. Estrutura de estádios ontogenéticos em população nativa da palmeira *Syagrus romanzoffiana* (Cham.) Glassman (Arecaceae). **Acta Botanica Brasilica**, 22, 119-130, 2007
- GALETTI, M. & ALEIXO, A. Effects of palm heart harvesting on avian frugivores in the Atlantic rain forest of Brazil. **Journal of Applied Ecology**, 35: 286–293, 1998.
- GALETTI, M., DONATTI, C.I., PIRES, A.S., GUIMARÃES JR., P.R. & JORDANO, P. Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation. **Botanical Journal of the Linnean Society**, 151: 141-149, 2006.
- HULME, P.E. Post-dispersal seed predation: consequences for plant demography and evolution. **Perspectives in Plant Ecology, Evolution and Systematics**, 1: 32-46, 1998.
- IPCC. Land–climate interactions. In: *Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems*. IPCC, 2019. Disponível em: <<https://www.ipcc.ch/srccl/>> Acesso 08/02/2020.
- JORDANO, P. **Fruits and frugivory**. Pp. 125-165 in Fenner, M. (ed.). *Seeds: the ecology of regeneration in plant communities* (2nd edition). CAB International, Wallingford, 2000.
- MENDES, C.P., RIBEIRO, M.C., GALETTI, M. Patch size, shape and edge distance influence seed predation on a palm species in the Atlantic forest. **Ecography** 39, 465-475, 2015.
- MORELLATO, L.P.C., ALBERTON, B., ALVARADO, S.T., BORGES, B., BUISSON, E., CAMARGO, M.G.G., CANCIAN, L.F., CARSTENSEN, D.W., ESCOBAR, D.F.E., LEITE, P.T.P., MENDOZA, I., ROCHA, N.M.W.B., SOARES, N.C., SILVA, T.S.F., STAGGEMEIER, V.G., STREHER, A.S., VARGAS, B.C., PERES, C.A. Linking plant phenology to conservation biology. **Biol. Conserv.** 195, 60–72, 2016.
- MURCIA, C. Edge effects in fragmented forests: implications for conservation. **Tree** 10: 58-62, 1995

MYERS, N., MITTERMEIER, R.A., MITTERMEIER, C.G., FONSECA, G.A.B. & KENT, J. Biodiversity hotspots for conservation priorities. **Nature**, 403: 853–858, 2000.

REZENDE, C.L., SCARANO, F.R., ASSAD, E.D., JOLY, C.A., METZGER, J.P., STRASSBURG, B.B.N., TABARELLI, M., FONSECA, G.A., MITTERMEIER, R.A. From hotspot to hopespot: Na opportunity fot the Brazilian Atlantic Forest. **Persp. In Eco. and Con.** 16, 208-214, 2018.