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AMANDA FREITAS CERQUEIRA

PALMEIRAS NATIVAS DA MATA ATLÂNTICA: REVELANDO AS LACUNAS CIENTÍFICAS E DESVENDANDO A INFLUÊNCIA DA PERDA DE HABITAT EM ASPECTOS ECOFISIOLÓGICOS E GENÉTICOS DE UMA ESPÉCIE AMEAÇADA (*Euterpe edulis* Mart.)

ILHÉUS - BAHIA
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Tese apresentada à Universidade Estadual de Santa Cruz, como parte das exigências para obtenção do título de Doutor em Ecologia e Conservação da Biodiversidade.
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Profª. Drª. Rita de Cássia Quitete Portela
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Prof. Dr. Marcelo Schramm Mielke
Universidade Estadual de Santa Cruz
(Orientador)

"...Os guardiões naturais não têm armas pro concreto
Mata Atlântica te levanta, deixo meu peito aberto
Pra te guardar na lembrança, pra te contar pros meus netos
No registrar dos meus olhos vou te cantar nos meus versos
Se pudesse eu te dava as asas do pensamento
Quem sabe te guardaria do jeito que eu te penso
Criando os teus nativos, crescendo no teu silêncio..."

Luís Perequê

Dedico essa tese a todos que contribuem para preservar nossas florestas. Dedico também a minha mãe que sempre me apoiou e ao meu filho Heitor, para quem eu quero ajudar a construir um mundo melhor.

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RESUMO

A Mata Atlântica (MA) é um dos biomas florestais com maior biodiversidade e endemismo no mundo, mas com a sua flora e fauna altamente ameaçadas pelo desmatamento e fragmentação. As palmeiras (Arecaceae) exercem grande relevância para a estrutura e funcionamento desse bioma, além de disponibilizarem recursos essenciais para animais frugívoros. No entanto, muitas de suas espécies estão atualmente em risco de extinção devido à sobre-exploração, perda e/ou fragmentação florestal. Assim, os objetivos dessa tese foram: (i) contribuir para o avanço do conhecimento sobre a produção científica das espécies de palmeiras nativas da MA; (ii) investigar a capacidade de aclimatação à perda de habitat e à disponibilidade de luz de *Euterpe edulis*; e (iii) avaliar como fragmentos florestais inseridos em paisagens com diferentes níveis de desmatamento influenciam as características fisiológicas e genéticas de progênies de *E. edulis* quando essas são submetidas a uma ampla faixa de luz em um experimento semicontrolado. Especificamente, no primeiro capítulo realizamos uma revisão sistemática com abordagem cenciométrica reportando as lacunas na produção científica sobre as 78 espécies de palmeiras nativas da MA. Observamos que os estudos realizados para grande parte das palmeiras ainda são escassos, principalmente para algumas áreas do conhecimento, como a produção e manejo por comunidades locais, que podem ser o ponto de partida para descobrir e estimular o uso de produtos florestais não madeireiros. Em particular, os gêneros *Desmoncus*, *Geonoma* e *Trithrinax* merecem mais atenção em pesquisas futuras por apresentarem as espécies com o menor número de publicações. Além disso, as espécies mais estudadas como *E. edulis*, *Acrocomia aculeata* e *Syagrus ramanzoffiana*, ainda carecem de estudos em algumas áreas do conhecimento, bem como de estudos que sejam desenvolvidos na porção nordeste da MA, região menor amostrada nas pesquisas. No segundo capítulo, avaliamos a influência da perda de floresta e da disponibilidade de luz em atributos foliares e na aclimatação de indivíduos jovens de *E. edulis* em um gradiente de perda de floresta em escala de paisagem. Os resultados desse capítulo forneceram novas evidências sobre ocorrência de *E. edulis* em locais mais sombreados dentro dos fragmentos. Além disso, observamos que tanto a paisagem (cobertura florestal) quanto o contexto local (abertura de dossel) afetam os atributos foliares dessa espécie, levando a ajustes bioquímicos, químicos e morfológicos. No terceiro capítulo, analisamos como fragmentos florestais inseridos em paisagens com diferentes níveis de desmatamento influenciam as características fisiológicas e genéticas de progênies de *E. edulis* submetidas a uma ampla faixa de luz. As progênies provenientes das matrizes que se desenvolveram em fragmentos florestais inseridos em uma paisagem mais florestada apresentaram maior vigor, demonstrado pelas variáveis de crescimento, bem como maior capacidade de se ajustar à ampla variação na disponibilidade de luz e de manter balanço de carbono positivo em baixa disponibilidade desse recurso. Já as progênies provenientes de matrizes de fragmentos florestais inseridos em paisagens mais desmatadas apresentaram baixo número de alelos exclusivos e devem ser monitoradas para evitar o colapso dessas populações. Dessa forma, essa tese traz novas evidências da importância de manter os fragmentos florestais inseridos em paisagens altamente florestadas para garantir a manutenção de espécies como *E. edulis*, que se encontra ameaçada de extinção, a longo prazo. Em paisagens mais desmatadas, torna-se essencial a implementação de programas de restauração, bem como a introdução de indivíduos de locais mais florestados para aumentar a diversidade genética e a capacidade dessa espécie se adaptar frente às mudanças ambientais.

Palavras-chave: Floresta tropical, distúrbios antrópicos, palmeiras, palmito juçara, tolerância à sombra; marcadores microssatélites.

ABSTRACT

The Atlantic Forest (AF) is one of the forest biomes with the greatest biodiversity and endemism in the world, but with its flora and fauna highly threatened by deforestation and fragmentation. Palm trees (Arecaceae) have great relevance to the structure and functioning of this biome, in addition to providing essential resources for frugivorous animals. However, many species are currently at risk of extinction due to over-exploitation, loss and/or forest fragmentation. Thus, the objectives of this thesis were: (i) to contribute to the knowledge progress about scientific production of AF native palm species; (ii) to investigate the acclimation ability to habitat loss and the availability of light from *Euterpe edulis*, one of the palm trees that is threatened and has fundamental importance for the AF functioning; and (iii) to evaluate how forest fragments inserted in landscapes with different levels of deforestation influence the physiological and genetic characteristics of *E. edulis* progenies submitted to a wide range of light in a semi-controlled experiment. Specifically, in the first chapter, we carried out a systematic review with a scientometric approach reporting the gaps in scientific production on 78 AF native species. We observed that studies carried out for most palm trees are still scarce, especially for some areas of knowledge, such as production and management by local communities, which can be the starting point for discovering and stimulating the use of non-wood forest products. In particular, *Desmoncus*, *Geonoma* and *Trithrinax* genera deserve more attention in future research because they present the species with the least number of publications. In addition, the most studied species such as *E. edulis*, *Acrocomia aculeata* and *Syagrus ramanzoffiana*, still lack studies in some areas of knowledge, as well as studies that are developed in the northeast portion of AF, the smallest region sampled in the research. In the second chapter, we evaluated the influence of forest loss and the availability of light on leaf traits and acclimatization of young *E. edulis* individuals in a forest scale gradient on a landscape scale. The results of this chapter provided new evidence about the occurrence of *E. edulis* always in more shaded places within the fragments. In addition, we observed that both the landscape (forest cover) and the local context (canopy openness) affect the leaf traits of this species, leading to biochemical, chemical and morphological adjustments. In the third chapter, we analyze how forest fragments inserted in landscapes with different levels of deforestation influence the physiological and genetic characteristics of *E. edulis* progenies subjected to a wide range of light, from an experiment carried out in semi-controlled conditions. The progenies from the mother plants that developed in forest fragments inserted in a more forested landscape showed greater vigor, demonstrated by the growth variables, as well as a greater capacity to adjust to the wide variation in the light availability and to maintain a carbon positive balance in a low availability of this resource. The progenies from mother plants of forest fragments inserted in more deforested landscapes showed a low number of exclusive alleles and must be monitored to avoid the collapse of these populations. Thus, this thesis brings new evidence of the importance of maintaining forest fragments inserted in highly forested landscapes to guarantee the maintenance of species such as *E. edulis*, which is threatened with extinction in the long term. In more deforested landscapes, the implementation of restoration programs is essential, as well as the introduction of individuals from more forested places to increase the genetic diversity and the capacity of this species to adapt in the face of environmental changes.

Keywords: Tropical forest, anthropic disturbances, palm trees, juçara hearts of palm, shade tolerance; microsatellites markers.

INTRODUÇÃO GERAL

Existe uma crescente preocupação com a conservação das florestas tropicais, onde se encontram as maiores áreas de biodiversidade de todo o mundo (GASTON 2000; MYERS *et al.* 2000; PAN *et al.* 2013; Bellard *et al.* 2014) e onde são gerados diversos serviços ambientais como a disponibilidade de água e oxigênio. No entanto, a constante demanda para transformação dessas áreas em outros usos antropogênicos da terra, têm levado à redução e a fragmentação das florestas e consequentemente influenciando tanto na persistência das espécies como na provisão dos serviços ecossistêmicos. A perda de habitat causada por esses processos é considerada como uma das principais ameaças a biodiversidade e vem sendo apontada como a causa da extinção de várias espécies florestais (PIMM *et al.* 1995; WRIGHT & MULLER-LANDAU 2006; BARNOSKY *et al.* 2011).

Todas as mudanças antrópicas são ainda mais críticas quando ocorrem em ambientes de alta diversidade e endemismo, como é o caso do bioma Mata Atlântica, uma das florestas tropicais mais ameaçadas globalmente (RIBEIRO *et al.* 2009; REZENDE *et al.* 2018, FARIA *et al.* 2021). A Mata Atlântica está presente ao longo de toda costa litorânea brasileira desde o Rio Grande do Norte até o Rio Grande do Sul, além de parte dos estados do Mato Grosso do Sul e Goiás, e incluindo parte dos territórios da Argentina e Paraguai (BRASIL 2004). Apesar de sua ampla distribuição pelo território brasileiro, estima-se que permaneçam cerca de 11 a 16% da cobertura original de florestas no país, em sua maioria formada por pequenos fragmentos florestais inseridos em paisagens com diferentes porcentagens de floresta nativa circundante (Fig. 1) (SAATCHI *et al.* 2001; MARTINI *et al.* 2007; RIBEIRO *et al.* 2009).

Figura 1. Fragmento florestal da Mata Atlântica situado no município de Belmonte no Sul da Bahia, inserido em uma paisagem altamente desmatada (Foto: Maíra Benchimol).

Dentre as espécies que ocorrem naturalmente na Mata Atlântica, destacam-se as palmeiras pertencentes à família Arecaceae, muitas das quais estão vulneráveis a um declínio de riqueza e abundância (GALETTI *et al.* 2006), e encontram-se ameaçadas por processos como a perda de habitat (BENCHIMOL *et al.* 2016). São conhecidos aproximadamente 200 gêneros e 1500 espécies de palmeiras com distribuição predominantemente neotropical, diversificadas composições filogenéticas e formas de vida (HENDERSON *et al.* 2019; MUSCARELLA *et al.* 2020). Do ponto de vista ecológico, a família destaca-se nas florestas tropicais, podendo contribuir com mais de 50% do conteúdo energético disponível para fauna a partir dos seus frutos (SCHAEFER *et al.* 2002).

As palmeiras podem atuar como espécies-chave na manutenção e funcionamento dos ecossistemas florestais, através da produção de flores e frutos nos períodos de maior escassez de recursos (JOHNSON 1996). Além disso, vale destacar a utilização dessa família pelo ser humano, sendo um dos grupos de plantas mais utilizados em todo o mundo. Possuem destacada importância especialmente para os povos indígenas, provendo matéria-prima para construção de moradias, fibras para elaboração de ferramentas e utensílios, além de alimento para a subsistência, proveniente dos frutos e meristema apical (onde se encontra o palmito) (HENDERSON *et al.* 2019). Assim, devido ao uso diversificado, as palmeiras são um dos principais produtos florestais não madeireiros da Mata Atlântica (GRIMES *et al.* 1994; VAN ANDEL *et al.* 2004).

Muitos fatores afetam o estabelecimento e a sobrevivência das palmeiras em paisagens fragmentadas, desde processos em maior escala, como defaunação (GALETTI *et al.* 2013) e predação de sementes (MENDES *et al.* 2016; ANDREAZZI *et al.* 2012), a escalas mais finas, como mudanças nas condições abióticas e na diversidade genética e fluxo gênico entre populações (SANTOS *et al.* 2016; BROWNE & KARUBIAN 2018). Assim, as populações remanescentes são mais propensas à perda de alelos, a redução do fluxo gênico e depressão por endogamia (YOUNG *et a*l 1996; BROWNE & KARUBIAN 2018). Dentre as palmeiras que vem sofrendo com a esses processos destaca-se *Euterpe edulis*, conhecida popularmente como palmito juçara ou palmeira juçara (Fig. 2). Essa espécie se encontra ameaçada de extinção devido à redução de seu habitat e a superexploração de seu meristema apical (GALETTI & FERNANDEZ 1998). Além desses fatores, *E. edulis* possui uma grande importância para funcionalidade dos ecossistemas da Mata Atlântica, uma vez que produz uma grande quantidade de frutos, os quais são utilizados como alimento por cerca de 58 espécies de aves e 21 espécies de mamíferos (GALETTI *et al.* 2013).

Figura 2. Indivíduos de *E. edulis* em diferentes estádios ontogenéticos em fragmentos florestais da Mata Atlântica no Sul da Bahia. **a.** Indivíduo adulto; **b.** Plântula. **c.** Jovem (Foto: acervo pessoal).

Devido à alta produção de frutos, *E. edulis* é uma espécie que pode ser utilizada para recuperar manchas florestais degradadas uma vez que possui alta capacidade para atrair dispersores de sementes que podem transportá-las para fragmentos florestais vizinhos (REIS *et al.* 2000). Além disso, essa espécie ainda possui potencial econômico de uso-múltiplo de seus subprodutos, uma vez que, além do palmito, podem ser comercializados tanto frutos para produção de polpa semelhante ao açaí amazônico, como mudas para a restauração da Mata Atlântica. Portanto, é considerada uma espécie-chave para a manutenção da biodiversidade e funcionalidade desse bioma que se encontra em constante pressão antrópica.

Além de mudanças em escala de paisagem, como a perda de cobertura florestal, utilizada como um *proxy* de desmatamento (FAHRIG 2003), também podem ocorrer mudanças em escala local, como alterações no dossel influenciando na variação de luz que chega ao sub-bosque (ROCHA-SANTOS *et al.* 2016). Em resposta ao aumento na disponibilidade de luz, as plantas podem apresentar ajustes relacionados a mudanças no balanço de carbono a nível foliar e de planta inteira (GIVNISH 1988; VALLADARES &

NIINEMETS 2008). Em escala de folhas, o balanço de carbono é dependente dos processos de fotossíntese e respiração celular.

Em escala de planta inteira, este processo está relacionado com a capacidade de assimilação do carbono pelas folhas e com a eficiência na alocação de biomassa e a respiração das diferentes partes da planta. As folhas são órgãos altamente plásticos e apresentam mudanças nos seus atributos em função da disponibilidade de luz, como taxa de fotossíntese e respiração, área foliar, massa foliar específica, conteúdos de clorofila e nitrogênio, entre outros. Estudos baseados nos atributos foliares vem sendo utilizados com sucesso para avaliar respostas complexas do ecossistema às ações antrópicas em diferentes paisagens, como nas pastagens (AUBIN *et al.* 2007) e em florestas (MLÁDEK *et al.* 2011). No entanto, a maioria desses estudos se concentram em respostas a pastagens, ervas e arbustos e estão concentrados em ambientes temperados (FORTUNEL *et al.* 2009), ainda sendo necessários estudos que relacionem esses atributos às espécies da Mata Atlântica (VITÓRIA *et al.* 2019).

A capacidade de aclimatação das plantas às variações na disponibilidade de luz também pode ser avaliada a partir de variáveis, em escala de planta inteira, como a taxa de crescimento relativo, que corresponde ao incremento em biomassa a partir da biomassa inicial (HUNT 2003), e que está relacionado com o crescimento e a eficiência de interceptação de luz pelas folhas (POORTER 1999). Outra variável que permite avaliar a capacidade de aclimatação das plantas às variações na disponibilidade de luz é o ponto de compensação de luz em escala de planta inteira (WPLCP), que prediz o mínimo de disponibilidade de luz utilizado pelas plantas no processo fotossintético, para que ocorra um balanço de carbono positivo (BALTZER & THOMAS 2007). Como medida da tolerância à sombra de plantas crescendo no sub-bosque, o WPLCP é avaliado como o intercepto da relação entre a taxa de crescimento relativo e disponibilidade de luz, podendo ser considerado como uma medida de eficiência do uso da luz no interior de florestas. Apesar de fornecer informações relevantes, principalmente para plantas que regeneram no sub-bosque, o WPLCP tem sido pouco utilizado uma vez que para o seu cálculo, é necessário que as plantas estejam aclimatadas a uma ampla faixa de luz (BALTZER & THOMAS 2007; LUSK & JORGENSEN 2013).

Para aumentar a compreensão sobre o conhecimento científico de palmeiras nativas da Mata Atlântica, no **capítulo 1** desta tese foi realizada uma revisão sistemática com abordagem cenciométrica de todas as 78 espécies de palmeiras nativas do bioma, buscando identificar as espécies e regiões mais bem estudadas, principais áreas de conhecimento, padrões gerais, tendências e lacunas na pesquisa científica associada a esta família.

Nos **capítulos 2 e 3** foram utilizados indivíduos jovens de *E. edulis* como modelo para estudos ecofisiológicos e genéticos (Fig. 2c). Assim, no **capítulo 2** investigamos, em condições de campo, a influência da perda de floresta e da disponibilidade de luz em atributos foliares e na aclimatação de indivíduos jovens de *E. edulis* em um gradiente de perda de floresta em escala de paisagem. Especificamente buscou-se entender (i) como a abertura do dossel e a luz transmitida no topo de jovens de *E. edulis*, e no fragmento florestal, são afetados pela cobertura florestal em escala de paisagem; e (ii) como as características locais e de paisagem, combinadas e separadamente, afetam alguns atributos foliares amplamente conhecidos por estarem relacionados ao crescimento e à aclimatação das plantas em relação à disponibilidade de luz.

No **capítulo 3,** foi investigado como fragmentos florestais inseridos em paisagens com diferentes níveis de desmatamento influenciam as características fisiológicas e genéticas de progênies de *E. edulis* submetidas a uma ampla faixa de luz em um experimento realizado em condições semicontroladas. Especificamente, buscou-se verificar: (i) se progênies de diferentes matrizes (em inglês, *mother plants*) de *E. edulis* localizadas em diferentes fragmentos florestais apresentam padrões diferentes em termos de capacidade de aclimatação a uma ampla faixa de luz; (ii) se existe uma relação entre a diversidade genética e a resposta fisiológica para as progênies originadas de diferentes matrizes; (iii) se existe apenas uma influência da luz e/ou da matrizes nas características fisiológicas em plantas jovens de *E. edulis*.

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CAPÍTULO 1

Trends and gaps in the literature on native palms of the Brazilian Atlantic Forest

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Acrocomia aculeata

Allagoptera caudescens

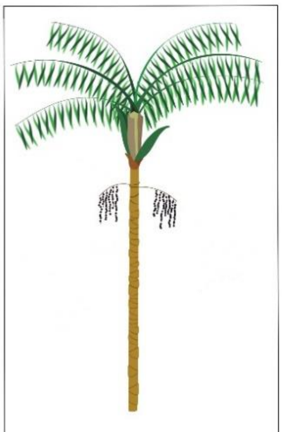
Astrocaryum aculeatissimum

Attalea funifera

Bactris setosa

Butia odorata

Desmoncus orthacanthos



Euterpe edulis

Geonoma pauciflora

Syagrus romanzoffiana

Trithrinax acanthocoma

Trends and gaps in the literature on native palms of the Brazilian Atlantic Forest

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ABSTRACT Palms (Arecaceae) exert great relevance to the structure and functioning of tropical forest ecosystems, in addition to comprise key resources for frugivorous animals. However, many species are currently at risk of extinction due to overexploitation and/or habitat loss. Our study aimed to perform a scientometric analysis of all 78 native palm species of the Brazilian Atlantic Forest, seeking to identify the best studied species, overall patterns, trends and gaps in scientific research associated with this botany family. In total, studies were carried out for 48 species belonging to 10 genera, with the number of studies exponentially increasing from the 70s and exhibiting great difference in the number of publications among species. In particular, *Euterpe edulis* was the most studied species (N=274), followed by *Acrocomia aculeata* (N=205), whereas *Bactris bahiensis* (1), *Geonoma litoralis* (1), *Syagrus santosii* (1), *Trithrinax acanthocoma* (0) comprised the less studied species. The largest number of studies was carried out in the southeastern states of Brazil. Regarding the type of studies, 34% and 27% were related to biochemical properties and ecological processes, respectively, while studies on entomology (N=26), tissue culture (N=23) and taxonomy (N = 7) showed the lowest number of studies. Given the key role of palms to tropical forests, our study suggests that future research should focus on less studied species, including *Desmoncus* spp., *Geonoma* spp. and *Trithrinax* sp, and on some less studied areas like the northeast portion of Atlantic Forest.

Keywords: Tropical forest, Arecaceae, palm trees, Scientometrics.

1. INTRODUCTION

Palm trees (Arecaceae) are among the main monocots in the world and comprise the most abundant vascular plants in the tropics (Dransfield et al., 2008). Species from this group comprise key components of forest structure and functionality in tropical ecosystems (Henderson et al., 2002), exhibiting great relevance from an ecological and socioeconomic perspective (Lieberman et al., 1985). Indeed, their flowers and fruits encompass fundamental resources for pollinator and fruit-eating animal species, since seeds and fruits are regularly available in periods of resource scarcity (Galetti & Aleixo, 1998; Genini, Galetti & Morellato, 2009). For this reason, several species are widely considered fundamental for biodiversity maintenance in tropical forests, including *Euterpe edulis* (Galetti et al., 2013) and *Attalea humilis* (Wright & Duber, 2001). Some palm species also have high economic and social value, being one of the main sources of non-timber forest products (Dos Reis et al., 2000; Oliveira et al., 2017) and/or being vastly used by local communities for different purposes, including food, medicine, and ornamental plants (Zambrana et al., 2007; Sosnowska & Balslev, 2009; Da Silva & Fish, 2012).

The Arecaceae family is predominantly distributed across the Neotropics (Muscarella et al., 2020), encompassing 200 genera and 2.500 species recognized worldwide (Pintaud et al., 2008). One of the centers of their diversity is South America, in which five genera stand out for their diversification at a specific level: *Attalea* (56 spp.), *Astrocaryum* (39 spp.), *Bactris* (61 spp), *Geonoma* (69 spp.) and *Syagrus* (35 spp.) (Pintaud et al., 2008). Among all neotropical biomes, the Brazilian Atlantic Forest (AF) harbors a great number of palm species, with 54 being endemic (Pitaud et al., 2008), in addition to retain one of the highest tree species richness worldwide (Myers et al., 2000). Distributed along the coast, this unique forest biome encompasses both tropical and sub-tropical climates and covers almost 15% of the Brazilian territory, but its domain also extends to the extreme northeast of Argentina and Uruguay and to the east of Paraguay. The AF is widely recognized a global biodiversity hotspot due to the eminent threats of extinction induced by anthropogenic activities combined with its great biological relevance (Myers et al., 2000; Ribeiro et al., 2009). Indeed, forest loss and fragmentation have drastically reduced the diversity of palms in forest patches in this biome (Benchimol et al., 2017) and coupled with overexploitation have led several species to the risk of extinction (Martinelli & Moraes, 2013).

Despite the paramount ecological and socioeconomic relevance of the AF, we still lack studies investigating quantitative and qualitative information of the scientific production associated with native palms from this biome. Some native species of AF also present distribution in other locations, including in the Amazon and Cerrado biomes in Brazil, in addition to nine other countries (Mesa & Galeano, 2013; Zambrana et al., 2007; Balslev et al., 2010; Alvez-Valles et al., 2018). Considering that the number of publications on palms in Brazil has been recently increased (Elias et al., 2015), an overall synthesis of studies focusing on native palms from AF throughout its geographic distribution would enhance our current scientific knowledge of this keystone group. Thus, it would turn possible to contribute to the identification of which taxa and types of studies (e.g., ecology, taxonomy, etc) have so far been mostly and uncommonly studied to therefore propose recommendations for future studies.

This study aimed to perform a scientometric analysis (i.e., quantitative and qualitative analysis of published articles, which examines the development and structure of scientific production; see Hood & Wilson, 2001) on native palm tree species native to the AF. For this, a comprehensive literature review was performed to include all studies that examined at least one Atlantic forest palm species, either within or outside the AF, intending to identify patterns, trends and gaps. In particular, it was evaluated: 1) the most (and least) studied species; 2) the time trend of publications; 3) the most addressed area of knowledge for each species; 4) the patterns of occurrence of keywords of the most studied species; 5) the geographic distribution of studies throughout the Neotropical region; and 6) priority areas for future research based on knowledge gaps.

2. METHODS

2.1 Search and database

We firstly consulted the list of all native palms species from the AF available in the Flora do Brasil 2020 database (http://floradobrasil.jbrj.gov.br) and in a book about the family (Lorenzi, 2010), which resulted in 78 species belonging to 11 genera. Based on this list, we subsequently conducted a Web of Science (https://www.webofknowledge.com/), SCOPUS (https://www.scopus.com/) and Google Scholar (https://scholar.google.com.br/) search, published throughout the period available in these databases until December 2020. To cover a larger number of studies, the search was made for each species separately, by including the scientific name in quotes, as well as its synonym - for example "*Allagoptera arenaria"* OR "*Cocos arenaria*" OR "*Allagoptera pumila*" OR "*Diplothemium littorale*" OR

"*Diplothemium maritimum*" OR "*Diplothemium arenarium*" (see Table S1). In particular, the search for "*Euterpe edulis*" (a valuable non-timber species, currently classified as vulnerable to extinction) resulted in a remarkable number of studies, so we added the term "Atlantic Forest" to restrict our search. Extinction risk category was also added to each species, when available, based on the Brazilian Red List (Martinelli & Moraes, 2013) (Table S1).

We used a strict set of criteria to select the studies compiled in our initial search. First, the study must have been conducted with species that naturally occur in the AF, based on either *in situ* or *ex situ* surveys. Studies available in English, Spanish or Portuguese were included in the database. Also, we considered all studies carried out within the occurrence distribution of species in the Neotropical region both within and outside the domain of the AF, because species such as *Acrocomia aculeata* occur not only in the AF, but also in Cerrado. Additionally, the study must have examined at least a single native palm species, focusing on any aspect of the knowledge related to ecological, physiological, genetic, morphological, production and use, biochemical or nutritional properties, taxonomic, entomology or tissue culture. We did not include neither studies focused on floristic surveys, which only reported species occurrence nor review studies. Thus, four stages for study selection were established: (*i*) identification, (*ii*) screening, (*iii*) eligibility and (*iv*) inclusion (Figure 1). During these stages, both duplicate articles and studies carried out outside the area of natural occurrence of the species were excluded. We considered studies from gray literature (e.g. theses and dissertations) in our search, only excluding those already related to a published article in order to avoid that different publications, but with the same data set, were counted twice. After the screening, the title and abstract were analyzed and articles that did not meet the criteria were excluded. Finally, the remaining articles were read and if achieved the established criteria for inclusion were incorporated into the final database.

2.2 Categorization and data analysis

We ranked the number of overall studies conducted per species. We thus assessed the temporal trend of publications by extracting the year of publication and related it to the number of published studies, considering all species together; the trend line was chosen based on the best fit - analysis was performed using the program R 3.5.2 (R Core Team, 2018). We subsequently categorized each study into nine areas of knowledge based on the obtained data compilation (Table 1).

TABLE 1 Categorization of area of knowledge for each native palm species studied in the Atlantic Forest.

Assigned number	**Area of knowledge**	**Description**
1	Ecology	Phenology, conservation, population dynamics, interactions, effects of disturbances or evolution
2	Production and use	Production and transformation of forest products, management/use by local communities
3	Biochemical and/or nutritional properties	Vegetable compounds used as raw material for the isolation of one or more biochemical substances, or use for nutritional purposes or biological activity testing for nutritional purpose
4	Physiology	Influence of abiotic factors on germination, growth and development, basic and applied physiology
5	Morphology	Description, biometrics, anatomy, establishment of methodologies to measure any morphological attribute
6	Genetics	Genetic diversity, population structure, gene flow, marker making, phylogenetics, genetic improvement or cytogenetics
7	Taxonomy	Description of new species, taxonomy or phylogeny.
8	Entomology	Description or study assessing the insects in palms
9	Tissue culture	In vitro germination, tissue culture analysis.

Considering that ecology and biochemical studies encompass a wide range of sub-areas, we also analyzed the data into two sub-categories– i.e., community and population-level for the former, and extraction and application for the latter. For "biochemical properties" the studies were classified as "characterization" when their main objective was to characterize biochemical compounds from parts of palms or describe the extraction of these compounds, whereas "application" protocols refer to those that used the extracted active principle for some practical purpose. For the ecological studies, we grouped into two subcategories “population” for studies focused on dynamics and aspects of the species of interest, and “community” for studies that evaluated the species of interest within a broader study which aimed to verify some pattern or process in the species within the community.

For those species encompassing a great number of studies (≥ 200), we performed a bibliometric analysis using VOSviewer (Van Eck & Waltman, 2007), and created a map of the keywords that were most frequently considering all studies, seeking to understand the structure of the academic literature. VOSviewer is a software for creating maps based on bibliographic data and for visualizing and exploring the maps for citations, authors, countries, keywords and others bibliometric metrics. In this study, this software was used for analyzing the co-occurrence of keywords, that is, the frequency of the same keyword being used in different studies. For this, we selected co-occurrence as the type of analysis and all keywords as the unit of analysis. We selected five shared keywords as a minimum threshold level. This software by means of algorithms, forms clusters classifying the most frequent keywords. The words present in the clusters are directly related to each other. The size of each word in the cluster is related to its weight, that is, its co-occurrence in publications.

We used the geographical coordinates of each site location to produce a spatial distribution map of studies on native Atlantic forest palms across the Neotropical region using the QGIS 3.2.1 program (2.18.26). The AF covers a very extensive latitudinal breadth, mainly in the Brazilian territory. Based on its similarities, we call the region that covers the Brazilian states from Rio Grande do Norte to Espirito Santo the northeast portion of AF, and the region that goes to the region from the state of Rio de Janeiro to Rio Grande do Sul of south/southeast portion of AF. For the studies carried out *in situ*, the geographic coordinates of the collection site were used, while the coordinates of research development (e.g., university laboratory, nurseries, and others) were used for *ex situ* studies. When the study included more than one location, the central coordinate of those sites was used. Studies investigating more than one species were counted separately for each species, where each row in the database referred to one species. We also created a map for each genus, to identify the priority areas for future studies where a small number of studies (i.e. none up to five publications) were recorded by state or country.

3. RESULTS

From the initial search for studies on palm species, a total of 19.390 publications were identified with all three used databases. Considering just the list of 78 palm species native to the AF and the exclusion criteria, a total of 16.521 articles were further selected, of which only 938 met the eligibility criteria and were included in subsequent analyses. These studies covered at least one species of palm, including 48 species of ten genera of the native palms of

AF (Figure 1). For a total of 30 species, no study has been obtained regarding any area of knowledge (Table S1).

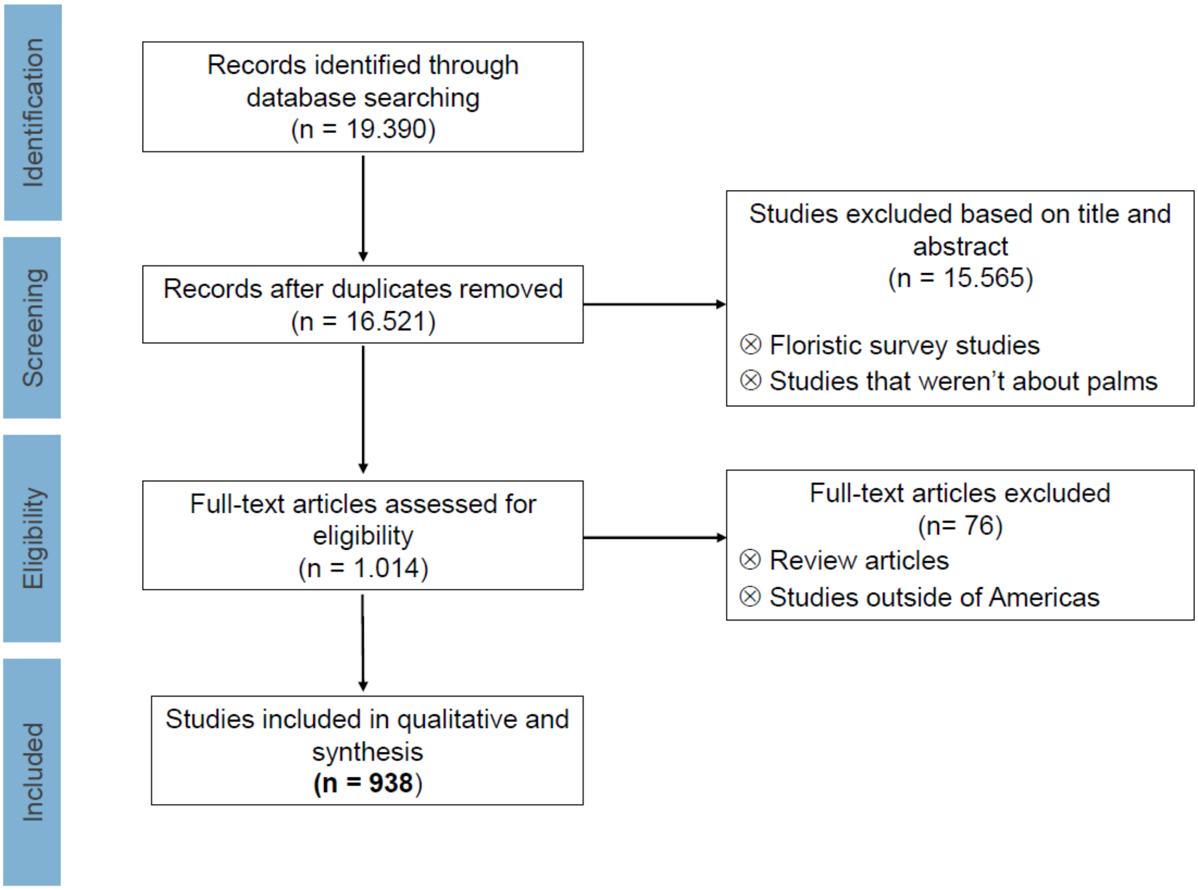

FIGURE 1 Steps for selecting studies on native palm trees occurring in the Atlantic Forest. The number of studies obtained at each stage is indicated in parentheses.

3.1 Most studied species

The number of publications per species greatly varied, but most species appeared in less than 10 studies (Figure 2). In particular, the threatened *Euterpe edulis* had the greatest number of studies (N= 274), followed by *Acrocomia aculeata* (N=205), *Syagrus romanzoffiana* (N=77), and *Attalea funifera* (N=60). On the other hand, nine species appeared in only one study: *Attalea burretiana*, *Bactris bahiensis*, *Bactris caryotifolia*, *Bactris horridispatha*, *Geonoma conduruensis*, *Geonoma litoralis*, *Syagrus amicorum*, *Syagrus picrophylla*, and *Syagrus weddeliana*.

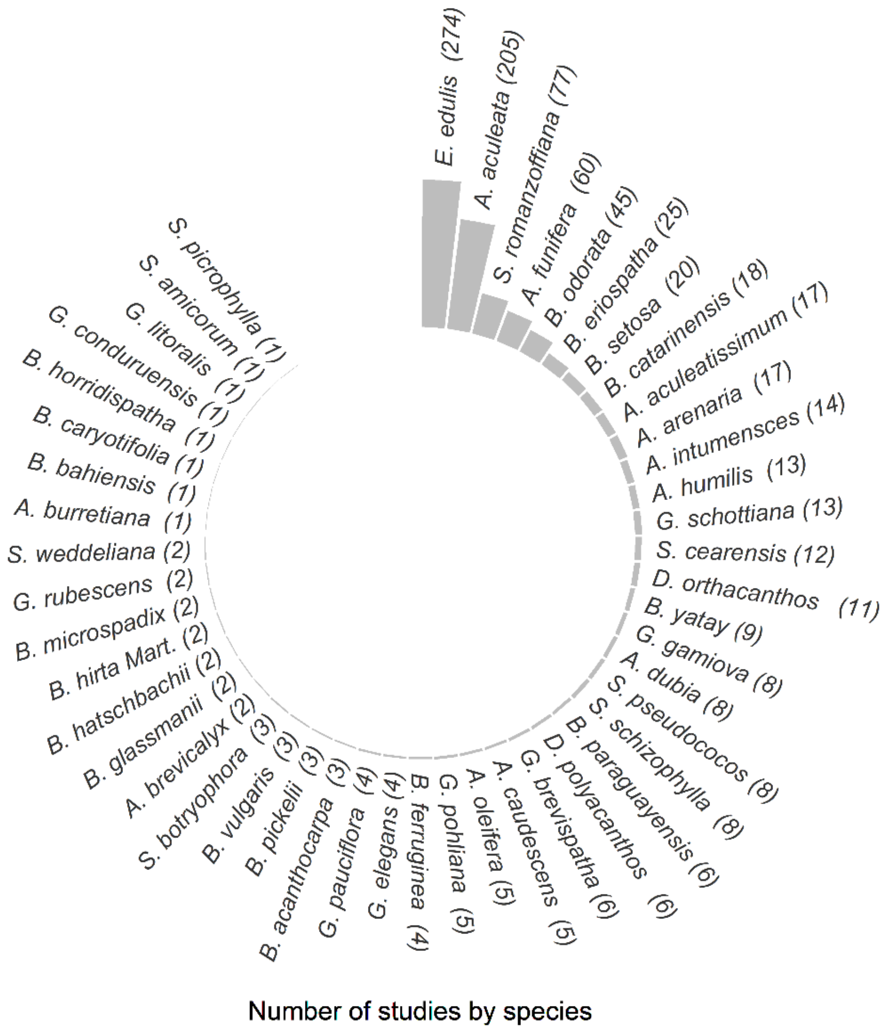

FIGURE 2 Total number of publications encompassing 48 palm species that presented at least one study published between 1974 and 2020 and indexed in the WOS, Scopus or Google Scholar databases.

3.2 Temporal trend of publications

The number of publications exponentially increased during the surveyed period ($R^2 = 0.94$; $p < 0.05$; Figure 3). Specifically, the number of studies has considerably grown since 2004, with 75% being published in the last decade.

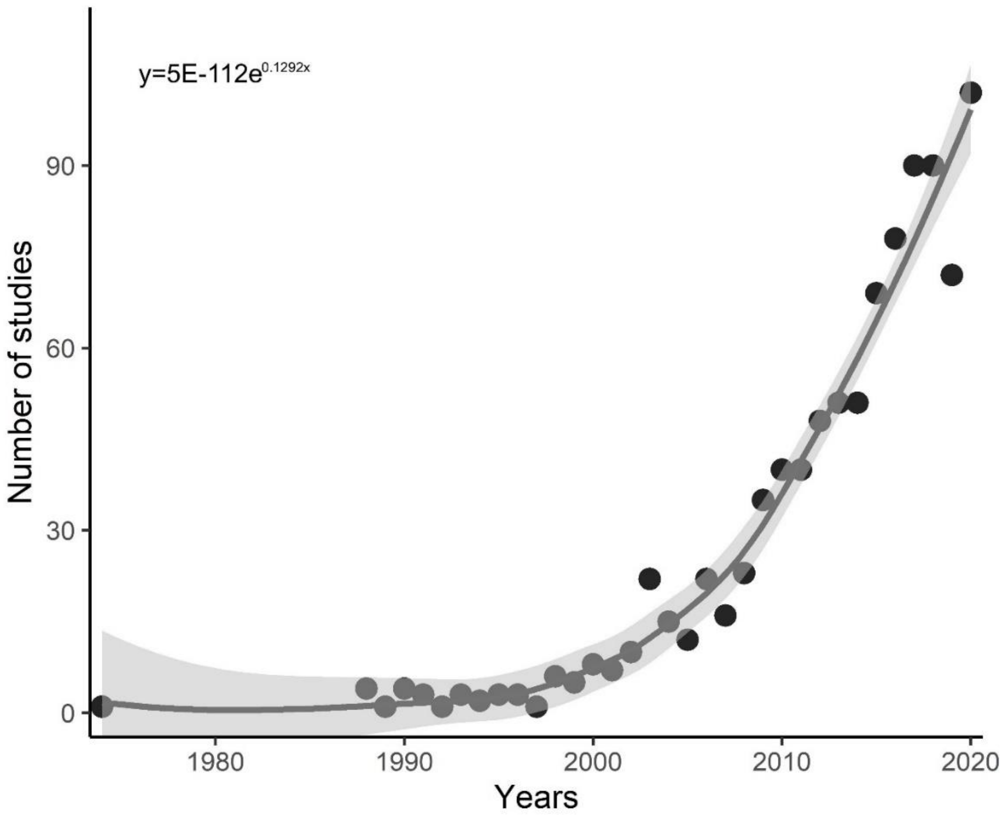

FIGURE 3 Time trend of the total number of publications indexed in the WOS, Scopus or Google Scholar databases (N=938) containing at least one palm species studied between 1974 and 2020.

3.3 Main areas of knowledge

Among all nine areas of knowledge, we observed that most studies belonged to "biochemical properties", followed by "ecology" (Figure 4 and Table S2). The genus that presented the largest number of study types were *Euterpe* (N = 274) and *Acrocomia* (N = 219), whereas *Astrocaryum* (N = 17) and *Desmoncus* (N = 17) presented lower numbers. Considering all genus, few studies encompassed "production and use" (N = 41), "entomology" (N = 26), tissue culture (N = 23) and "taxonomy" (N = 7). Among the area of knowledge, only "ecology" was recorded for all genera, and also presented the largest proportion of studies by genus for *Astrocaryum* (88%, N = 15), *Bactris* (63%, n = 23), *Geonoma* (55%, N = 24), *Syagrus* (42%, n=46), *Desmoncus* (41%, N = 7), *Euterpe* (33%, N = 92), *Allagoptera* (32%, N = 7), *Attalea* (28%, N = 24) and *Acrocomia* (3,5%, N = 7). We found 137 studies about "physiology", which were accomplished all the existing genera at AF except for *Bactris* that no study was registered. Other areas reasonably studied were "genetics" (N = 72), followed by "morphology" (N = 52) and "production and use" (N = 41) (Table S1).

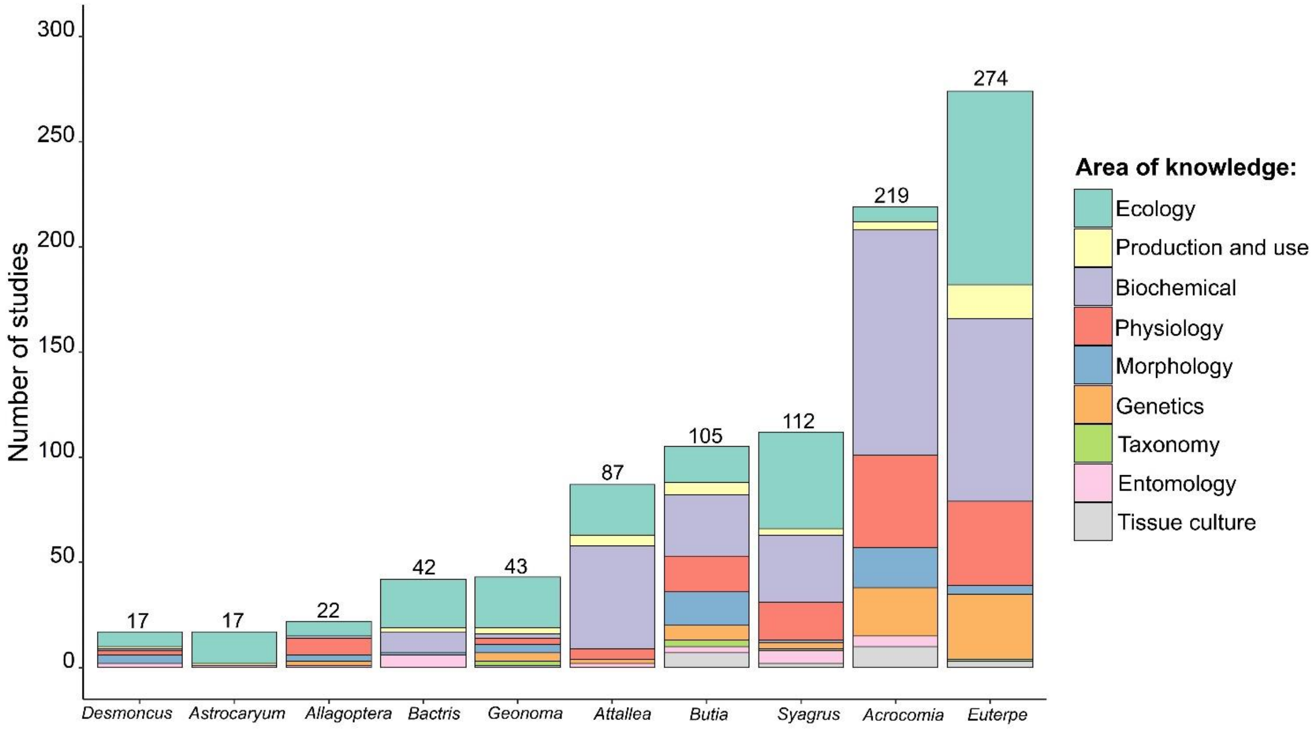

FIGURE 4 Number of publications in relation to the area of knowledge for palm species. (A) Number of publications referring to ten genera of palm trees for each study type. 1 = Ecology; 2 = Production and use; 3 = Biochemical and/or nutritional properties; 4 = Physiology; 5 = Morphology, 6 = Genetics; 7 = Taxonomy; 8 = Entomology; 9 = Tissue culture.

Regarding sub-categories herein considered for biochemical properties and ecological studies, we observed that those nine genera with studies in "biochemical" and "ecology" had a balanced number of studies among the subcategories, except *Bactris* spp., which presented a smaller number of studies for "application" (Figure 5). Additionally, for *Allagoptera* spp., *Desmoncus* spp. and *Geonoma* spp. we found few studies for this area of knowledge. For example, we detected only one study focused on 'application' for *Allagoptera* spp., a single study on 'characterization' for *Desmoncus* spp. and one study in each subcategory for *Geonoma* spp. For ecological studies, the genera that had the smallest amount of study for these "ecological" subcategories were *Acrocomia* spp. in which no studies were carried out at the community level and for *Desmoncus* spp. where one study fell into this subcategory. For the other genera, we observed no differences, except for *Euterpe* sp and *Syagrus* spp., where the number of studies was higher for the subcategory "population" (Figure 5).

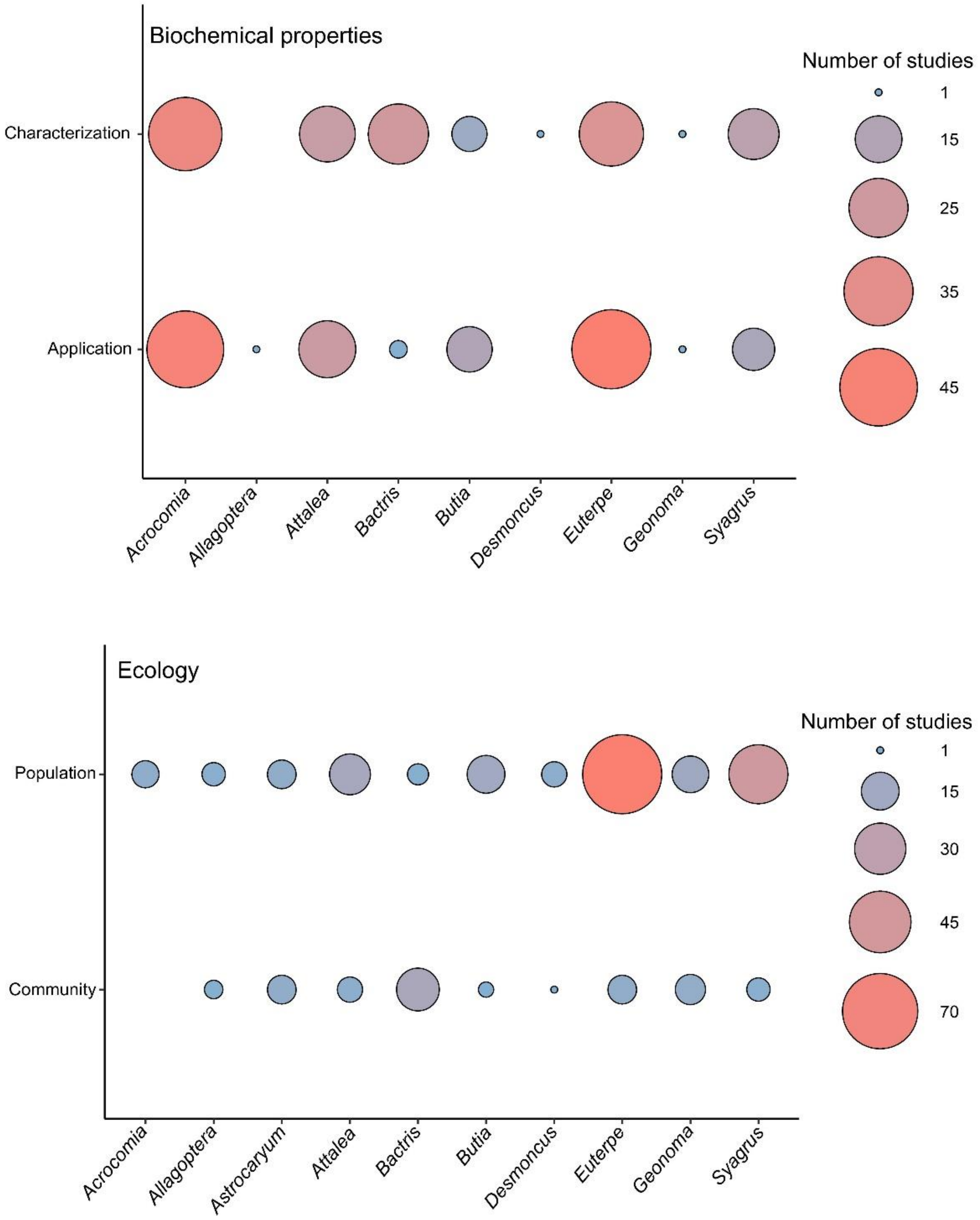

FIGURE 5 Subcategories for the two areas of knowledge showing the largest number of studies for the ten genera of palms native to the Atlantic Forest. (a) Biochemical properties and (b) Ecology.

Given that only a single species, *E. edulis*, exhibited greater than 250 studies, we subsequently investigated the pattern of its co-occurrence of keywords (Figure 6). Among the 274 articles analyzed, 2.621 keywords were found. Among them, 178 keywords were shared at least 5 times among these articles. Based on the analyses, we found that 43% from keywords were related to “ecology” (such as predation and regeneration) and 57% grouping words such as anthocyanins and antioxidants related to studies that investigated the biochemical of the analyzed palm species.

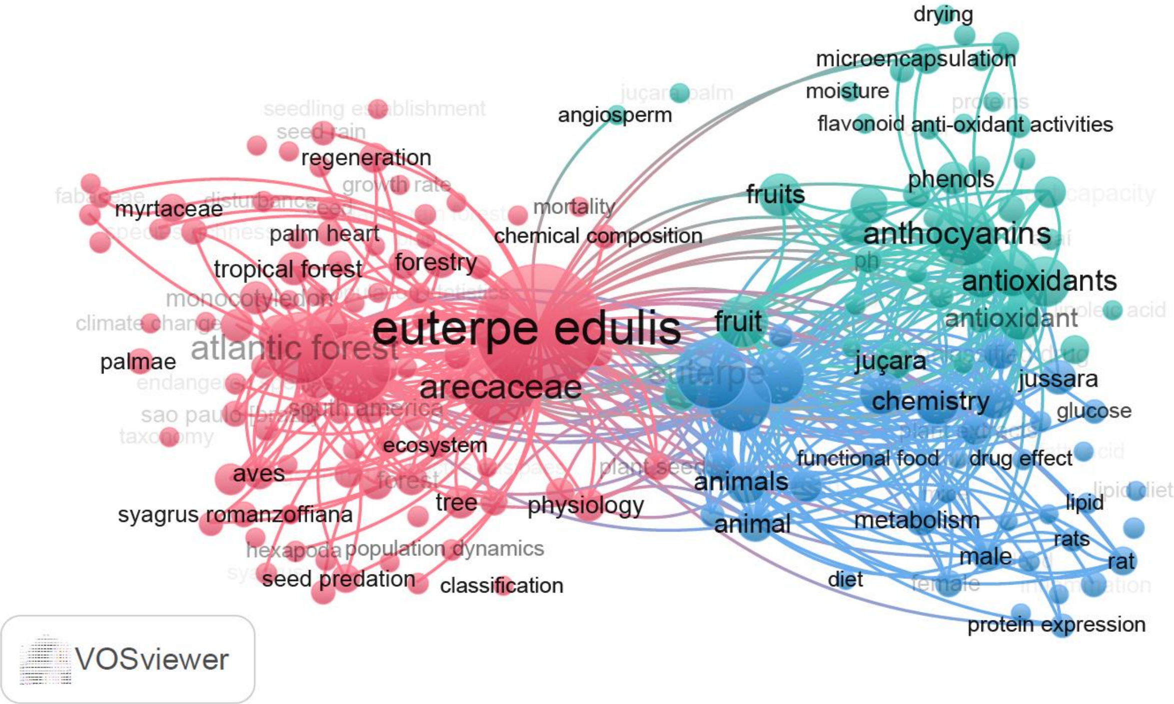

FIGURE 6 Keyword co-occurrence network built with 274 studies for *E. edulis*, published between 1974 and 2020. The 178 dots with different colors represent the 178 keywords. The size of a dot represents the frequency of the keywords. The line between two dots represents that both keywords occurred in one study.

3.4 Geographic distribution of studies

The studies examining native palms covered the entire AF biome, with a small number of studies being conducted outside of AF. In general, the greatest number of research was carried out in the south/southeast portion of AF and the smallest in the northeast portion of AF (Figure 7). In addition, we also observed few isolated studies for some species that also occur outside Brazil, such as *Euterpe* sp., *Acrocomia* spp., and *Butia* spp. in Argentina and *Desmoncus* spp. in Peru. Despite the low number, it is noted that studies referring to the *Syagrus* spp. have the highest concentration in the northeast portion of AF and in Argentina. While for the *Geonoma* spp., the studies were restricted to São Paulo and a few others spread over other regions, like the coast of Bahia. Studies carried out for *Attalea* spp. have concentrated on the southern coast of Bahia, some isolates in the Amazonas state, and also in the southeastern states of Brazil. For *Bactris* spp., isolated publications were observed in some states and only one research was developed with *Desmoncus* spp. in the AF, with isolated research in northern Brazil and some countries like French Guiana, Peru and Mexico (Supporting Information).

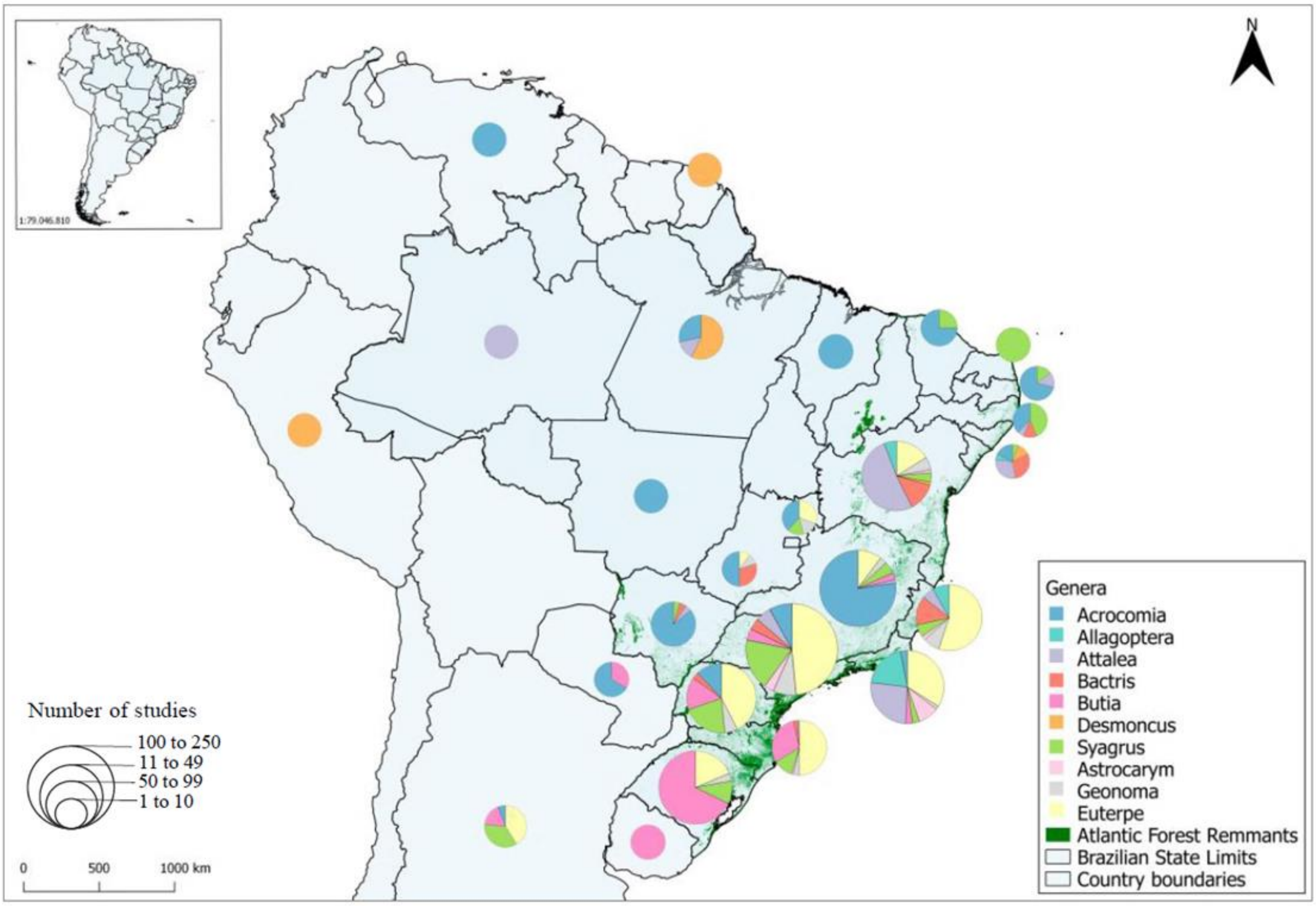

FIGURE 7 Distribution of publications in South America per genus indexed in the WOS, Scopus or Google Scholar databases for palms studied between 1974 and 2020.

Based on the potential occurrence of each genus related to the distribution of studies (Figure S1), we were able to identify areas that should be prioritized for future research. For instance, although *Desmoncus* spp. have a wide potential for occurrence throughout South America, studies with this genus are quite sparse; we therefore indicate several states that should be prioritized for future studies (Table 2). For *Euterpe* sp., we observed a distribution of studies throughout its occurrence area, although places such as the northeast portion of AF and Argentina should be prioritized for future research as we discuss ahead. A summary of the ten genera of palms and the regions that should be prioritized for future research is presented in Table 2.

TABLE 2 Genera of palm trees native to the Atlantic Forest with their respective areas of knowledge and region that should be prioritized for future research.

Genus	Areas that should be prioritized for future research	Priority locations for future research
Acrocomia	Ecology, production and use, taxonomy, entomology and tissue culture	Bahia, Pará, Mato Grosso, Rio de Janeiro, Espírito Santo (all in Brazil), Argentina and Paraguay
Allagoptera	Genetics, production and use, morphology, biochemical and / or nutritional properties	Bahia, Espírito Santo, Sergipe and Paraná (all in Brazil)
Attalea	Morfology and genetics	Bahia, Espírito Santo and São Paulo (all in Brazil)
Bactris	Production and use, morphology, ecophysiology, taxonomy and genetics	Bahia, Sergipe, Minas Gerais, Rio de Janeiro, Paraná, Rio Grande do Sul and Santa Catarina.
Butia	Production and use, taxonomy, entomology and tissue culture	Bahia, Santa Catarina (all in Brazil)
Desmoncus	Production and use, physiology, genetics and taxonomy	All Atlantic Forest
Euterpe	Physiology, production and use, morphology, taxonomy and genetics	Bahia, Sergipe, Alagoas, Pernambuco (all in Brazil), Argentina and Paraguay
Geonoma	Physiology, biochemical and / or nutritional properties, morphology	Alagoas, Bahia, Espírito Santo, Rio de Janeiro, Minas Gerais and Pernambuco (all in Brazil)
Syagrus	Physiology, ecology, morphology, and production and use	Espírito Santo, Sergipe (all in Brazil)
Trithrinax	All types of studies	Rio grande do Sul, Santa Catarina and Paraná (all in Brazil)

4. DISCUSSION

4.1 Most studied species and time trend in publications

This is the most comprehensive review of palm studies showing natural distribution in the Brazilian Atlantic Forest, one of the most threatened biomes on Earth (Myers et al., 2000). Out of 78 species occurring in the AF, 61% have been studied at least once, with the endangered *E. edulis* accounting for the greatest number of studies. It is notable the increase in studies on palm trees over the past 40 years, yet they are specific to a few species, limiting the knowledge of the Arecaceae family in terms of ecological and socio-environmental importance. Species with low number of studies is rare. They have been recently described or exhibit a narrow range of distribution. For instance, *G. bondariana e G. conduruensis* have been described in 2009 (Lorenzi et al., 2010) and *Trithrinax acanthocoma,* which despite described for a long time, has a very limited distribution (Santa Catarina and Rio Grande do Sul states of Brazil). Given the crucial importance of palm species for the structure and function of Atlantic forests (Lieberman et al., 1985) and their high economic and social value, further research poses as necessary aiming to either propose conservation strategies or disseminate their importance.

Our results show that *E. edulis* and *A. aculeata* were the most studied palm species across the AF. In fact, we observed the greatest number of ecological studies for *E. edulis*, probably due to its key importance as food resource for frugivorous animals, especially in times of scarcity, being considered a key species for the biodiversity maintenance (Galetti et al., 2013). Other reason can be related to its inclusion in the list of endangered species in 2008 (MMA, 2008). This species has also been suffering intensive extractive exploitation, as well as the fragmentation and reduction of its habitat, leading to drastic reduction in their natural population in Atlantic Forest remnants (Martinelli & Moraes, 2013; Portela & Dirzo 2020). The main reason for anthropogenic exploitation is due to its meristem (heart of palm), which is used in Brazilian cooking (Galetti & Fernandez, 1998). Over the last years, several studies have been carried out with *E. edulis* to mitigate this scenario, mainly at the population level and seeking to understand the mechanisms involved in its germination (Pizo et al., 2006; Barros Leite et al., 2012), dispersion (Da Silva et al., 2017; Dos Santos et al., 2018), phenology (Galleti et al., 1999; Tres et al., 2020), predation (Fleury & Galetti, 2004, Soares et al., 2015), and genetics (Santos et al., 2015; Soares et al., 2019; Coelho et al., 2020). Community-level studies, although few, have brought advances in analyzing processes such as habitat loss and fragmentation (Portela et al., 2014; Benchimol et al., 2017) besides the influence of altitude on palm species (Oliveira et al., 2014). In addition to its ecological importance, *E. edulis* is one of the main sources of non-timber forest products in AF, being widely used as a food, ornamental, and handicraft product (Oliveira et al., 2017). Thus, the properties and different ways of processing its fruits for human consumption have been extensively studied to enable species persistence (Inácio et al., 2013; Geraldi et al., 2018).

Indeed, several studies included in our review have focused on biochemical properties of *E. edulis*, mainly on the bioactive compounds of its fruit (Schulz et al., 2016; Cardoso et al., 2018). Another important aspect revealed by this study is the lack of interdisciplinary studies, i.e., those coupling more than one area of knowledge, such as “genetics” and “biochemical properties” or “genetic” and “physiology”. This could substantially enhance the management actions focused on species conservation of *E. edulis*.

The second species with the greatest number of studies, *A. aculeata*, popularly known as “macaúba” or “macaw palm”, is a palm tree native to Central and South America (Lorenzi, 2006). Most of studies carried out were due to its various applications and uses, since it has been exploited as a source of raw material for food, pharmaceuticals, cosmetics and mainly for biofuels (Colombo et al., 2018). Indeed, the use of oil from its mesocarp to produce biodiesel is the main factor associated to the growing number of studies. Additionally, *A. aculeata* fits into the new perspective of sustainability awakened in recent years, which seeks to reduce the emission of pollutants generated by the combustion of fuels fossils and the search for renewable alternatives in the production of biofuels (Cavalcanti-Oliveira et al., 2015; Teixeira et al., 2017). For this reason, much research has focused on the characterization and analysis of compounds (Oliveira et al., 2014; Evaristo et al., 2016) or on the application for this nutritional aspect (Ferreira et al., 2018; Prates-Valério et al., 2019) besides the production of biofuel (Iha et al., 2014; Da Conceição et al., 2017). Given that the germination in *A. aculeata* occurs slowly even when seeds are removed from the fruit (Ribeiro et al., 2011), and seed dormancy has limited their wider commercial use, some studies have investigated the physiological aspects of the germination of this species (Pires et al., 2013; Bicalho et al., 2016; Coelho et al., 2019).

The growing number of publications with native palms from AF followed a global trend of exponential growth in the number of scientific publications over recent decades (Nabout et al., 2012; Tinoco et al., 2015; Pereira et al., 2018). Scientometric analyses have also shown a significant increase in scientific production of native palms in the state of Santa Catarina, Brazil (Elias et al., 2015). Furthermore, there are some factors that have increased the number of publications over the years, including the beginning of the indexing of studies in databases, the increase in number of scientific journals, as well as the expansion of research grants with the increase of postgraduate courses in Brazil. In fact, these courses expanded in the 1990s, boosting research and further contributing to disseminate the thesis and dissertations related to palms (Mugnaini et al., 2004).

4.2 Area of knowledge

For palms of the genus *Syagrus*, the most studied area of knowledge was "ecology". The characteristics of the species most studied in this genus, *S. romanzoffiana*, justify the greater number of studies in this area, once its fruits are consumed by many frugivores, including a wide variety of insects as well as vertebrates such as rodents, squirrels, agoutis, among others (Galetti et al., 1992; Silva et al., 2011; Sica et al., 2014). It is therefore considered a key species for neotropical frugivores (Giombini, Bravo & Martínez, 2009), which may explain the interest in ecological studies with this species. Popularly known as "Jerivá", it is a palm widely distributed from northeastern Brazil to Argentina, being one of the only palms that occurs in the transition from the AF and the Pampa biomes (Henderson, 2002). Other characteristics of *S. romanzzofiana*, as its seeds rich in oil, explain the class of "biochemical properties" appearing as the second most studied for this species with the aim of investigating the oil properties of this palm for biodiesel production (Falasca et al., 2012; Moreira et al., 2013). Knowledge areas such as genetics and tissue culture have been little studied and deserve therefore attention in future research due to the potential of this species, especially for genetic improvement in the optimization of the biodiesel production.

For *Butia* spp., most studies have focus in its "biochemical and nutritional properties" as a potential source of phenolic compounds, carotenoids, and vitamin C (Beskow et al., 2015; Hoffmann et al., 2017), as well as its antioxidant and anti-tumor activities (Boeing et al., 2020). The most studied species was *Butia odorata*, known as "jelly palm". Its fruits are very appreciated for consumption *in natura* or processed in juice, liquor, pulp or frozen, which justifies the greater number of studies for this class. Another area of knowledge with a notable number of studies was "physiology". Due to the increase in publications with this species, there was a great demand for seedlings, whose production is restricted by seed dormancy, a characteristic that can delay its germination in more than two years (Schlindwein et al., 2013). Thus, physiological studies that seek to identify the most appropriate conditions for germination and cultivation are extremely important for obtaining quality seedlings. Despite their social and economic importance, the natural populations of *B. odorata* have been constantly suffering the consequences of anthropogenic action, mainly due to the implantation of monocultures, extensive livestock and urbanization, especially in coastal areas (Rivas & Barilani, 2004). Thus, areas of knowledge little explored such as genetics are extremely important to assess the genetic variability of the remaining natural populations and provide subsidies for the establishment of conservation strategies, sustainable management and genetic improvement of this species.

The most evident area of knowledge for the *Attalea* spp. was “biochemical and nutritional properties” probably due to the main species *A. funifera,* known as “piassava da Bahia”, which is native and endemic to the Atlantic coast of the state of Bahia. Most of the studies carried out were due to the great use of its fibers. Because they are long, non-elastic and show high flexibility, they are used in the national and international market for the manufacture of brooms and industrial use (D’Almeida et al., 2006). Thus, scientific production has been focused on evaluating its physical, chemical or mechanical properties (Aquino et al., 2003) and the traction property when subjected to certain treatments (Reis & Mota, 2014). Another important characteristic is the possibility of using this species to recover degraded areas, which may explain the number of studies related to the ecology. This species has a high germination rate in acidic and low fertility soils, considered unsuitable for the production of other species (Melo, 2001) and due to its various uses and ease of production, it generates benefits for the economy of local communities (Voeks et al., 1996). In fact, the vegetable fiber of *A. funifera* occupies the 5th position among the most commercialized Brazilian non-timber forest products (Pimentel et al., 2020). Despite the importance of this species for the conservation of forest remnants, in generating income from agro-extractive families and the historical use of their products, few studies have been found focused on understanding the processes of their use by local communities, which should be prioritized in future research. In addition, further studies that investigate the physiology of this highly tolerant species to germinate in acidic soils deserve to be highlighted in future investigations due to the high demand to restore degraded areas in which AF is currently found.

The *Geonoma* spp. comprises about 50 species, widely distributed throughout Central and South America (Ostrorog & Barbosa, 2009). The largest number of studies for this genus was found in “ecology”, mainly due the species *G. schottiana,* which exhibited the greater number of publications for this genus. Similar to other species of this genus, it is an understory palm associated with humid soils, with its distribution from the AF to the gallery forests in central Brazil (Chazdon, 1991; Oliveira-Filho & Ratter, 1995). The main influence for the great number of publications within the “ecology” area of knowledge probably is that this palm comprises a key species in many communities through its supply of food for the fauna once has the characteristic to bear fruit every year, plus the production of more than one fruit at a time (Sampaio & Scariot, 2008). Despite the importance of its fruits as a food source for the fauna, only one study analyzed its biometric and morphological aspects (Sousa et al., 2007), which we believe should be the focus for future research.

Among the species of *Bactris* spp., the most studied area of knowledge was "ecology" where publications until the past decade studied patterns such as demography (Monteiro & Fish, 2005), ecological processes related to fruit phenology (Genini, Galetti & Morellato, 2009), and predation (Ribeiro et al., 2010). Among the species of this genus, *B. setosa* is the one with the widest distribution (Fernandes, 1995), which justifies the greater number of studies found for this species. Currently, studies have been carried out mainly with the chemical characterization of its fruits due to its high antioxidant activity (Rosa et al., 2016; Boeing et al., 2017; Campos et al., 2018). Even with several potentials to be investigated, no study has been carried out in areas such as genetics, physiology and tissue culture; topics that we recommend for future studies.

The focus on ecological and physiological research with *Allagoptera* is due to the characteristics of the species *A. arenaria*: i) under high temperatures they have a high germination rate (Menezes et al., 2017); ii) as a pioneer species, it colonizes open areas favoring the entry of other species into the community (Scarano et al., 2001); iii) by creating a microclimate conducive to germination and development of other species, it can play the role of facilitator (Menezes et al., 2017); and iv) after the fire, it will germinate in a few days (Menezes & Araújo, 2004). This palm is the most abundant in the *restinga* area, a marginal ecosystem associated with the AF, where all plant species survive under high temperatures with water and nutritional deficiency in the soil (Scarano et al., 2001). Thus, due to these characteristics and the high plasticity of this species that aroused the interest of research, recent studies are focusing on understanding how *A. arenaria* would be influenced in a climate change scenario with high temperatures (Zani, 2017; Valfré, 2018). Even though this species has so many characteristics that give it a high germination plasticity, no study has been carried out to investigate the properties of its fruits and seeds, which we believe should be a prime area in future research.

In this study, *Astrocaryum aculeatissimum* was the only representative of the genus *Astrocaryum*. Even though it is one of the genera with the low number of studies, 88% of the publications sought to understand its ecological process. This species is endemic to the AF, occurring in Brazil from Bahia (in the northern region of AF) to Santa Catarina (in the south region of AF) (Henderson et al., 2002). In addition to its large size, the absence of additional pulp reduces the range of frugivorous vertebrates consuming its fruits, but the most publications have investigated this process (Donatti et al., 2009; Andreazzi et al., 2012; Pires & Galetti, 2012). According to these studies, the main dispersers of its seeds are *Proechymis* spp., *Sciurus* spp. and mainly *Dasyprocta leporina* (Pires & Galetti, 2012). Thus, areas that suffered reduction or local extinctions of *Dasyprocta* spp. populations, either due to hunting or habitat loss, may present less dispersion of seeds of *A. aculeatissimum*, impairing its recruitment and seedling density (Galetti et al., 2006). For this species, several areas of knowledge deserve attention, since only "ecology", “production and use” and “entomology” studies were performed, often at the community level. Thus, future research must prioritize the understanding of its biochemical properties, physiology, as well as investigate the genetic diversity of this palm.

Species belonging to Desmoncus (*D. orthacanthos* and *D. polyacanthos*) had the low number of studies in relation to the others and the predominant area of knowledge was “ecology”. These species are mainly distributed in the north and east of Brazil, in the Amazon region. In the AF, species of the genus *Desmoncus* are distributed mainly on the Atlantic coast of Bahia and Espírito Santo states (Lorenzi et al., 2010). Despite its potential as a non-timber forest product, since its fibers are used to manufacture ropes, baskets and furniture (Escalante et al., 2004), only one study was carried out in the AF (Benchimol et al., 2017) and all the others were carried out in the state of Pará (Troy et al., 1997; Silva, 2018), showing a great gap in relation to the studies carried out in the Atlantic Forest with these species. Given its potential for use in the production of handicrafts, further studies focused on the use by communities and the properties of their fibers deserve attention.

4.3 Study distributions across AF

Most references for the Arecaceae family in Brazil are restricted to the Amazon region, which is located mainly in the north of the Brazilian territory. Furthermore, in other countries, as in Argentina for *E. edulis* (Gatti et al., 2011, 2014), in Mexico for *Desmoncus orthacanthos* (Ramos-Zapata et al., 2006; Quiroz et al., 2008) and in Peru for *Desmoncus polyhacanthos* (Torres-Vasques et al., 2009). In AF, a large number of the scientific production on palm trees is concentrated in south and southeast, where the large research centers with the largest number of doctoral researchers are located (CNPq, 2016). In addition, the genus with a stricter distribution such as *Butia* and *Geonoma* tend to have their studies concentrated only in that location, unlike species of the genus *Euterpe* or *Syagrus* that have a wide occurrence and consequently influence the wide range of distribution of the studies carried out. However, even with the species of widespread occurrence, we note that locations such as the Brazilian states of Espírito Santo, Bahia, Sergipe and Alagoas should be prioritized in future research due to the absence or low number of studies performed.

In general, for all species, the least number of studies was in the northeast portion of the AF which according to the climate change panel (PBMC, 2013), is the region that will be the most affected by climate change. Thus, thinking that most of the native species of the AF are understory species and need a humid environment for their development, future studies should prioritize this northeast portion of this biome. Beyond this worrying scenario, according to the red list (Martinelli & Moraes, 2013), there are currently 9 species of palm trees native to the AF included into threatened categories with risk of extinction. Thus, special attention should be given to species that are vulnerable, which are facing a real risk of extinction (such as *Allagoptera brevicalyx*, *Butia eriospatha*, *Butia microspadix*, *Butia yatay*, *Euterpe edulis,* and *Syagrus picrophylla*).

4.1 Conclusions

Palm trees have long provided a wide range of services to humanity (Eiserhardt et al., 2011; Levis et al., 2017). Given the morphological and physiological distinction of palm trees, they can play important roles in the ecosystem of tropical forests, such as carbon sequestration (Muscarella et al., 2020). It still needs attention since there are gaps, depending on the genus, both for regions and for areas of knowledge. The development of studies with palm trees will directly assist in their conservation and the maintenance of the AF biodiversity, which, despite being considered one of the 35 biodiversity hotspots worldwide, has been increasingly deforested due to human pressures (Rezende et al., 2018). Even with all the threats, the AF offers ecosystem services, such as climate regulation, water supply and nutrient cycling, which depend on the adequate conservation of this area and consequently its species, such as palm trees.

This study represents a contribution in the scope of scientometrics on studies conducted with palm tree species from the AF. It was possible to notice the relevance that species of *Euterpe* sp., *Acrocomia* spp. and *Syagrus* spp. have in the amount of publications, although more research needs to be carried out in different areas of knowledge. *Desmoncus* spp., *Geonoma* spp. and *Trithrinax* sp. deserve more attention in future research since they presented the least number of publications to investigate related processes such as their biochemical properties, their use by communities and aspects related to genetics. As of of the major gaps we found that the most studied palm species, *E. edulis*, still needs interdisciplinary studies to assist in the conservation of this endangered species, which is essential for AF. The studies carried out for a large part of the palm trees is still scarce, mainly for some study areas, such as the production and management by local human communities, which can be the starting point for discovering and encouraging the use of non-timber forest products contributing to the conservation of these species. In addition, palm trees produce a wide variety of organic compounds that need further investigation, since they have the potential for new products to be discovered from their fruits and seeds. Finally, our review demonstrates the existence of both geographic and areas of knowledge biases in native palms of the AF researched in South America. We found that the southern portion of AF have been greatly sampled compared to the northeast portion, which deserves due attention for future investigations.

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AUTHOR S ' CONTRIBUTIONS

AFC, MSM and MB conceived this study. AFC and CSS collected the data. AFC analyzed the data with contributions from CSS and MSS. AFC wrote the manuscript with all co-authors contributing.

DATA AVAILABILITY STATEMENT

Data will be available from the Figshare Repository.

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SUPPLEMENTARY INFORMATION

TABLE S1 List of native palm tree species of the Atlantic Forest (N=78), with their respective synonyms and number of publications found for each study type. Source: Lorenzi 2010 and JBRJ (2020). Total represented by species (Total$_{Sp}$) and by study type (Total$_{St}$). 1-Ecology; 2-Production and use; 3-Biochemical and / or nutritional properties; 4-Physiology; 5-Morphology, 6-Genetics; 7-Taxonomy; 8-Entomology; 9-Tissue culture. The threat categories in the Brazilian red list (Martinelli & Moraes, 2013) are informed for each species– CR Critically endangered; Endangered; VU Vulnerable; NT Near threatened; LC Least concern; - no information.

Species (Threat status)	**Synonym**	**Study type**									**Total$_{Sp}$**
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	
Acrocomia aculeata (Jacq.) Lodd. ex Mart (-)	*Acrocomia subinermis* León ex L.H.Bailey. *Acrocomia tenuifrons* Lodd. ex Mart. *Acrocomia quisqueyana* L.H.Bailey *Acrocomia antioquiensis* Posada-Ar.	7	4	97	44	16	23	0	4	10	**205**
Acrocomia intumescens Drude (-)	*Diplothemium* Mart. *Orania* Zipp. *Polyandrococos* Barb.Rodr.	0	0	10	0	3	0	0	1	0	**14**
Allagoptera arenaria (Gomes) Kuntze (LC)	*Allagoptera pumila* Nees *Cocos arenaria* Gomes	5	0	0	8	3	1	0	0	0	**17**

	Diplothemium arenarium (Gomes) Vasc. & Franco *Diplothemium littorale* Mart. *Diplothemium maritimum* Mart.										
Allagoptera brevicalyx Moraes (VU)	-	0	0	0	0	0	0	0	0	0	**0**
Allagoptera caudescens Mart. Kuntze (-)	*Ceroxylon niveum* H.Wendl. *Diplothemium caudescens* Mart. *Diplothemium pectinatum* Barb.Rodr. *Orania nivea* Linden ex W.Watson *Polyandrococos caudescens* (Mart.) Barb.Rodr. *Polyandrococos pectinata* (Barb.Rodr.) Barb.Rodr.	2	0	1	0	0	1	0	1	0	**5**
Astrocaryum aculeatissimum (Schott) Burret (LC)	*Toxophoenix aculeatissima* Schott	15	1	0	0	0	0	0	1	0	**17**
Attalea apoda Burret (-)	*Attalea camposportoana* Burret	0	0	0	0	0	0	0	0	0	**0**
Attalea burretiana Bondar (-)	*Attalea concentrista* Bondar *Attalea salvadorensis* Glassman	0	0	0	0	0	1	0	0	0	**1**
Attalea dubia (Mart.) Burret (-)	*Attalea indaya* Drude *Orbignya dubia* Mart.	6	0	2	0	0	0	0	0	0	**8**

	Scheelxea dubia (Mart.) Burret *Attalea concinna* (Barb.Rodr.) Burret										
Attalea funifera Mart. Ex Spreng (NT)	*Attalea acaulis* Burret	3	4	47	4	0	0	0	2	0	**60**
Attalea humilis Mart (-)	*Attalea borgesiana* Bondar ex Dahlgren *Attalea butyrosa* Lodd. ex H.Wendl. *Attalea compta* var. acaulis Mart.	11	1	0	1	0	0	0	0	0	**13**
Attalea oleifera Barb.Rodr (LC)	-	4	0	0	0	0	1	0	0	0	**5**
Attalea seabrensis Glassman (-)	-	0	0	0	0	0	0	0	0	0	**0**
Attalea voeksii Noblick ex Glassman	-										
Bactris acanthocarpa Mart (-)	*Bactris mindellii* Barb.Rodr. *Bactris bicuspidata* Spruce	2	0	0	0	0	0	0	1	0	**3**
Bactris bahiensis Noblick ex A.J. Hend (-)	-	1	0	0	0	0	0	0	0	0	**1**
Bactris caryotifolia Mart. (-)	-	1	0	0	0	0	0	0	0	0	**1**
Bactris ferruginea (NT)	-	2	0	0	0	0	0	0	2	0	**4**
Bactris glassmanii Med.- Costa & Noblick ex A. J. Hend (-)	-	1	0	0	0	0	0	0	1	0	**2**
Bactris hatschbachii Noblick ex A.J.Hend. (LC)	-	2	0	0	0	0	0	0	0	0	**2**
Bactris hirta Mart. (-)	*Amylocarpus hirtus* (Mart.)	1	0	0	0	0	0	0	1	0	**2**

	Barb.Rodr.										
Bactris horridispatha Noblick ex A. J. Hend (-)	-	1	0	0	0	0	0	0	0	0	**1**
Bactris pickelii Burret (LC)	-	2	0	0	0	0	0	0	1	0	**3**
Bactris setosa Mart. (-)	*Bactris setosa* var. *santensis* Barb.Rodr.	7	2	10	0	1	0	0	0	0	**20**
Bactris soeiroana Noblick ex A.J.Hend. (-)	-	0	0	0	0	0	0	0	0	0	**0**
Bactris timbuiensis H.Q.B.Fern. (-)	-	0	0	0	0	0	0	0	0	0	**0**
Bactris vulgaris Barb. Rodr. (-)	*Bactris glazioviana* Drude *Bactris polyclada* Burret	3	0	0	0	0	0	0	0	0	**3**
Butia catarinensis Noblick & Lorenzi (-)	-	7	3	6	1	1	0	0	0	0	**18**
Butia eriospatha (Mart. ex Drude) Becc. (VU)	*Cocos eriospatha* Mart. ex Drude *Syagrus eriospatha* (Mart. ex Drude) Glassman *Butia punctata* Bomhard	3	0	7	4	3	4	1	1	2	**25**
Butia exilata Deble & Marchiori (-)	-	0	0	0	0	0	0	0	0	0	**0**
Butia microspadix Burret (VU)	*Syagrus hatschbachii* Glassman	0	0	0	0	2	0	0	0	0	**2**
Butia odorata (Barb.Rodr.) Noblick (-)	*Butia capitata* var. *virescens* Becc. *Butia capitata* var. *erythrospatha* (Chabaud) Becc. *Butia capitata* var.	6	1	15	11	5	2	0	0	5	**45**

	nehrlingiana (Abbott ex Nehrl.) L.H.Bailey *Butia capitata* var. *strictior* L.H.Bailey *Butia nehrlingiana* (Abbott ex Nehrl.) Abbott ex Nehrl. *Butia pulposa* (Barb.Rodr.) Nehrl.										
Butia paraguayensis (Barb.Rodr.) Bailey (LC)	*Butia yatay* var. *paraguayensis* (Barb.Rodr.) Becc. *Syagrus amadelpha* (Barb.Rodr.) Frambach ex Dahlgren *Syagrus paraguayensis* (Barb.Rodr.) Glassman *Syagrus dyeriana* (Barb.Rodr.) Becc.	0	0	0	0	3	1	1	1	0	**6**
Butia pubispatha Noblick & Lorenzi (-)	-	0	0	0	0	0	0	0	0	0	**0**
Butia yatay (Mart.) Becc (VU)	*Butia capitata* subsp. *yatay* (Mart.) Herter *Butia quaraimana* Deble & Marchiori *Butia noblickii* Deble, Marchiori, F.S. Alves & A. S. Oliveira *Syagrus yatay* (Mart.) Glassman	1	2	1	1	2	0	1	1	0	**9**

Desmoncus orthacanthos Mart. (-)	*Atitara ataxacantha* (Barb.Rodr.) Kuntze *Atitara lophacantha* (Mart.) Barb.Rodr. *Atitara orthacantha* (Mart.) Barb.Rodr. *Desmoncus orthacanthos* var. mitis Drude *Desmoncus lophacanthos* Mart.	5	0	0	2	3	0	0	1	0	**11**
Desmoncus polyacanthos Mart. (-)	*Desmoncus phoenicocarpus* Barb.Rodr. *Desmoncus prestoei* L.H.Bailey *Desmoncus polyacanthos* Mart. var. *polyacanthos* *Atitara aerea* (Drude) Barb.Rodr. *Desmoncus ulei* Dammer *Atitara oxyacantha* (Mart.) Kuntze *Atitara polyacantha* (Mart.) Kuntze *Desmoncus oxyacanthos* Mart. *Atitara caespitosa* (Barb.Rodr.) Barb.Rodr. *Desmoncus mirandanus* L.H.Bailey *Desmoncus peraltus*	2	1	1	0	1	0	0	1	0	**6**

	L.H.Bailey *Desmoncus maguirei* L.H.Bailey *Desmoncus polyacanthos* var. *oxyacanthos* (Mart.) Drude *Desmoncus campylacanthus* Burret										
Euterpe edulis Mart. (VU)	*Euterpe edulis* var. clausa Mattos *Euterpe espiritosantensis* H.Q.B.Fern.	92	16	87	40	4	31	1	0	3	**274**
Geonoma bondariana Lorenzi (-)	*Geonoma pohliana* Mart. subsp. pohliana	0	0	0	0	0	0	0	0	0	**0**
Geonoma brevispatha Barb.Rodr. (-)	*Geonoma caudulata* Loes. *Geonoma chapadensis* Barb.Rodr. *Geonoma altissima* Barb.Rodr. *Geonoma calophyta* Barb.Rodr. *Geonoma aricanga* Barb.Rodr. *Geonoma brevispatha* Barb.Rodr. var. *brevispatha*	5	0	0	1	0	0	0	0	0	**6**
Geonoma conduruensis Lorenzi (-)	-	1	0	0	0	0	0	0	0	0	**1**
Geonoma elegans Mart. (-)	*Geonoma elegans* var. *robusta* Drude	3	0	0	0	1	0	0	0	0	**4**

	Geonoma bifurca Drude & H.Wendl. *Geonoma caudescens* H.Wendl. ex Drude										
Geonoma fiscellaria Mart. ex Drude (-)	*Geonoma pohliana* subsp. *fiscellaria* (Martius ex Drude & Wendland) Henderson	0	0	0	0	0	0	0	0	0	**0**
Geonoma gamiova Barb.Rodr. (LC)	*Geonoma meridionalis* Lorenzi	4	2	0	0	1	0	1	0	1	**9**
Geonoma gastoniana Glaz. ex Drude (-)	*Geonoma pohliana* subsp. *gastoniana* (Glaziou ex Drude) Henderson	0	0	0	0	0	0	0	0	0	**0**
Geonoma litoralis Noblick & Lorenzi (-)	-	1	0	0	0	0	0	0	0	0	**1**
Geonoma kuhlmannii Burret (-)	*Geonoma pohliana* subsp. *kuhlmannii* (Burret) Henderson	0	0	0	0	0	0	0	0	0	**0**
Geonoma pauciflora Mart. (-)	*Geonoma caespitosa* H.Wendl. ex Drude *Geonoma porteana* H. Wendl.	2	0	1	0	0	1	0	0	0	**4**
Geonoma pohliana Mart. (-)	*Geonoma barbosiana* Burret *Geonoma barbigera* Barb.Rodr *Geonoma pohliana* Mart. subsp. p*ohliana*	2	2	0	0	0	1	0	0	0	**5**

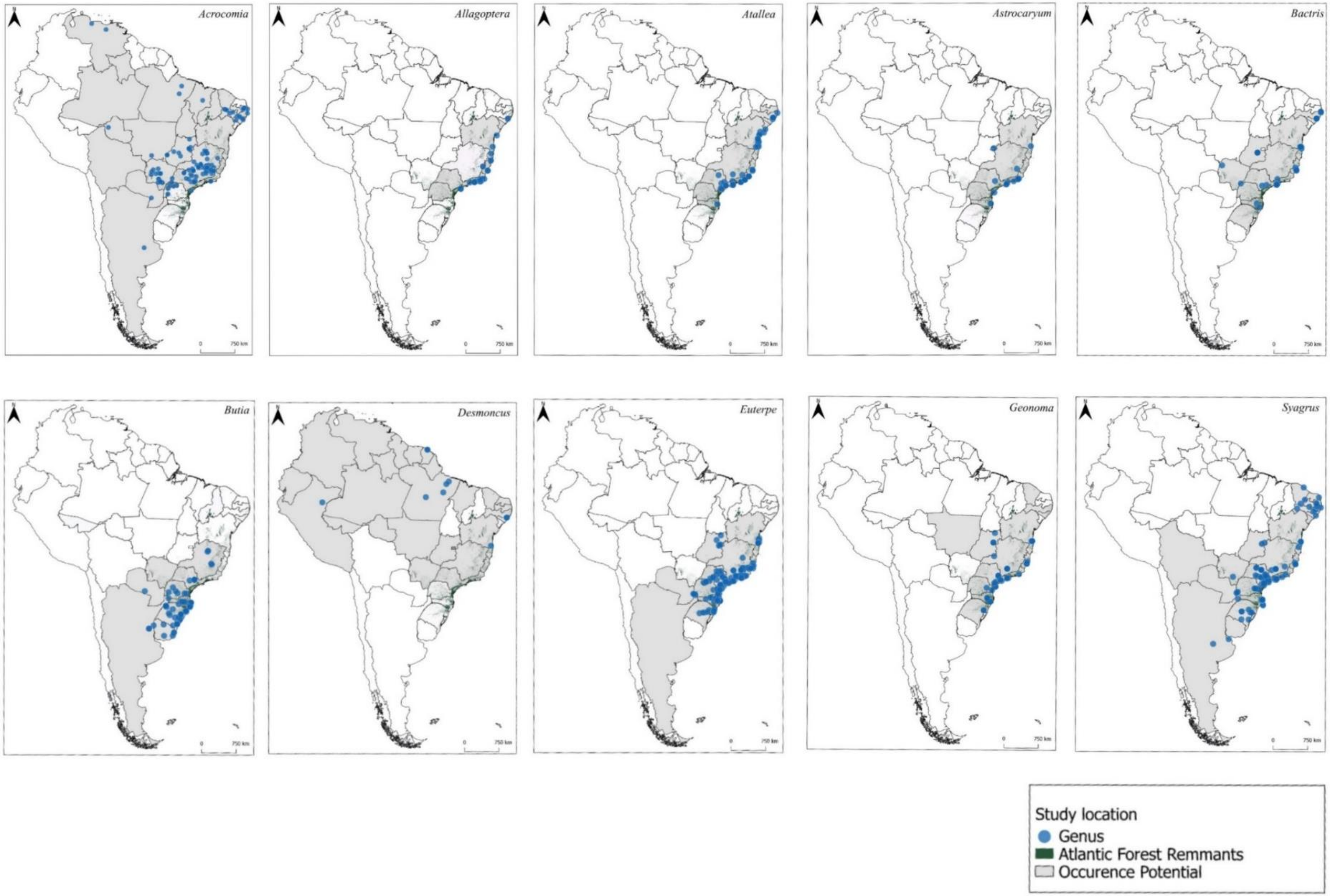
Geonoma rodeiensis Barb.Rodr. (-)	-	0	0	0	0	0	0	0	0	0	**0**
Geonoma rubescens H Wendl. Ex Drude (-)	*Geonoma platycaula Drude* *Geonoma pohliana* subsp. *rubescens* (Wendland ex Drude) Henderson	0	0	0	0	0	1	0	0	0	**1**
Geonoma schottiana Mart. (LC)	*Geonoma hoehnei* Burret *Geonoma erythrospadice* Barb.Rodr.	6	0	1	2	2	1	1	0	0	**13**
Geonoma trinervis Drude & H.Wendl. (-)	*Geonoma pohliana* subsp. *trinervis* (Drude & Wendland) Henderson	0	0	0	0	0	0	0	0	0	**0**
Geonoma wittigiana Glaz. ex Drude (-)	*Geonoma pohliana* subsp. *wittigiana* (Glaziou ex Drude) Henderson	0	0	0	0	0	0	0	0	0	**0**
Syagrus amicorum K. Soares & C. A. Guim. (-)	-	0	0	0	0	0	0	1	0	0	**1**
Syagrus ×andrequiceana K. Soares & L.C. Assis (-)	-	0	0	0	0	0	0	0	0	0	**0**
Syagrus botryophora (Mart.) Mart (LC)	*Arecastrum romanzoffianum* var. *botryophorum* (Mart.) Becc. *Cocos botryophora* Mart. *Calappa botryophora* (Mart.) Kuntze	2	0	0	1	0	0	0	0	0	**3**
Syagrus ×camposportoana (Bondar) Glassman (-)	-	0	0	0	0	0	0	0	0	0	**0**
Syagrus cearensis Noblick (-)	-	1	1	9	0	0	1	0	0	0	**12**

Syagrus ×cipoensis K. Soares & L.C. Assis (-)	-	0	0	0	0	0	0	0	0	0	**0**
Syagrus guaratinguensis Noblick (-)	-	0	0	0	0	0	0	0	0	0	**0**
Syagrus hoehnei Burret (-)	*Lytocaryum hoehnei* (Burret) Toledo	0	0	0	0	0	0	0	0	0	**0**
Syagrus insignis (Rob.) Becc (-)	*Syagrus insignis* (Drude) Becc. *Lytocaryum insigne* (Drude) Toledo	0	0	0	0	0	0	0	0	0	**0**
Syagrus itapebiensis (Noblick & Lorenzi) Noblick & Meerow (-)	*Lytocaryum itapebiensis* Noblick & Lorenzi	0	0	0	0	0	0	0	0	0	**0**
Syagrus kellyana Noblick & Lorenzi (-)	-	0	0	0	0	0	0	0	0	0	**0**
Syagrus ×lacerdamourae K. Soares & C. A. Guim. (-)	-	0	0	0	0	0	0	0	0	0	**0**
Syagrus lorenzoniorum Noblick & Lorenzi (-)	-	0	0	0	0	0	0	0	0	0	**0**
Syagrus macrocarpa Barb.Rodr (-)	*Syagrus getuliana* (Bondar) Glassman *Cocos macrocarpa* (Barb.Rodr.) Barb.Rodr	0	0	0	0	0	0	0	0	0	**0**
Syagrus picrophylla Barb.Rodr. (VU)	*Cocos picrophylla* (Barb.Rodr.) Barb.Rodr. *Syagrus catechucarpa* (Barb.Rodr.) Becc.	0	0	0	1	0	0	0	0	0	**1**
Syagrus pseudococos (Raddi) Glassman (LC)	*Syagrus mikaniana* (Mart.) Mart. *Barbosa pseudococos* (Raddi) Becc.	8	0	0	0	0	0	0	0	0	**8**

	Langsdorffia pseudococos Raddi										
Syagrus romanzoffiana (Cham.) Glassman (LC)	*Arecastrum romanzoffianum* (Cham.) Becc. *Arecastrum romanzoffianum* var. *ensifolium* (Drude) Becc. *Cocos martiana* Drude & Glaz. *Cocos australis* Mart. *Arecastrum romanzoffianum* (Cham.) Becc. var. *romanzoffianum*	34	2	20	10	1	2	0	5	2	**76**
Syagrus ruschiana (Bondar) Glassman (-)	*Cocos ruschiana* Bondar *Arikuryroba ruschiana* (Bondar) Toledo	0	0	0	0	0	0	0	0	0	**0**
Syagrus santosii K. Soares & C. A. Guim. (-)	-	0	0	0	0	0	0	0	0	0	**0**
Syagrus schizophylla (Mart.) Glassman (NT)	*Arikury schizophylla* (Mart.) Becc. *Arikuryroba capanemae* Barb.Rodr. *Arikuryroba schizophylla* (Mart.) L.H.Bailey *Cocos arikuryroba* Barb.Rodr. *Cocos capanemae* (Barb.Rodr.) Drude *Cocos schizophylla* Mart.	0	0	2	4	0	0	0	1	0	**7**

Syagrus ×serroana K. Soares & L.C. Assis (-)	-	0	0	0	0	0	0	0	0	0	**0**
Syagrus ×tostana (Bondar) Glassman (-)	-	0	0	0	0	0	0	0	0	0	**0**
Syagrus weddelliana (H.Wendl.) Becc. (-)	*Lytocaryum weddellianum* (H.Wendl.) Toledo *Syagrus weddelliana* var. *cinerea* Becc. *Syagrus weddelliana* var. *pinaertii* (G. Nicholson & Mottet) Becc. *Syagrus weddellianus* (H. Wendl.) Becc. *Cocos weddelliana* H.Wendl.	1	0	0	1	0	0	0	0	0	**2**
Trithrinax acanthocoma Drude (-)	-	0	0	0	0	0	0	0	0	0	**0**
Total$_{ST}$		**262**	**42**	**317**	**136**	**53**	**72**	**7**	**26**	**23**	**938**

Figure S1. Distribution of studies and potential area of occurrence of 78 native species of the Brazilian Atlantic Forest grouped in ten genera (N= 921).


Acrocomia
Allagoptera
Atallea
Astrocaryum
Bactris
Butia
Desmoncus
Euterpe
Geonoma
Syagrus
0
750 km
Study location
● Genus
🟩 Atlantic Forest Remmants
☐ Occurence Potential

CAPÍTULO 2

Habitat loss and canopy openness mediate leaf trait plasticity of an endangered palm in the Brazilian Atlantic Forest

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Habitat loss and canopy openness mediate leaf trait plasticity of an endangered palm in the Brazilian Atlantic Forest

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Abstract

Forest cover and light availability comprise key factors for plant establishment in tropical forests. In the Brazilian Atlantic Forest (AF), *Euterpe edulis* (Areacaceae) is an endangered and keystone food resource contributing to forest functionality. We investigated the influence of forest loss and light availability on leaf traits and acclimatization of young individuals of *E. edulis* in AF fragments. We aimed to understand (i) how canopy openness and transmitted light are affected by forest cover at the landscape scale and the individual palm level; and (ii) how local and landscape features, combined and separately, affect key leaf traits widely known to be related to plant growth. The study was carried out in 15 forest fragments, ranging from 16-97% of surrounding forest cover. In each fragment, we sampled 10-20 individuals of *E. edulis* and analyzed nine leaf traits related to morphological, biochemical and chemical aspects. We also took hemispherical photographs to estimate canopy openness on the top of each *E. edulis* and also within fragment plots. We found that young plants predominantly occurred in more shaded environments. Additionally, *E. edulis* succeeded to acclimate in six of the nine traits analyzed, with most traits being affected by local and landscape features. It is likely that the lack of variation in traits related to protection against herbivory are limiting the species establishment in highly deforested landscapes. Our results provide novel evidence that both landscape and local contexts affect the leaf traits of *E. edulis* young plants leading to biochemical, chemical and morphological adjustments.

Key words: tropical forest, landscape change, palm tree, acclimation, canopy openness, plasticity.

Introduction

Habitat loss comprises one of the major drivers of biodiversity decay around the globe, with tropical regions experiencing the highest rates of species extinction (Fahrig 2013; Vamosi and Vamosi 2008). A parameter widely used as an indicator of habitat loss is landscape forest cover (Fahrig 2003). In fact, this metric has been widely used as a proxy of deforestation by several studies considering the amount of forest surrounding the landscape (Carvalho et al. 2015; Lima and Mariano-Neto 2014; Morante-Filho et al. 2015). Among several pervasive effects of habitat loss, changes in forest canopy structure (Rocha-Santos et al. 2016), promote profound alterations in understory light regime at a local scale, and also lead to a decay in floristic diversity in tropical forests (Nicotra, Chazdon and Iriarte 1999; Benchimol et al. 2017b).

The availability of understory light radiation is one of the main abiotic factors conferring environmental heterogeneity to tropical forests, playing a key role in plant establishment and recruitment (Valladares and Niinemets 2008; Laurans et al. 2014). Although light intensity greatly varies within forest sites, mainly due to the variation in canopy openness, juvenile plants of the same species exhibit a range of adjustments to their phenotype through phenotypic plasticity to acclimate to different light gradients (Valladares et al. 2006; Dos Anjos et al. 2015). Leaves are the most plastic organs of the plant since they determine light energy capture and carbon assimilation. Thus, adjustments of leaf traits such as leaf area (Álvarez-Clare and Avalos 2007), leaf toughness (Kitajima and Poorter 2010), leaf mass per area (Poorter et al. 2009) and chlorophyll content (Hallik, Niinemets and Kull 2011) comprise the most efficient ways that plants can acclimate to the local light regime (Rozendaal et al. 2006; Vitória et al. 2019). Leaf traits of the same species exhibit great variation related to light availability. For instance, leaves of plants exposed to low-light availability are usually thinner, present greater leaf area and chlorophyll content, and smaller leaf mass per area than the leaves of plants exposed to high-light availability (Teraschima et al. 2006), which can optimize the use of available light and ensure the survival of plants in the understory (Valladares and Niinemetes 2008; Avalos 2019). Despite the expression of adjustment mechanisms, shade tolerant, or preferentially interior forest species, cannot cope with high light intensities, and therefore are unlikely to be established in open or less shaded areas (Avalos 2019). This condition is evidenced in young plants that are under development and exhibit greater susceptibility to abiotic factors (Valladares and Niinemets 2008). Thus, assessing changes in leaf traits, mainly in young plants, can enhance our understanding of species responses to environmental changes (Silva and Batalha 2009; Rodriguez, Maiti and Kumari 2016), such as human-induced disturbances.

Among the most current anthropogenic activities, deforestation directly affects the availability of light radiation in a forest patch (Fauset et al. 2017), limiting the recruitment of species that preferentially regenerate in more shaded environments. This is the case of the neotropical palm *Euterpe edulis* Mart. (Areacaceae) (Gatti, Campanello and Goldstein 2011), which regenerates in the shaded understory, growing preferentially under the closed forest canopy, and tending to be absent in large gaps (Gatti 2011). In fact, in comparison with the coexisting species of dicotyledonous trees, palm have evolutionary strategies allowing a better adaptation in forest-shaded environments, as the low dark respiration and high leaf phosphorus concentration (Ma et al. 2018). This species comprises a keystone food resource in the Brazilian Atlantic Forest (hereafter, AF), a biome extremely reduced, which currently has about 10% of forest remnants from its original area (Rezende et al. 2018). In fact, *E. edulis* produces large fruit crops in times of resource scarcity in the AF and therefore provides crucial resources for a wide range of frugivorous birds and mammals (Galetti et al. 2013). This species exhibits high economic potential since its meristem is cut for human consumption. Yet, its regeneration fails to occur after meristem’s removal, leading to the death of the individual (Ferri and Cavalcante 1997). Given its over-exploitation since the 1970s, in addition to forest loss and fragmentation of the AF, *E. edulis* is currently classified as threatened by the Brazilian Official List of Endangered Species (MMA 2014) and has already been extirpated in several fragmented forest landscapes in the AF (Benchimol et al. 2017b). Although there is evidence that species like *E. edulis* has a wide range of germination rates under light and water availabilities (Donohue et al. 2010; Braz et al. 2014), they are more likely to germinate in altered environmental conditions. For instance, no individual has been recorded in severely deforested landscapes in the southern region of the state of Bahia in Brazil (Leal 2019), and the main causes for its absence are still unknown.

Here, we investigated the influence of habitat loss and light availability on leaf traits and acclimatization of young individuals of *E. edulis* in forest fragments in the AF. Specifically, we seek to understand (i) how canopy openness and transmitted light on the top of young *E. edulis*, and in the forest fragment, are affected by landscape forest cover (ii) how local (canopy openness) and landscape (forest cover) features affect key leaf traits widely known to be related to plant growth and light requirements. For this, we measured nine leaf traits in young individuals recorded in 15 forest fragments exhibiting different levels of landscape forest cover and assessed the canopy openness and transmitted light on both the top of each individual and within fragment forest plots. We expected that the canopy openness and transmitted light would be lower in fragments embedded within highly forested landscapes, and also on the top of young *E. edulis* in comparison with the average canopy openness of each fragment, due to its preference for more shaded environments (Gatti, Campanello and Goldstein 2011; Gatti et al. 2014). In addition, we predicted that landscape forest cover would act synergistically with canopy openness in shaping morphological (i.e., leaf area, leaf thickness, leaf toughness, leaf mass per area), biochemical (i.e., chlorophyll index) and chemical traits (i.e., magnesium, nitrogen, phosphorus and potassium concentrations) of young *E. edulis* plants. Specifically, we expected that forest cover positively affects some leaf traits, with more forested landscapes harboring young individuals exhibiting greater leaf areas, with greater toughness and higher leaf chlorophyll index and leaf nutrient concentrations (Álvarez-Clare and Avalos 2007; Kitajima and Poorter 2010; Zhao and Oosterhuis 1998; Hallik, Niinemets and Kull 2011). For leaf thickness and leaf mass per area, we expected that forest cover would negatively affect these traits (Terashima, Miyazawa and Hanba 2001; Poorter et al. 2009). Concomitantly, we predicted an opposite relationship as the canopy openness increases for all leaf traits.

Material and methods

Study area

This study was conducted in AF fragments located in the municipalities of Una, Belmonte and Mascote in southern Bahia, Brazil (15º 28'S and 39º 30'W). Firstly, sampling sites were selected based on the mapping of high-resolution satellite images (RapidEye from 2009 to 2010, QuickBird and World View from 2009 to 2011). The mapping was performed by manually digitizing the land cover features as visually interpreted at a scale of 1:10,000, which is adequate for identifying patches based on differences in color, texture, and shape. After intensive ground-truthing, we mapped the vegetation and land use over an area of 3500 km^2. Together with a process of checking the areas in the field, these images enabled the elaboration of a land use map of the region and consequently the identification of 58 potential forest fragments at least 1 km apart and suitable for road access. These fragments were selected on the basis of the amount of native forest cover at the landscape scale, i.e., the percentage of mature and successional forest cover within a radius of 2 km around forest fragments or ~13 km^2 landscapes (for more details see Morante-Filho et al. 2015; Rocha-Santos et al. 2017). We selected forest fragments located in areas exhibiting similar characteristics of soil, topography and vegetation, avoiding sandbank areas and montane forests. These forest fragments were surrounded by different types of matrices, composed mainly of rubber tree and *Eucalyptus* sp. plantations, cocoa agroforests and/or cattle pastures.

The vegetation of the region is characterized as Tropical Rainforest (Thomas 2003). The climate is Af type in the Köppen classification, hot and humid, with average annual temperature and precipitation of 25ºC and 1200 mm, respectively (Mori et al. 1983).

For this study, we thus selected 15 forest fragments along a gradient of forest cover at the landscape scale (i.e., 16-97% considering 1 km radii from the center of each sampled fragment; hereafter, FC) (please, see Table S1 in the Supplementary Material), following two main criteria − (i) each fragment needed to be spaced at least 1 km from the other sites to avoid overlapping, and (ii) sampling of *E. edulis* was previously occurred and a minimum of ten young individuals of *E. edulis* was recorded within the fragment (see Santos et al. 2015; Leal 2019; Soares et al. 2019).

Sampling surveys

On each forest fragment, we performed 4-hours of active search method, and sampled all young individuals of *E. edulis* found, keeping a minimum distance of 30 m among each sampling individual. We ended up with 10 to 20 sampling individuals per site, totaling 222 individuals considering all surveyed forest fragments (mean ± standard deviation = 14.8 ± 5.9 individuals per forest fragment). There are six ontogenetic stages that are well delimited for *E. edulis*: Seedling, Juvenile I, Juvenile II, Immature I, Immature II, and Adult (Silva 1991; Reis et al. 1996; Silva et al. 2009). We used ‘Juvenile I’, which comprised individuals with less than 0.15 m of insertion height, and presenting two to four leaves, to estimate the different leaf traits (Fig. S1). We chose this stage because the seedling (previous ontogenetic stage) still presented endospermic reserves, directly influencing its ability to adjust to environmental variations. In addition, adult individuals of tree species in general may persist for a long time in the landscape even after land use transformation (Metzger et al. 2009), and thus sapling or young individuals is expected to be more sensitive to habitat loss when compared to adults (Rigueira et al. 2013). All selected individuals did not show apparent signs of pathogen and herbivore attacks. On each individual, we detached the larger and fully expanded leaf for subsequent laboratory analyses.

On the top of each individual, we took one hemispheric photograph using a Nikon Coolpix 4300 digital camera equipped with a hemispherical fish-eye lens (180°) set on a tripod 1.5 m above the ground, and positioned towards the magnetic north (Andrade et al. 2015). The percentage of both canopy openness (CO_I) and total transmitted gap light (TT_I) just above each individual was calculated using Gap Light Analyzer (GLA) (Frazer, Canhan and Lertzman 1999). Although CO is the most used variable in the literature to provide information about the available light in the forest understory (Sterck and Bongers 2001; Santos et al. 2012; Lusk 2019), we also calculated the TT. Transmitted light radiation is a more proximal indicator of seedling growth and survival in the understory (Montgomery and Chazdon 2001; Kitajima, Mulkey and Wright 2005). CO represents the percentage of open sky seen from below a forest canopy, whereas TT is the sum of direct and diffuse solar radiation transmitted by the canopy (Frazer, Canham and Lertzman 1999). We took the photos either in the late afternoon or in cloudy days to avoid overexposure. To test our first hypothesis, additional hemispheric photos were taken in the center of ten forest plots of 40 m^2 randomly selected on each sampled fragment, keeping a minimum of 50 m from the nearest forest edge and between fragments. Additional hemispheric photos were taken according to the same methodology described above. We thus calculated the average of these ten canopy openness measurements, which we considered represented the fragment (CO_F).

Leaf traits

We selected a set of leaf traits closely related to light requirements for tropical forest plant species, comprising morphological, biochemical, and chemical traits (Poorter and Bongers 2006; Kitajima and Poorter 2010; Lusk et al. 2019) (Table 1). Considering that young individuals of *E. edulis* have compound leaves with usually five to eight leaflets, all leaf trait measurements were performed on three leaflets per leaf, always in the middle region of each leaf. Firstly, a biochemical trait, the Chlorophyll index (CI), was measured on those same three leaflets per leaf, before removing it from the plant, using a portable chlorophyll meter ClorofiLog (Falker, Brazil). Regarding the morphological leaf traits, leaf toughness (LTO) was measured using a penetrometer IP-90DI, tip ø 3 mm (Impac, Brazil). For this, the leaflets were positioned on a base, and the tip pressed avoiding the main rib. We also estimated the leaf blade thickness (LT) using an external digital micrometer 0-25 mm, 0.001 mm (Zaas Precision, Brazil). After these measurements, we scanned the entire leaf and calculated the leaf area (LA) using the Image J software (Abramoff, Magalhaes and Ram 2004). To determine the leaf dry mass, the leaves were dried in a forced ventilation oven at 50°C until constant mass. From the ratio between leaf dry mass and LA, the leaf mass per area (LMA) was calculated. Also, after leaf drying, the leaves were ground in a ball mill (Tecnal, model TE-3500), in a sample composed of all individuals recorded per fragment, to obtain a minimum amount for macronutrient content analysis, according to the protocol of Embrapa

(2009). We performed all analyzes for chemical leaf traits at the Plant Tissue Analysis Laboratory of the Cocoa Research Center (CEPEC/CEPLAC), in Ilhéus, Bahia, Brazil. The concentrations of magnesium (Mg), nitrogen (N), phosphorus (P) and potassium (K) were then obtained. Subsequently, we performed Pearson pairwise correlation analyses, which showed high correlation among N and K (r=0.71) and between N and P (r=0.79, see Table S2). However, we considered all four nutrients separately in subsequent analyses, given that they perform different functions and represent different relationships between plants and the environment (Table 1).

TABLE 1 Leaf traits measured in young plants of *E. edulis*, with their respectively main functions.

Classification	**Leaf trait**	**Function**	**References**
Morphological	Leaf area (LA)	Fundamental for light energy capture and photosynthesis, being an indicator of plant productivity.	Niinemets, 2010; Zhang and Pan 2011; Avalos, 2019.
	Leaf thickness (LT)	Related to the water use efficiency, since thicker leaves reduce transpiration, representing an important mechanism against the effects of desiccation and overheating of the leaves.	Terashima *et al*., 2001; Ville *et al*., 2005; Monteiro *et al*., 2016;
	Leaf toughness (LTO)	Related to leaf protection against herbivory and physical damages. Additionally, is linked to the increase of leaf lifespan and carbon assimilation.	Peeters, Sanson and Read, 2007; Markesteinjn, Poorter and Bongers, 2007; Kitajima and Poorter, 2010.
	Leaf mass per area (LMA)	Key leaf measuring investment in dry mass per unit of leaf area and is associated to the plant regeneration strategy.	Wrigth and Westoby, 2002; Wrigth *et al*., 2004; Poorter *et al*., 2009.
Biochemical	Chlorophyll index (CI)	Related to the amount of leaf nitrogen and photosynthetic capacity, it is a quick and practical way of estimate chlorophyll contents in an instantaneous, indirect and nondestructive way.	Schilichting *et al*., 2015; Vieira Silva *et al*., 2016.
Chemical	Magnesium content (Mg)	Component of the chlorophyll molecule and is involved in some processes such as enzyme activation, synthesis of nucleic acids and proteins, and photosynthetic capacity.	Li, Liu and Zhuang, 2000; Chen *et al*., 2018; Wang *et al*., 2018.
	Nitrogen content (N)	Nitrogen content is considered as one of the most important nutrients in plant nutrition and provide information on the plant nutritional state, representing a direct indicator of photosynthetic capacity and plant productivity.	Novoa and Loomis, 1981; Zarco-Tejada *et al*., 2004.
	Phosphorus content (P)	Is a major component of biological membranes, nucleic	Bieleski, 1973; Reich, Oleksyn and Wright,

	acids, sugar phosphates, ATP, all which play important roles in photosynthetic carbon assimilation, and together with N are the most common nutrients limiting net primary productivity.	2009; Mo *et al*., 2019.
Potassium content (K)	Is largely related to osmotic potential and stomatal control being an important osmoregulator. Controls the functioning of stomata in photosynthesis and transpiration such as maintenance of plant turgor.	Clarkson and Hanson, 1980; Cakmak, 2005; Ahmad *et al*., 2018.

Landscape forest cover

Given that multi-scale analysis is considered the most appropriate approach for defining a landscape size (see Holland et al. 2004; Fahrig 2013; Jackson and Fahrig, 2015; Arroyo-Rodríguez et al. 2020), we firstly measured the amount of forest cover (FC) at different spatial scales and thus analyzed the strength of the relationship among each estimate of forest cover and our response variables. This procedure was carried out to investigate the most appropriate spatial scale to assess the landscape influence on biodiversity (Holland et al. 2004; Ordóñez-Gómez et al. 2015). Then to calculate FC, we delimited five buffers of different radii around the central point of each sampling site, and calculated the percentage of native forest, independent of its successional stage (i.e., intermediate and advanced successional stages), and excluded all plantations such as shaded cocoa (*Theobroma cacao*) and eucalyptus (*Eucalyptus* spp.). Buffers were delimited every 200 m, ranging from 200 to 1000 m, based on two criteria – (*i*) to maintain independence of the fragments (maximum 1000 m); and (*ii*) due the dispersal capacity of the species that consume and disperse *E. edulis* fruits, which corresponds to approximately 700 m for toucans of the genus *Ramphastos*, the main dispersers of *E. edulis* (Holbrook 2011). We thus evaluated which spatial scales of FC best explained the variation in leaf traits, by comparing the coefficient of determination (R^2) between each leaf trait and FC obtained in different radius sizes. The radius of 1000 m was the one that obtaining the highest R^2 value for eight of the nine leaf traits analyzed, and therefore was used in subsequent analyses (Table S3).

Data Analysis

We firstly performed Pearson correlation analysis among FC, CO_I and TT_I, with results demonstrating that FC is correlated with CO_I (r = -0.45) and TT_I (r = -0.41). However, CO_I

and TT_I presented a high correlation (r = 0.71), and because the CO_I showed the highest correlation with FC, we thus opted by using CO_I in subsequent analyses (Fig. S2). Furthermore, we performed an analysis of covariance (ANCOVA) to examine the relationship between CO (CO_F and CO_I) and FC. We used CO as a response variable, FC as covariate and CO_F and CO_I as categorical variables.

We performed Generalized Mixed Models (GLMMs) to evaluate the influence of FC and CO_I, combined and separately, on each leaf traits of *E. edulis,* considering the fragment as a random effect and FC and CO_I as fixed effects. For the nutrient-related leaf traits (i.e., N and Mg), we ran Generalized Linear Models (GLMs) instead, since there was only one sample per fragment. We then tested for multicollinearity among FC and CO_I in the full model using Variation Inflation Factors (VIF) for each evaluated trait, with results demonstrating that both variables were neither moderately nor highly collinear in all cases (VIF $\leq$2; see Table S4). We finally adopted a model selection approach in which the models used were: 1. null, to test the absence of effects; 2. FC; 3. CO_I; 4. CO_I + FC. The Akaike Information Criterion (AICc) was used for small samples, considering as the best models all those exhibiting ΔAIC $\leq$ 2.00. When the null model was among the most parsimonious models, we considered that no other model explained the pattern better than chance. All the statistical analyses were carried out in R software (R Core Team 2016).

Results

We observed that CO decreased significantly with increase of FC (Fig. 1), and this pattern was also significantly different among values obtained by CO_F and CO_I ($R^2 = 0.858$, F = 88.91; $P < 0.01$). Indeed, measurements of CO taken on the top of the individual (CO_I) were always lower than the ones taken in the fragment forest plots (CO_F). This demonstrates that *E. edulis* predominantly occurs in more shaded areas in our study landscape.

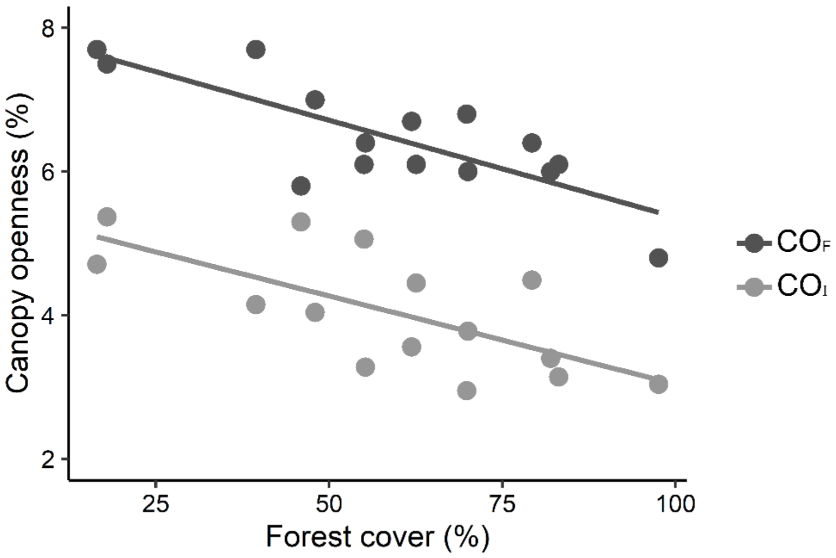

FIGURE 1. Relationship between the percentage of forest cover and the percentage of canopy openness taken within forest plots (CO_F, in black dots), and on top of each surveyed young *E. edulis* (CO_I, grey dots). Analysis of covariance indicated a significant difference on the categories of canopy openness used in relation to forest cover (ANCOVA, $p < 0.05$).

Leaf traits greatly varied across the 15 surveyed forest sites (Table S4). Both landscape and local factors, either independently or combined, were included in the best model explaining the effect of patterns of most morphological, biochemical and chemical leaf traits herein examined. Indeed, the best model explaining LA included CO_I alone, followed by CO_I plus FC (Table 2), in which greater leaf area of *E. edulis* was obtained in fragments surrounded by higher landscape forest cover and lower individual canopy openness (Fig. 2 a,b). Conversely, for LMA, the most predictive model included only FC followed by CO_I plus FC, where lower LMA values were obtained in forest fragments with higher amount of forest cover and lower CO (Fig. 2 c,d). Regarding the CI, the most parsimonious model was those containing CO_I and FC, followed by model with only FC, which indicates that leaves with higher content of chlorophyll were recorded in more forested landscapes and for individuals under lower CO (Table 2; Fig. 2 d,e). The null model was the most parsimonious for LT and LTO, so these traits were unaffected by landscape and local factors in young *E. edulis* (Table 2).

TABLE 2 Ranking of Generalized Linear Models (GLMMs) predicting the influence of forest cover (FC) and canopy openness (CO_I) on each morphological and biochemical leaf trait of young *E. edulis* in 15 surveyed forest fragments of the Brazilian Atlantic Forest. The most parsimonious models are in bold. ΔAICc: difference of AICc from the best model; df: number of model parameters; wi: AICc weight.

Leaf traits	**Model**	**ΔAICc**	**Df**	**Wi**
Leaf area (cm^2) - LA	**CO_I**	**0.00**	3	0.440
	CO_I+FC	**0.57**	4	0.331
	Null	2.46	4	0.129
	FC	2.96	5	0.100
Leaf thickness (mm) - LT	**Null**	**0.00**	3	0.981
	CO_I	8.23	4	0.016
	FC	11.25	4	0.003
	CO_I+FC	21.21	5	0.000
Leaf toughness (N mm^{-1}) - LTO	**Null**	**0.00**	3	0.962
	FC	7.53	4	0.022
	CO_I	9.42	4	0.009
	CO_I+FC	17.10	5	0.000
Leaf mass per area (g m^{-2}) - LMA	**FC**	**0.00**	4	0.499
	CO_I+FC	**0.02**	5	0.493
	CO_I	9.74	4	0.004
	Null	9.82	3	0.004
Chlorophyll index - CI	**CO_I+FC**	**0.00**	5	0.487
	FC	**0.08**	4	0.468
	CO_I	5.81	4	0.027
	Null	6.56	3	0.018

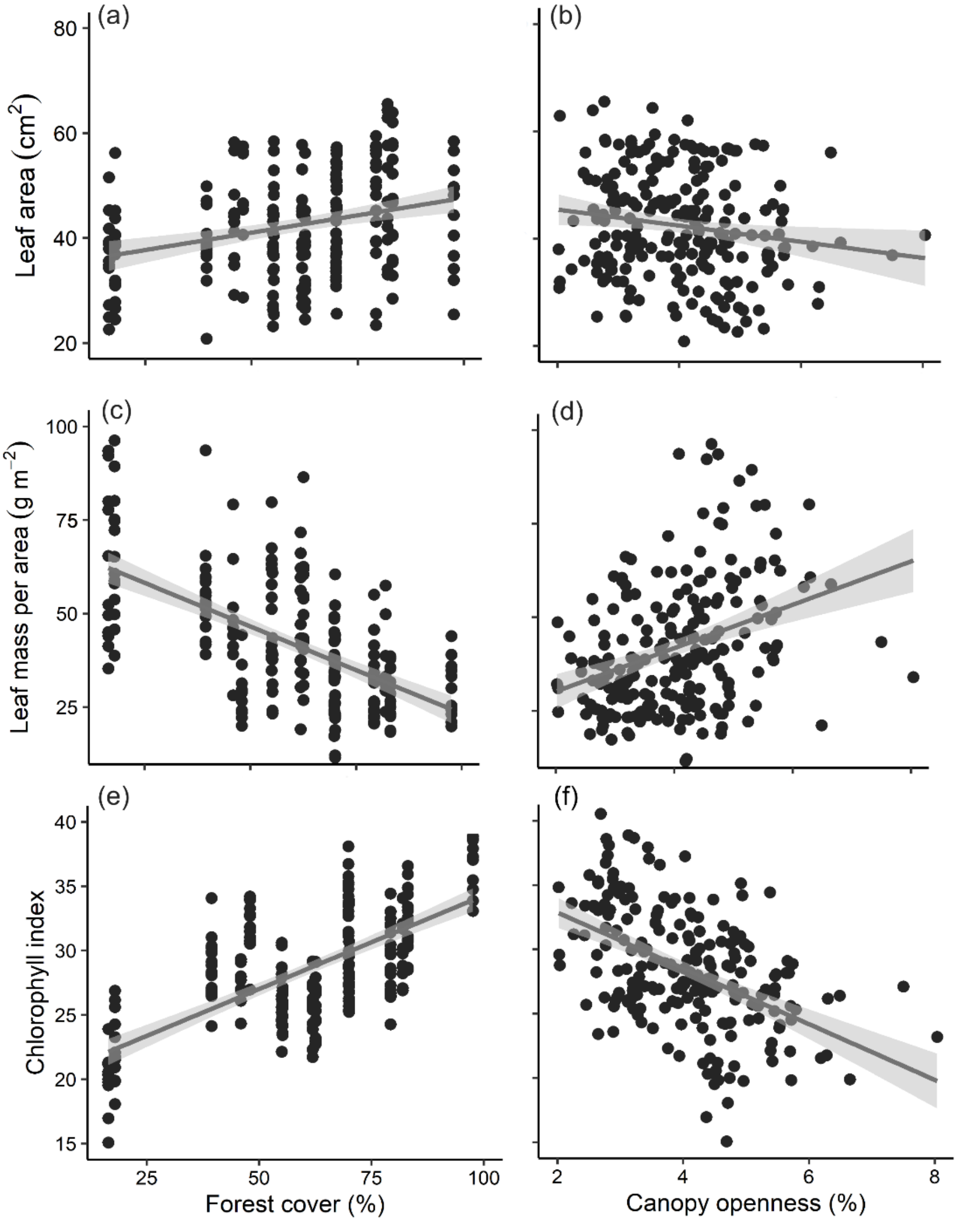

FIGURE 2. Relationships between percentage of forest cover (a, c, e) and canopy openness (b, d, f) with leaf traits of young *E. edulis*.

For leaf chemical traits, the best model explaining Mg concentration included only FC followed by the model with only CO_I (Table 3), which presented a higher Mg concentration in landscapes showing higher percentage of forest cover and lower individual canopy openness (Fig. 3 a,b). Regarding N the most predictive model included CO_I alone, followed by CO_I plus FC (Table 3), with the same pattern found for N in relation to the increase of forest cover and canopy openness (Fig. 3 c,d). For P the most parsimonious model was the model containing only FC, which indicates that leaves with higher concentration of P were recorded in more forested landscapes (Table 3 and Fig. 3 e,f). Finally, the null model appeared amongst the best models explaining K concentration, and therefore we considered that that K was not affected by the predictor variables. (Table 3).

TABLE 3 Ranking of Generalized Linear Models (GLMs) predicting the influence of forest cover (FC) and canopy openness (CO_I) on chemical leaf traits of young *E. edulis* in 15 surveyed forest fragments of the Brazilian Atlantic Forest. The most parsimonious models are in bold. ΔAICc: difference of AICc from the best model; Df: number of model parameters; wi: AICc weight.

Leaf traits	**Model**	**ΔAICc**	**Df**	**Wi**
Magnesium concentration (g kg^{-1}) - Mg	**FC**	**0.00**	3	0.569
	CO_I	**1.73**	3	0.239
	CO_I+FC	2.84	4	0.138
	Null	4.72	2	0.054
Nitrogen concentration (g kg^{-1}) - N	**CO_I**	**0.00**	3	0.658
	CO_I+FC	**1.83**	4	0.263
	FC	4.31	3	0.076
	Null	11.14	2	0.003
Phosphorus concentration (g kg^{-1}) - P	**FC**	**0.00**	3	0.687
	CO_I	3.20	3	0.139
	CO_I+FC	3.32	4	0.131
	Null	5.55	2	0.043
Potassium concentration (g kg^{-1}) - K	**CO_I**	**0.00**	3	0.411
	FC	**0.62**	3	0.302
	Null	**1.43**	2	0.202
	CO_I+FC	3.15	4	0.085

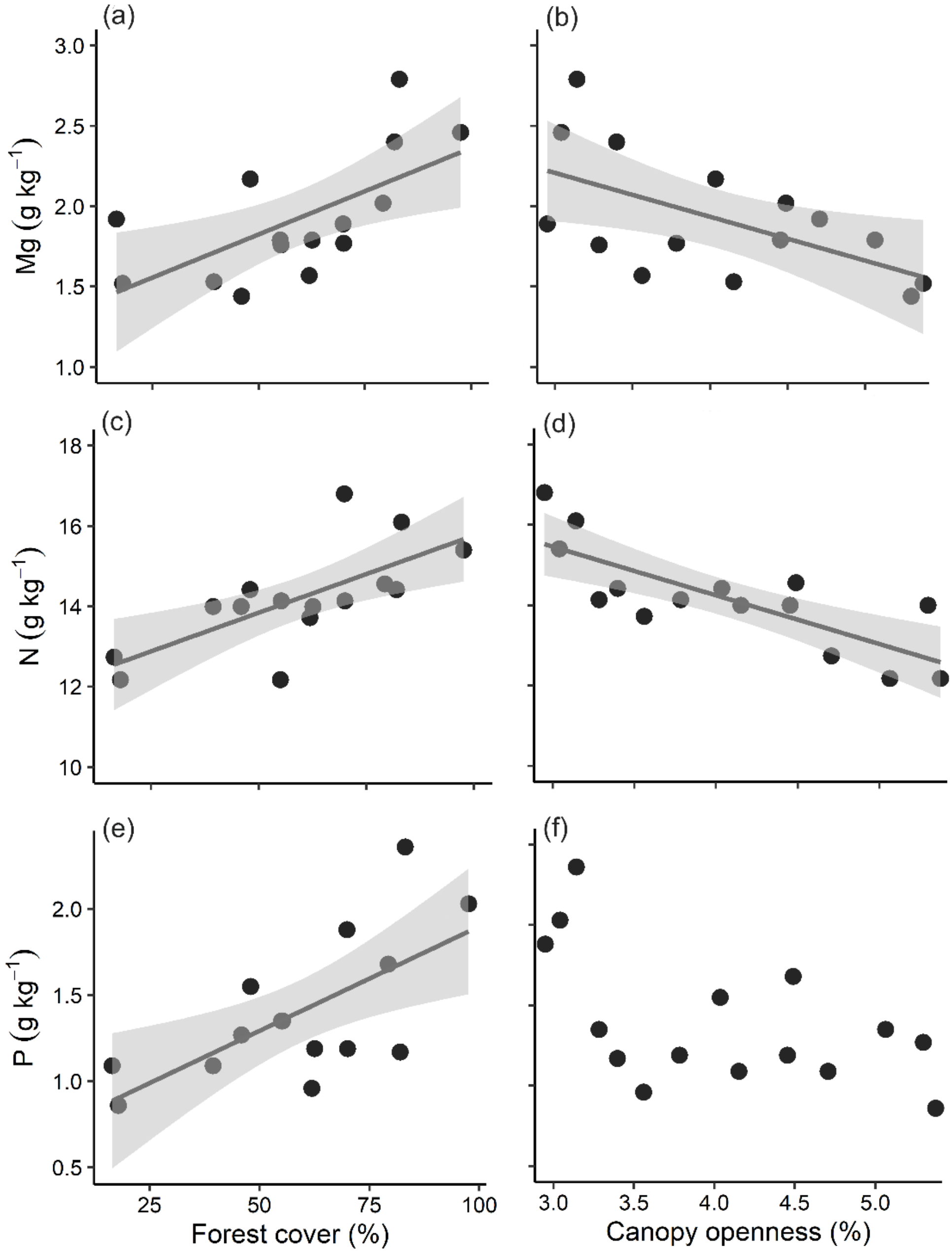

FIGURE 3. Relationships between percentage of forest cover (a, c, e) and canopy openness (b, d, f) on leaf nutrients concentrations of young *E. edulis* in each forest fragment.

Discussion

Our study clearly demonstrates that landscape forest loss and increasing understory light conditions affect most of leaf traits analyzed in this study. Indeed, the majority of analyzed leaf traits (leaf area, leaf mass per area, chlorophyll index, and nutrient concentrations) were substantially influenced by forest cover and canopy openness either together or separately. This suggest that fragments embedded within highly deforested landscapes exhibit greater canopy openness and light transmission, with low potential for the growth and survival of young *E. edulis*. Considering the key role of this palm species for forest functioning, this result demonstrates the pervasive consequence of increasing levels of deforestation in the AF (SOS Mata Atlântica 2020) for the maintenance of healthy populations of *E. edulis* in the long term.

Most of the morphological traits of *E. edulis* were robustly affected by either landscape and/or local factors, indicating that young plants are managing to adjust their leaf traits to the gradient of forest cover and canopy openness. Specifically, leaf area increased in more forested landscapes exhibiting lower canopy openness above the plants. Plants growing under moderate and dense shade increased leaf area to enhance light capture (Lusk 2002). This compensates for their low light availability, as previously documented in the literature (Mendes et al. 2001). On the other hand, when subjected to high light radiation, the plants reduced leaf area to avoid water loss through transpiration (Valladares et al. 2016). In addition, unlike other palm species with entire leaves, young plants of *E. edulis* produce fan-shaped and pinnatisect leaf blades. This pattern of leaf production can reduce the damage caused by herbivory, which has a more pronounced and damaging effect in humid and shaded environments (Carvalho et al. 1999; Kitajima and Poorter 2010).

Leaf mass per area consisted of another morphological trait affected by landscape forest loss and canopy openness, in which palms from more deforested fragments with greater canopy openness exhibited higher leaf mass per area. Plants exposed to high-light availability generally have leaves with greater leaf mass per area than plants exposed to low-light availability (Poorter et al. 2009). Similarly, Prado et al. (2015) observed that as the degree of disturbance increased, lower specific leaf area was detected (the inverse of leaf mass per area), as a consequence of the greater canopy openness. All these changes together increase the water use efficiency and prevent possible photoinhibition of photosynthesis (Takahashi and Murata 2008), since thicker leaves generally contain a larger amount of water per unit leaf area and thus minimize damage from possible photoinhibition by preventing leaf overheating (Kitao et al. 2000). As a result, this might enhance the ability of juveniles of *E. edulis* to survive and achieve other ontogenetic stages (Fini et al. 2010; Matthews, Chabrand and Lawson 2017).

Contrary to our expectations, neither local nor landscape scale features influenced the leaf thickness and leaf toughness. Commonly, leaves exposed to high-light availability tend to be thicker and exhibit a higher toughness than leaves exposed to low-light (Kitajima and

Poorter 2010). These characteristics give protection to these leaves, which are tougher and usually less susceptible to herbivory (Peeters et al. 2007). In this study, all young plants of *E. edulis* were detected in environments showing low values of canopy openness (i.e., below 10%). Two of the main hypotheses explaining the mechanism by which plants are able to grow under low light availability are related to the maximization of net carbon gain in low light (Givnish 1988) and the stress tolerance to biotic and abiotic factors (Kitajima 1994). The first hypothesis predicts that any physiological and morphological characteristic associated with maximizing net carbon gain under low light availability improves shade tolerance and, consequently, the ability of a given species to establish and grow in the forest understory. The stress tolerance hypothesis states that survival in the shade is more related to resistance to biotic and abiotic stresses. However, studies have showed that these two hypotheses are not mutually exclusive (Sánchez-Gomez et al. 2006; Valladares and Niinemets 2008). In our study, we reveal that in fragments with lower forest cover in the landscape, the young plants of *E. edulis* decreased leaf area and increased leaf mass per area (traits related to capturing light in the shade – Givnish 1988), but there was no change in leaf thickness and toughness (related to protection - Kitajima 1994). Previous studies analyzing the survival of *E. edulis* showed that the mortality of small plants may be related to herbivory (Matos et al. 1999). Since leaf herbivory of other tree species and all understory species of Rubiaceae in the same studied region increased with forest cover loss (Dodonov et al. 2016; Morante-Filho et al. 2016), the lack of variation in these traits may be another limiting factor for the acclimatization of young *E. edulis* plants in severely deforested landscapes.

Regarding biochemical and chemical traits, only the response of chlorophyll index corroborated our initial hypothesis, in which the combined influence of landscape and local factors best predicted this trait. The higher concentrations of leaf nutrients in young plants of *E. edulis* in more conserved forest fragments may be related to the greater litter production and soil fertility (Moraes 2017) in these fragments, which results in a greater nutrient cycling and greater availability of nutrients (Rode 1995; Boeger, Wisbievski and Reissmann 2005). Interestingly, the greatest differences between the leaf nutrient concentrations in plants growing in the fragments with the highest and lowest forest cover were observed for P, followed by Mg and N. Mycorrhizal associations in *E. edulis* seedlings provided a greater accumulation of P and other nutrients in the leaves (Moreira and Junior 2016) as well as a greater biomass accumulation (Sgrott et al. 2012). Generally, the diversity of mycorrhizae is lower in AF areas at initial stages of succession than in more advanced or mature forests

(Stürmer et al. 2006, Zangaro et al. 2008; Bonfim et al. 2013), which we believe may be occurring in the most deforested and most conserved fragments, respectively, contributing to the higher leaf nutrient content in these young plants. In fact, leaves in shaded environments tend to invest in higher concentration of photosynthetic pigments to maximize light capture efficiency, as larger amounts of chlorophyll (Mendes et al. 2001). Nitrogen and magnesium are components of the chlorophyll molecule and are involved in photosynthetic capacity (Wang et al. 2018). This ability is generally positively related to leaf nitrogen because a large portion of nitrogen is invested in photosynthetic machinery (Kattge, Raddatz and Wirth 2009). As expected for young *E. edulis* plants, the concentrations of nitrogen and magnesium followed the same trend as in the total chlorophyll index, indicating that *E. edulis* has a more favorable environment in fragments embedded within great native vegetation cover.

Even though most of the leaf traits changed in relation to the forest cover gradient, our results clearly demonstrate that young *E. edulis* individuals (Juvenile I) (Silva 1991; Reis et al. 1996; Silva et al. 2009) preferentially occur in more shaded environments within forest fragments. Most neotropical palm trees widely vary in the regeneration strategies of initial life stages (Hodel 1992). For several palm species, increased disturbance favoring recruitment and growth is associated with changes in canopy structure (Cintra and Horna 1997; Terborgh and Davenport 2001; Avalos 2016), even if light increases are minor. An example is *Euterpe precatoria*, which is usually abundant in light gaps and disturbed environments, with seedlings under low canopy openness showing higher mortality rates and slower growth than those found in more open areas (Avalos et al. 2013; Brum and Souza 2020). Conversely, there are some disagreements between studies in relation to tolerance and preference of *E. edulis* for shaded environments–while some studies consider that this species needs understory shading to grow and regenerate (Lavinsky et al. 2014), others suggest intermediate light for its growth (Gatti, Campanello and Goldstein 2011). In this study, all recorded *E. edulis* were under low light (i.e., under a mean canopy openness of 6%, which corresponds to approximately 8.6 to 9% of transmitted solar radiation; Fig. S2). Considering that the average radiation in full sun is around 35 mol photons m^{-2} day^{-1} in the study region (Feijó et al. 2009; Cerqueira et al. 2018), this means that young plants of *E. edulis* were under approximately 3.5 mol photons m^{-2} day^{-1}. These values represent more closed canopies with low light input (Valladares et al. 2000; Montgomery and Chazdon 2001), such as non-disturbed forests. It is worth mentioning that the amount of variation found between leaf traits in relation to the gradient of forest cover and canopy openness may also be related to the intrinsic variation of the regenerants in a natural environment, as well as the opening and closing of gaps that occur in the fragments. Although the changes in some leaf traits related to shade tolerance, and that young *E. edulis* have a clear preference for the more shaded environments within forest fragments, experiments that explicitly quantify light availability and quality need to be done to clarify the main controversies of species shade tolerance. However, we provide clear evidence that fragments in more deforested landscapes are less appropriate for the establishment of young *E. edulis*. Given the rapid pace of deforestation combined to the advance of climate change, this scenario can be damage to the long-term persistence of this species.

As previous studies demonstrated, forest fragments within lower amount of forest cover at landscape scale have been experienced disruption in forest structure and are subjected to greater light input (Rocha-Santos et al. 2016; Fauset et al. 2017). In addition, there are other microclimatic factors that concomitantly operate with increasing light availability in forest understories, as the high air temperature and low air humidity (Chen et al. 1999), which can act as environmental stress factors, hampering the establishment of young *E. edulis* individuals. Our results provide novel evidence that the landscape forest loss together with the local context given by the light regime greatly influence the leaf traits of young *E. edulis*, leading to morphological and physiological adjustments. Other studies in this same region have shown that landscape-scale deforestation has caused a reduction or even disappearance of this key palm species (Benchimol et al. 2017). Even the young plants of this species favored in more shaded forest understories, with the ability to adjust its leaf traits and presenting a wide geographical distribution (*E. edulis* occurs throughout the AF), are unable to acclimate to survive within severely deforested landscapes. Naturally occurring evolutionary events, such as local adaptation, may be influencing these populations to persist and grow in diverging environmental conditions (Brancalion et al. 2018). Additionally, other ecological processes may be related to the disappearance of *E. edulis* in fragments surrounded by lower vegetation cover, including seed dispersal (Galetti et al. 2013), seed predation by invertebrates (Soares et al. 2015) and vertebrates (Portela et al. 2020), and higher frequency of palm heart harvest (Prevedello et al. 2020). Hence, forests fragments within deforested landscapes seem to be unfavorable for the establishment of typical shade tolerant species even for those showing great plasticity and wide geographical distribution, with potential severe ecological and ecosystems consequences, including reduction in seed dispersion and carbon storage.

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Data availability statement

Data will be available from the Figshare Repository.

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Supplementary material

Figure S1 Photograph of a young *E. edulis* sampled within one of the surveyed forest fragments in southern Bahia, Brazil.

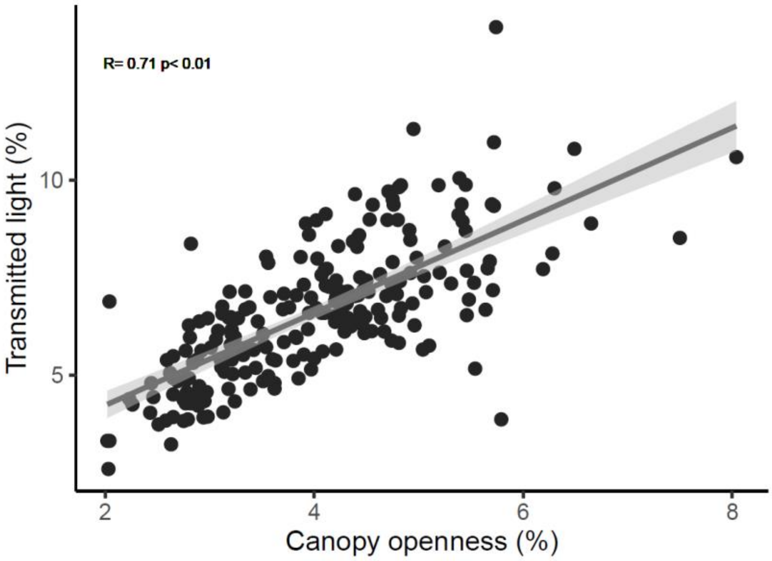


FIGURE S2 Relationship between transmitted light and canopy openness above each sampling individual in 15 forest fragments in southern Bahia, Brazil. The grey zone represents the 95% confidence level interval.

TABLE S1 Mean values and standard deviation of the biochemical, chemical and morphological leaf traits of young plants of *E. edulis* in each forest fragment (N = 222). Forest Cover (FC); Canopy openness (CO); Number of samples (N_S) co Leaf area (LA); Leaf thickness (LT); Leaf toughness (LTO); Leaf mass per area (LMA); Chlorophyll index (CI); Magnesium concentration (Mg); Nitrogen concentration (N); Phosphorus concentration (P); Potassium concentration (K).

FC	**CO**	**N_S**	**LA (cm^2)**	**LT (mm)**	**LTO (N mm^{-1})**	**LMA (g m^{-2})**	**CI**	**Mg (g kg^{-1})**	**N (g kg^{-1})**	**P (g kg^{-1})**	**K (g kg^{-1})**
16.46	4.71	12	36.21 ± 8.35	0.19 ± 0.02	0.59 ± 0.12	60.13 ± 20.76	20.01 ± 2.21	1.92	12.74	1.09	6.15
17.91	5.37	14	36.75 ± 8.58	0.20 ± 0.03	0.38 ± 0.04	65.65 ± 16.58	22.26 ± 2.64	1.52	12.18	0.86	5.40
39.43	4.15	20	38.26 ± 5.88	0.18 ± 0.02	0.65 ± 0.08	55.15 ± 11.42	28.50 ± 2.13	1.53	14.00	1.09	6.60
45.91	4.45	10	43.66 ± 9.15	0.19 ± 0.02	0.70 ±0.05	48.90 ± 14.11	27.32 ± 1.44	1.44	14.00	1.27	6.30
47.98	4.04	12	48.55 ± 8.56	0.17 ± 0.02	0.76 ± 0.11	28.60 ± 6.63	31.96 ± 2.03	2.17	14.42	1.55	6.45
55.04	5.06	13	35.78 ± 7.31	0.21 ± 0.04	0.50 ± 0.09	53.32 ± 13.97	26.53 ± 2.51	1.79	12.18	1.35	6.00
55.22	3.28	11	43.55 ± 10.70	0.19 ± 0.01	0.66 ± 0.17	35.49 ± 11.13	25.47 ± 1.28	1.76	14.14	1.35	6.45
61.89	3.56	16	40.15 ± 8.97	0.19 ± 0.03	0.44 ± 0.03	47.26 ± 14.49	25.51 ± 1.93	1.57	13.72	0.96	5.40
62.57	5.23	15	36.30 ± 8.44	0.20 ± 0.02	0.62 ± 0.08	50.95 ± 15.33	25.97 ± 2.06	1.79	14.00	1.19	6.60
69.86	2.95	19	40.65 ± 7.54	0.16 ± 0.02	0.91 ± 0.09	34.26 ± 9.18	33.59 ± 2.38	1.89	16.80	1.88	7.20
70.02	3.78	20	48.45 ± 8.24	0.18 ± 0.01	0.68 ± 0.10	30.92 ± 12.96	28.22 ± 2.45	1.77	14.14	1.19	5.40
79.27	4.49	20	47.68 ± 10.41	0.18 ± 0.01	0.85 ± 0.10	30.61 ± 9.18	29.30 ± 2.68	2.02	14.56	1.68	6.30
81.97	3.40	11	49.43 ± 11.98	0.17 ± 0.01	0.70 ± 0.17	35.55 ± 9.80	29.67 ± 2.20	2.40	14.42	1.17	6.60
83.13	3.14	16	46.53 ± 10.83	0.16 ± 0.01	0.80 ± 0.10	28.72 ± 6.91	32.49 ± 2.35	2.79	16.10	2.36	6.75
97.56	3.04	13	43.12 ± 10.46	0.17 ± 0.01	0.75 ± 0.08	29.25 ± 7.53	37.26 ± 2.41	2.46	15.40	2.03	7.35

Table S2 Pearson correlation matrix between chemical traits in young plants of *E. edulis*.

	Nitrogen	Magnesium	Potassium	Phosphorus
Nitrogen	-	0.56	0.71	0.79
Magnesium		-	0.55	0.76
Potassium			-	0.70
Phosphorus				-

TABLE S3 Coefficient of determination (R^2) of the relationship between each leaf traits and landscape forest cover at different spatial scales (200 to 1000 m of radii), considering 15 forest landscapes. The highest value of R^2 is highlighted in bold for each variable.

Leaf traits	**Scales**				
	200m	400m	600m	800m	1000m
Leaf area - LA	0.006	0.082	0.346	**0.433**	0.425
Leaf thickness - LT	0.091	0.166	0.311	0.408	**0.432**
Leaf toughness - LTO	0.106	0.096	0.197	0.314	**0.380**
Leaf mass per area - LMA	0.147	0.298	0.403	0.531	**0.593**
Chlorophyll index – CI	0.052	0.140	0.348	0.544	**0.647**
Magnesium concentration - Mg	0.053	0.141	0.297	0.370	**0.409**
Nitrogen concentration - N	0.122	0.153	0.281	0.436	**0.487**
Phosphorus concentration - P	0.097	0.132	0.239	0.361	**0.441**
Potassium concentration - K	0.069	0.032	0.051	0.014	**0.233**

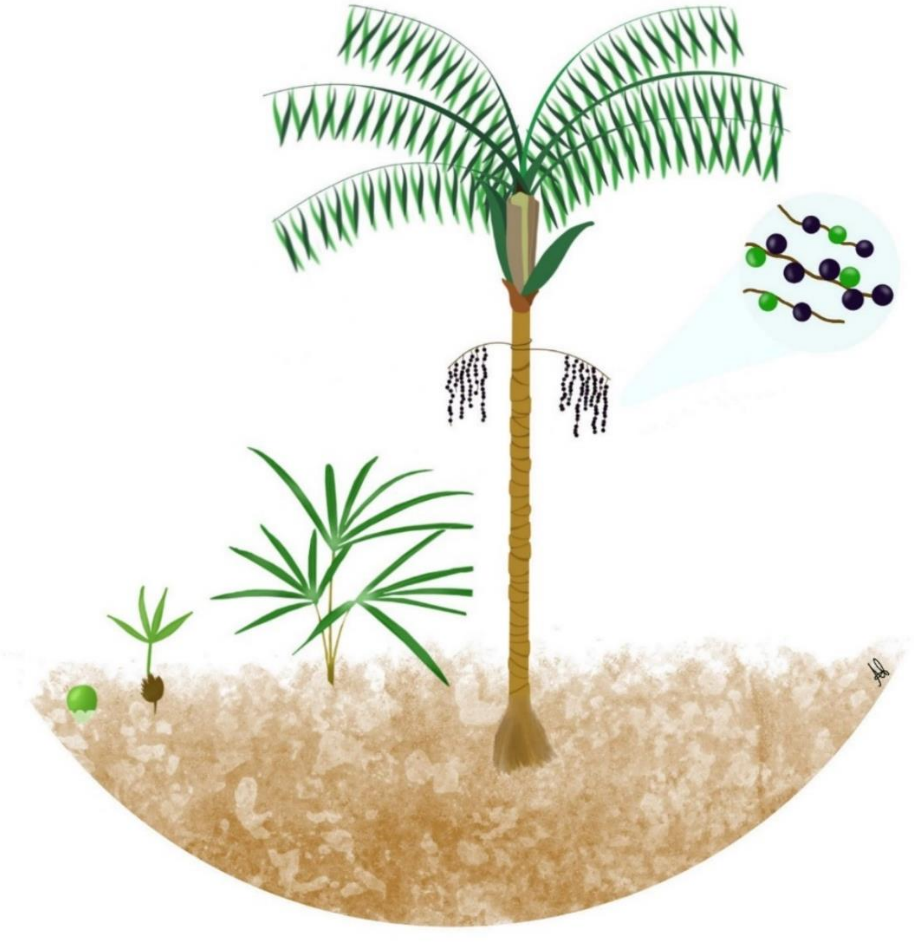
TABLE S4 Variance inflation factor values for each biochemical, chemical and morphological leaf traits of young *E. edulis* plants considering the full model.

Leaf trait	**Forest cover**	**Canopy openness**
Leaf area	1.128	1.128
Leaf thickness	1.100	1.100
Leaf toughness	1.022	1.022
Leaf mass per area	1.226	1.226
Chlorophyll index	1.023	1.023
Magnesium concentration	1.898	1.898
Nitrogen concentration	1.898	1.898
Phosphorus concentration	1.898	1.898
Potassium concentration	1.898	1.898

CAPÍTULO 3

Landscape conservation and maternal environment affect genetic diversity and the physiological responses of *Euterpe edulis* (Arecaceae) progenies to light availability

Article prepared for submission to Environmental and Experimental Botany (IF: 5.54, A1).



Landscape conservation and maternal environment affect genetic diversity and the physiological responses of *Euterpe edulis* (Arecaceae) progenies to light availability

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Abstract

The Brazilian Atlantic Forest (AF) is severely deforested and the remaining forest fragments are generally reduced and disconnected. *Euterpe edulis* (Arecaceae) is a native AF palm rarely found in forest fragments inserted in more deforested landscapes. We investigate how forest fragments inserted in landscapes with different levels of deforestation influence both the genetic diversity and physiological traits of *E. edulis* progenies. For this, we evaluate the genetic diversity and physiological variables associated with carbon balance at leaf and whole-plant leaf scales of *E. edulis* progenies to light availability. We collected fruits from six mother plants, being three from a forest fragment inserted in a more forested landscape (83% of forest cover) and three from a forest fragment inserted in a more deforested landscape (55% of forest cover). The seeds were germinated and, after reaching the juvenile stage, 17 microsatellite markers were used to perform a genetic diversity analysis. The progenies were subjected to 18 light treatments (0.72 to 22.1 mol photons m^{-2} day^{-1}) for the analysis of the carbon balance at leaf and whole-plant scales. We found that the origin of the mother plant proved to affect some genetic parameters, since progenies from mother plants of a forest fragment inserted in the more forested landscape had a greater number of private and effective alleles. In addition, progenies from this forest fragment had a great acclimation capacity to the light levels, with higher growth rates and vigor. Our results provide evidence that conservation actions are necessary for this species, including selecting and replanting progenies from the forest fragments inserted in more forested landscapes. It could be a way for alternative genotypes to raise the levels of alleles and thus avoid the collapse of these populations in fragments inserted in deforested landscapes where a low number of adult and juvenile individuals are found.

Keywords: Daily light integral; molecular marker; photosynthesis; shade tolerance; tropical rainforest.

1. Introduction

The increase habitat loss around the world affects several taxonomic groups, mainly in tropical forests, where the highest rates of forest loss are recorded (Lewis et al., 2015; De Oliveira Roque et al., 2018). In the Brazilian Atlantic Forest, for example, the remaining fragments are generally reduced and disconnected (Ribeiro et al. 2009), causing negative impacts on species diversity (Tabarelli et al., 2010). Severely degraded forest fragments are subjected to strong changes in their structure and function, including the increase in solar radiation reaching the understory. This transition leads to changes in microclimate conditions, as increased temperature and decreased air relative humidity, and increased light radiation available for the plants (Murcia, 1995; Hilário and Toledo, 2016). In addition to the consequences of habitat loss, the remaining plants populations are more vulnerable to changes on genetic parameters. These populations are prone to loss of alleles, reduced gene flow and inbreeding depression (Young et al., 1996; Browne and Karubian, 2018). Thus, there is a reduction in the potential of their individuals to adapt to changes in the environment, reducing the fitness (Reed and Frankham, 2003; Leimu et al., 2006).

Forest landscapes subjected to great disturbances tend to suffer a decrease in available resources (as the diversity of pollinators and dispersers, and availability of nutrients and water) for adult trees (Aizen and Feinsinger, 1994; Aguilar et al., 2006). The environment experienced by the mother plant during its development can affect the seed nutritional supply, which can influence the formation of more vigorous seedlings (Roach and Wulff, 1987). This process refers to the particular phenomenon in which the external ecological environment of parental individuals influences the genotype and/or phenotype of their progeny (Donohue, 2009). This is the case for plant populations in fragmented forests, where limited pollination increases the inbreeding, or when changes in abiotic conditions can result in the decreasing vigor of produced seeds (Kramer et al., 2008). Hence, the initial establishment, growth and survival of young individuals are negatively influenced by the environment where the mother plant is developed (Jacquemyn et al., 2001; Li et al., 2011). In general, seedlings and saplings are the most sensitive groups to habitat loss when compared to adults (Rigueira et al., 2013). Moreover, plants are sessile organisms, with ability to adapt to environmental changes depends on the genetic characteristics of the population (Alfaro et al., 2014), since higher levels of genetic diversity guarantee greater adaptive capacity in face to environmental changes.

In tropical forests, as the Atlantic Forest from the South America (AF), many Arecaceae species are threatened due to habitat loss, being vulnerable to a biodiversity decline as such richness, and abundance (Galetti et al., 2006; Benchimol et al., 2017). This biome is considered a biodiversity hotspot due to its high levels of biodiversity and endemism associated with the worrying threatened status (Ribeiro et al., 2009, Rezende et al., 2018). Among the several plant species that are native to AF, *Euterpe edulis* Mart. stands out. This palm tree is the producer of a large number of fruits, which influences the recovery of degraded forest sites through the high potential to attract seed dispersers that often transport their genes to neighboring forest fragments (Reis et al., 2000). Besides, being an allogamous species and with the potential to be dispersed over long distances (Gaiotto et al., 2003, Santos et al., 2016). However, *E. edulis* is threatened to extinction due to fragmentation and habitat loss, as well as its intensive exploitation (Martinelli and Moraes, 2013). During the cutting of its meristem (“heart of palm”), adult individuals are killed, causing a reduction in seed production and, consequently, a decline in *E. edulis* populations (Freckleton et al., 2003).

Many factors affect the establishment and survival of *E. edulis* in deforested landscapes, from processes at a large scale, such as defaunation (Galetti et al., 2013) and predation by vertebrates (Portela and Dirzo, 2020), to fine scales, as changes in genetic diversity and gene flow between populations (Santos et al., 2016; Soares et al., 2019). In particular, when deforestation increases, the local vegetation shrinks, and the forest becomes shorter, thinner, less dense, and, with an increase in canopy gaps (Rocha-Santos et al., 2016). It has already been found that under field conditions, with the forest loss and changes in the understory light regime, young *E. edulis* plants showed plasticity of some leaf traits to acclimatize to light gradient (Cerqueira et al., 2021) and have a quick response to the light availability in the understory (Santos et al., 2012; Lavinsky et al., 2014). However, we have no scientific evidence of such changes in fragments inserted in more deforested landscapes, where only a few or no individuals of this species can be found (Leal, 2019). Remaining populations facing contrasting microclimate environments, with different regimes of light, temperature and humidity can, together, create different selective pressures which could influence their persistence for the long term.

Despite the growing number of studies with *E. edulis* (see Chapter 1 of this thesis), there is still a lack of integrated studies comparing variations in leaf traits in a controlled environment with genetic diversity in order to elucidate the processes that involve the disappearance of young individuals in more deforested landscapes. In addition, new research has shown that the maternal light environment during seed development can affect the quality of the seed of this palm (Alabarce et al., 2017). Therefore, a detailed understanding of the mechanisms involved in the natural regeneration, especially the relationship among the genetic diversity and the habitat loss, will help to elucidate the mechanisms involved in the acclimatization capacity of *E. edulis* in desforested landscapes. Therefore, we investigated, for the first time, how forest fragments inserted in landscapes with different levels of deforestation influence both the physiological and genetic traits of *E. edulis* progenies subjected to a wide range of light in a semi-controlled experiment. Specifically, we aimed to answer the following questions: (i) is there a relationship between genetic diversity and the physiological response for the progenies from different mother plants?; (ii) the progenies from mother plants of *E. edulis* inserted in different forest fragments have distinct ability patterns to acclimatize in a wide range of light?; (iii) the morphophysiological traits of *E. edulis* progenies are influencied by the light gradient and/or for the mother plant environment? Based on the possible influence of the mother plants growth environments on the growth and development of its progenies, we believe that there is a genetic difference between the progenies and that these differences influence aspects of the carbon balance in leaf scale (organ) and in whole-plant scale (organism). In addition, we expect that progenies from a fragment inserted in a more forested landscape will have a greater capacity to adjust to the light gradient under semi-controlled conditions.

2. Material and methods

2.1 Study area and mother plant environment

This study was conducted in two forest fragments in the AF in landscapes with contrasting forest cover, located in the municipality of Una, southern Bahia, Brazil. These forest fragments were selected from a study carried out on 15 forest fragments inserted in a forest cover gradient at landscape scale (for more details see chapter 2 of this thesis). In this study, we consider as a landscape, a radius of 1000m from the center of the sampled fragment. We used the 1000 m radius, as it was the best scale found to predict changes in forest loss in leaf traits related to growth and influence of the availability of light in young plants of *E. edulis*

(Cerqueira et al., 2021). So, these two fragments were inserted in a landscape with greater forest cover (site 1; 83% forest cover) and another with a smaller one (site 2; 55% forest cover). Subsequently, the size of each fragment within a radius of 1000 m was also estimated using the Fragstat 4.2.1 software (Mcgarigal et al., 2012) (Table 1). In 2015, this region suffered a strong drought event that lasted for almost the middle of the following year (CPTEC/INPE, 2018; Gateau-Rey et al., 2018) and, thus, fruit production was very scarce in subsequent years. Thus, in the year 2018 among the forest fragments only two with presented at least three mother plants (hereafter, M_P) with signs of fruiting. In each fragment, we selected reproductive individuals carrying bunches with mature fruits, located at least 40 m apart from each other, being called A, B and C in the largest forest cover, and D, E and F the one with the lowest forest cover (Table 1). So, we collected one fruit bunch from each of the $M_{P.}$

For a better characterization of these forest fragments where each M_P developed, hemispheric photos were taken, and the percentage of canopy openness (CO) was obtained (Table 1). For that, in each fragment ten plots of 40 m^2 were randomly selected, keeping a minimum of 50 m from the nearest edge of the forest. Then, photographs were taken in the center of each plot. We used a Nikon Coolpix 4300 digital camera equipped with a fisheye (180º) hemispheric lens attached to a tripod 1.5 m above the ground, and positioned towards the magnetic north (Andrade et al., 2015; Cerqueira et al., 2021). The percentage of canopy openness for each forest fragment was calculated using the free software Gap Light Analyzer (GLA) (Frazer, Canhan and Lertzman, 1999). We took the pictures in the late afternoon or on cloudy days to avoid overexposure.

Table 1. Description of the sites where *E. edulis* fruits were collected in Southern Bahia, Brazil.

Forest Fragment	M_P	Coordinates	FS (ha)	FC (%)	CO (%)
1	A, B, C	39° 05' 24"W 15° 15' 38"S	268.03	83.12	4.8
2	D, E, F	39° 02' 44"W 15° 20' 53"S	154.36	55.04	6.7

M_P, mother plant; FS, fragment size; FC, forest cover at landscape scale considering a 1000m buffer of radius; CO, canopy openness.

2.2 Plant material and experimental growth conditions

After collecting *E. edulis* fruits, they were manually pulped, washed in running water, dried in the shade and placed to germinate in a bed containing sand washed on the nursery. The experiment was carried out between July 2018 and February 2019 and lasted 229 days. After germination, the seedlings were transplanted into 1.5 L plastic bags, containing substrate and black soil and subjected to an acclimatization period of approximately 30 days. After this time, seedlings were placed in PVC tubes of 100 mm in diameter and 250 mm in height and then were subjected to 18 light environments. Each of them measuring 1.2 x 1.2 x 1.0 m were installed, arranged under a metal bench, covered with different layering arrangements of black shading screens, ranging from 0.72 to 22.1 mol photons m^{-2} day^{-1} of daily light integral (DLI). In each light environment, between 4 and 6 progenies of each M_P were placed, totaling 462 seedlings of *E. edulis* throughout the experiment. However, M_P E and F did not present enough fruits to be considered for physiological analysis.

To estimate DLI within each light environment, a light radiation sensor S-LIA-M002 was used, coupled to a Hobo Micro Station Data Logger H21-000 datalogger (Onset Computer, Massachusetts, USA). Microclimatic conditions were monitored during the experimental period using the Hobo Pro V2 Data Logger station (Onset Computer, Massachusetts, USA), from which air temperature and relative humidity were obtained and the deficit of air vapor pressure (DPV) was calculated. Average daily temperatures of 27ºC were recorded. The average daily DPV was 0.45 kPa. From the compiled data extracted from the light sensors, we obtained the DLI values of 0.7, 0.8, 1.8, 1.9, 2.0, 3.2, 4.6, 5.3, 10.2, 10.6, 11.5, 12.0, 14.0, 15.1, 19.2, 20.2 and 22.1 mol photons m^{-2} day^{-1} for the 18 light environments.

2.3 DNA extraction and genotyping with microsatellite loci

For genetic analysis, we wait to the progenies reach the ontogenetic stage of Juvenile I (which comprised individuals with less than 0.15 m of insertion height and presenting two to four leaves) (Silva, 1991; Reis et al., 1996; Silva et al., 2009), which occurred approximately in 6 months after the seedlings were placed in the light environments. We chose this stage because the seedling still had endospermic reserves, directly influencing its ability to adjust to environmental variations. Subsequently, we randomly sampled leaf tissue from 10 progenies of each of the six $M_{P,}$ totaling 60 samples (Table 2). Since these are half-siblings of open reproductive pollination, it was not necessary to genotype all the plants in the experiment, since in each family the maternal genome was common among all samples. We performed the DNA extraction using the Doyle and Doyle (1987) protocol. The DNA samples were quantified by comparing each sample to the standard DNA (phage lambda) with known concentration in 1% agarose gel, stained with GelGreen proceeding the photo documentation in a transilluminator under blue light. To carry out genetic analyzes with the 60 sampled individuals, we used 17 nuclear microsatellite markers following the laboratory conditions for PCR reactions as established by Gaiotto et al. (2001). Subsequently, we performed the genotyping in the automatic DNA analyzer ABI3500 (Applied Biosystems) in a multiload system. For genotyping, the sizes of the obtained fragments were analyzed using the GeneMarker program version 2.2 (SoftGenetics, State College, PA, USA).

2.4 Growth variables

At the beginning of the experiment, 10 progenies from each M_P were collected randomly for biomass analysis. Height (H), stem diameter, (D), number of leaves (LN), leaf area (LA) and dry root mass (RDM), stems (SDM), leaves (LDM) and their total (TDM). At the end of the experimental period when reaches the ontogenetic stage of Juvenile I, the same variables were evaluated to estimate the growth variables. LA was estimated using an automatic leaf area meter LI-3000 (Li-Cor Bioscience, Lincoln, NE, USA). To determine the dry mass, the plants were separated into roots, stems and leaves and the samples were placed to dry in a forced ventilation oven for plant material at 50°C until constant mass. From the data obtained, the leaf area ratio (LAR = LA/TDM) was calculated, relative growth rate ($RGR = \ln TDM_{225} - \ln TDM_0/225$ (days)) and net assimilation rate ($NAR = (TDM_{225}-TDM_0/LA_{225}-LA_0)(\ln LA_{225}-\ln LA_0/225$ (days)) (Hunt, 2003).

2.5 Whole-plant compensation point (WLCP)

In order to estimate the minimum DLI value required to maintain a positive carbon balance on an entire plant scale, the WLCP was calculated. The WPLCP was estimated from the DLI value at which the line intersects the x-axis, when RGR = 0 (Lusk and Jorgensen, 2013), using the average DLI values obtained in each of the 18 light environments.

2.6 Light-response curves

We performed light-response curves of photosynthesis using a portable photosynthesis measurement system, LI6400 (Li-Cor, USA), equipped with a light source, 6400-02B RedBlue. The measurements were made on a mature and fully expanded leaflet from two progenies of each M_P in the 18 light environments. To avoid damage caused by photoinhibition, the equipment was programmed to provide different values of photosynthetically active radiation (PAR) depending on the light environments. For the progenies that were in the light environments from 0.7 to 2 mol photons m^{-2} day^{-1} the values were: 600-400-300-150-100-50-25-15-10-5 e 0 and 0 µmol photons m^{-2} s^{-1}; from 3.2 to 11.5 mol photons m^{-2} day^{-1} the values were: 800-600-400-200-100-50-25-10-5 and 0 µmol photons m^{-2} s^{-1} ; from 12.0 and 22.1 mol photons m^{-2} day^{-1} the values were 1000-800-600-400-200-50-25-10-5 and 0 µmol photons m^{-2} s^{-1}. The chamber temperature of 27 °C and CO_2 concentration of 400 µmol mol^{-1}. Then, we tested nine different models to adjust the light curves (Lobo et al., 2013), and the model with the best fit was identified as a non-rectangular hyperbola developed by Prioul and Chartier (1977). Based on this model, we obtained the following parameters: maximum rate of gross photosynthesis in saturating light (A_{max}), apparent quantum yield (α), dark respiration rate (R_d), light compensation point (LCP) and light saturation point (LSP).

2.7 Chlorophyll fluorescence

For the measurements of chlorophyll fluorescence, just after the measurements of leaf gas exchange, a clip was placed on the same leaflet, to maintain dark conditions for at least 30 minutes, ensuring total oxidation of the electron transport of the photosynthetic system. We used a portable fluorimeter Pocket PEA (Hansatech Instruments, UK). (Hansatech Instruments, United Kingdom), in which the leaves were exposed to a saturating pulse light (3500 µmol of photons m^{-2} s^{-1}, wavelength of 650 nm, for 1 s). The transient fluorescence of chlorophyll a was analyzed using the OJIP test (Strasser and Strasser, 1995). Among the parameters obtained by the OJIP test, we selected those most used in studies with light stress (Gonçalves et al., 2010; Pollastrini et al., 2014; Cerqueira et al., 2017): potential quantum efficiency of photosystem II (Fv/Fm), performance index (PI_{ABS}) and Probability that an absorbed photon moves an electron further than QA^- (φEo).

2.8 Data analysis

The genetic diversity of *E. edulis* was estimated using GenAlex 6.5 (Peakall and Smouse, 2012). We calculated the following genetic diversity parameters: number of alleles (Na), effective alleles (Ne), inbreeding coefficient (*f*), exclusive alleles (A). To estimate the frequency of null alleles and identify possible genotyping errors, we previously performed an analysis with the MICRO-CHECKER 2.2.3 program (Van Oosterhout et al., 2004). The progenies had a low mean frequency of null alleles (≤0.05), not compromising our results.

Subsequently, using the corrected genotypes from MICRO-CHECKER, we carried out the genetic analyses. We also used the pairwise relatedness of Lynch and Ritland (1999) in GenAlex program to verify if the forest fragments inserted in landscapes with different levels of deforestation could influence the parentage pattern of the progenies. Then, using these values of relatedness between pairs of individuals, we performed three heatmap analysis in heatmaply package in software R (Galili et al. 2018): 1) using all the progenies of the six M_P sampled in forest fragment 1 and 2; 2) using only the progenies of the M_P sampled in forest fragment 1 and; 3) using only the progenies of the M_P sampled in forest fragment 2. Then, we used the hierarchical clustering algorithm with the Euclidean distance and the average method, implemented in heatmaply package. Subsequently, we evaluated the genetic structure of the progenies using the Bayesian model in the Structure program (Evanno et al., 2005). In the configurations of the Bayesian model, the number of distinct genetic groups was automatically inferred according to the mixed model. The analysis of the number of clusters (K) was performed for values ranging from 1 to 6 (considering that the progenies of each matrix could form a cluster) with ten independent chains, each chain with a burn-in length of 50,000 iterations, followed by for 100,000 repetitions of the MCMC (Markov and Monte Carlo chain). The ΔK (real number of groups) was determined based on the average values of L (K) produced by ten repetitions for each K, according to the method of Evanno et al. (2005), using the Structure Harvester website (Earl and VonHoldt, 2012).

We analyzed the relation between the variables of a leaf and whole-plant scale along the light environments with analyses of covariance (ANCOVA), in which we considered the variables at leaf and plant scale as response variables separately, the M_PA (progeny from mother plant A), M_PB, M_PD and M_PE as a factor, and the light environment as a covariate (DLI). We previously tested data normality by applying the Shapiro-Wilk test and variance homoscedasticity by applying the Bartlett test. To meet the assumptions of the adjustments, transformations in DLI were made when necessary (Logn). We also evaluated the homogeneity of slopes by adding the interaction term in the ANCOVA. When slopes were not homogenous, we performed linear regressions for each M_P. For variables with significant effect on the categorical variable (M_P), we performed a post-hoc test of multiple comparisons using the Tukey test, excluding the effect of the covariate (DLI). Regarding the WPLCP values from the confidence intervals and the error estimates, we compared the values found for the progenies of the different M_P (Lusk and Jorgensen, 2013). We considered that there was no significant difference between the points of compensation between the progenies of the different M_P only if the value of the WPLCP of each one was within the confidence interval of the WPLCP of the other M_P. All analyzes were performed using Software R (R Core Team, 2018).

3. Results

The progenies of all M_P showed low Na and Ne except from the M_PA, which presented twice the value of Ne when compared to the others M_P (Table 2). The values of *f* were extremely high, except for M_PD that presented the lowest values. All populations had private alleles, however the values for M_PA, M_PB and M_PC were much higher when compared with M_PD, M_PE and M_PF (Table 2).

Table 2. Genetic diversity of *E. edulis* progenies considering six mother plants sampled in two forest fragments in the Atlantic Forest of Southern Bahia, Brazil. The mother plants in bold represent the progenies that were used in the light availability experiment.

Mother plants	N	Na	Ne	*f*	A
A	10	5.706	4.169	0.326	35
B	10	4.235	2.854	0.412	14
C	10	3.824	2.594	0.381	15
D	10	3.765	2.704	0.193	9
E	10	4.118	2.871	0.320	8
F	10	3.471	2.508	0.389	4

N = Number of individuals; Na, number of alleles; Ne, effective alleles; *f*, inbreeding coefficient; A, exclusive alleles.

The heatmap with clustering using the pairwise relatedness for analysis with all progenies sampled, two groups were formed, separating the progenies with origin of forest fragment (Figure 1a; Figure S1). However, when we performed the analysis separated by progenies of the different landscapes, we observed that the progenies of forest fragment 1 with the largest forest cover, revealed only two clusters, according to the mother plant (Figure 1b; Figure S2). In contrast, the progenies of forest fragment 2 with less forest coverage originated eight clusters (Figure 1c; Figure S3). The Bayesian cluster analysis showed that the sampled progenies form two well-defined genetic clusters, separating the progenies from mother plants A, B and C, from those originating from mother plants D, E and F (Figure 2; Figure S4).

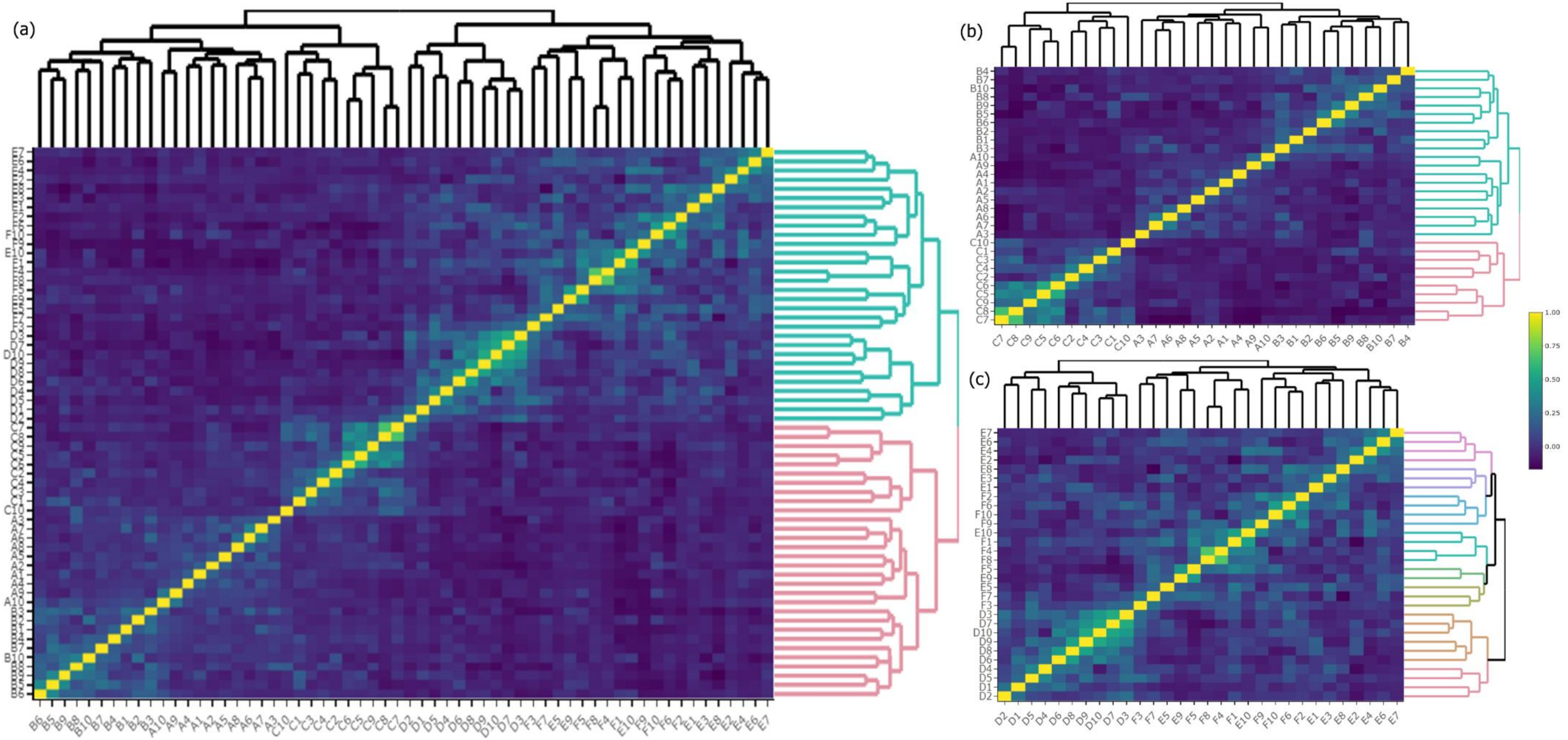

Fig. 1. Heatmap of relatedness values for *E. edulis* progenies of six mother plants in two forest fragments. **a** all progenies of the six mother plants sampled in forest fragment 1 and 2, with the pink cluster representing individuals from plant mothers A, B and C of the forest fragment 1 and the blue cluster individuals from plant mothers D, E and F of the forest fragment 2; **b** progenies of the plant mothers sampled in forest fragment 1, the blue cluster represents individuals from plant mothers A and B and pink cluster individuals from mother C; **c** progenies of the plant mothers sampled in forest fragment 2, with individuals from plant mothers D, E and F distributed into eight clusters.

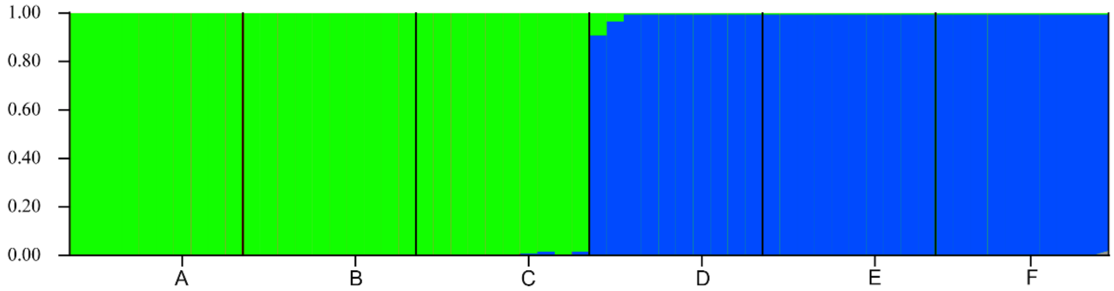

Fig. 2. Summary plot from STRUCTURE software for *E. edulis* progenies of six mother plants (A-F). Each sampled individual of *E. edulis* is represented by a single vertical line broken into two predefined populations which were coincident with two different colors (clusters), green and blue.

At whole-plant scale, we observed that there was a significant relationship between these growth variables and the light environments, and this relationship was affected by the origin of the *E. edulis* progenies (MP) (Table 3). For RGR we observed a significant increase with the increments in light availability (Figure 3a), in which MPA and MPB were similar to each other (p> 0.05) as well as the MPE and MPD (p> 0.05) (Table 4). In addition, the RGR values were always higher for MPA and MPB than the values of MPE and MPD (Figure 3a). For LAR, the values tended to be lower in environments with greater light availability (Figure 3b), but we still observed that the MPA and MPB were the same (p> 0.05) as well as the MPE and MPD (p> 0.05) (Table 4). Contrary to that was observed for the RGR, LAR values were always higher for MPD and MPE than the values of MPA and MPB. For NAR we observed that there was a significant increase with the increase in the availability of light (Figure 3c). However, all progenies differed significantly from each other (p <0.05) and only the MPD and MPE were equal in relation to the availability of light (p> 0.05) (Table 3). In addition, the NAR values were always higher in environments with greater light availability and for the MPA and MPB when compared with the values of the MPD and MPE.

Table 3. Summary of the analysis of covariance (ANCOVA) for variables in scale of whole-plant and leaf scale for progenies of *E. edulis*. p values obtained for covariate DLI, p-level for the four mother plants (M_P) e p-interaction between PAR and M_P.

	Variable	DLI	p-level (M_P)	p-interaction (DLI*M_P)
Whole-plant scale	RGR	0.000***	0.000***	0.549
	LAR	0.000***	0.000***	0.743
	NAR	0.000***	0.000***	0.000***
Leaf scale	A_{max}	0.000***	0.415	0.880
	A	0.000***	0.448	0.567
	R_d	0.000***	0.001**	0.058*
	LCP	0.000***	0.011*	0.047*
	LSP	0.000***	0.002**	0.000***
	Fv/fm	0.000***	0.450	0.289
	PI_{ABS}	0.000***	0.134	0.144
	φEo	0.000***	0.001**	0.159

$p > 0.05$ (not significant); $p < 0.05$(*); $p < 0.01$(**); $p < 0.001$(***). DLI, Daily light integral; M_P, mother plants; RGR, Relative growth rate; LAR, Leaf area ratio; NAR, Net assimilation rate; A_{max}, Maximum rate of gross photosynthesis in saturating light; (α) Apparent quantum yield; R_d, Dark respiration rate; LCP, Light compensation point; LSP, Light saturation point; Fv/fm, Potential quantum efficiency of photosystem II; $PI_{ABS,}$ Perfomance index; φEo, Probability that an absorbed photon moves an electron further than QA^- .

Table 4. Significance values of the Tukey test for the different variables of progenies of *E. edulis* and their pairwise comparisons between mother plants.

	Mother plants					
Variable	B-A	D-A	E-A	D-B	E-B	E-D
RGR	0.333	**0.000**	**0.000**	**0.000**	**0.000**	0.723
LAR	0.508	0.018	0.025	**0.000**	**0.000**	0.999
NAR	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.995
R_d	**0.000**	0.086	0.087	0.305	0.302	0.999
LCP	0.613	0.026	**0.024**	0.355	0.332	0.999
LSP	0.111	0.928	0.403	**0.025**	**0.001**	0.772
φEo	0.999	0.738	0.025	0.691	**0.031**	**0.001**

RGR, Relative growth rate; LAR, Leaf area ratio; NAR, Net assimilation rate; R_d, Dark respiration rate; LCP, Light compensation point; LSP, Light saturation point; φEo, Probability that an absorbed photon moves an electron further than QA^-. Values of $p > 0.05$

there is no significant difference between the mother plants and values of $p < 0.05$ there is a difference between the mother plants.

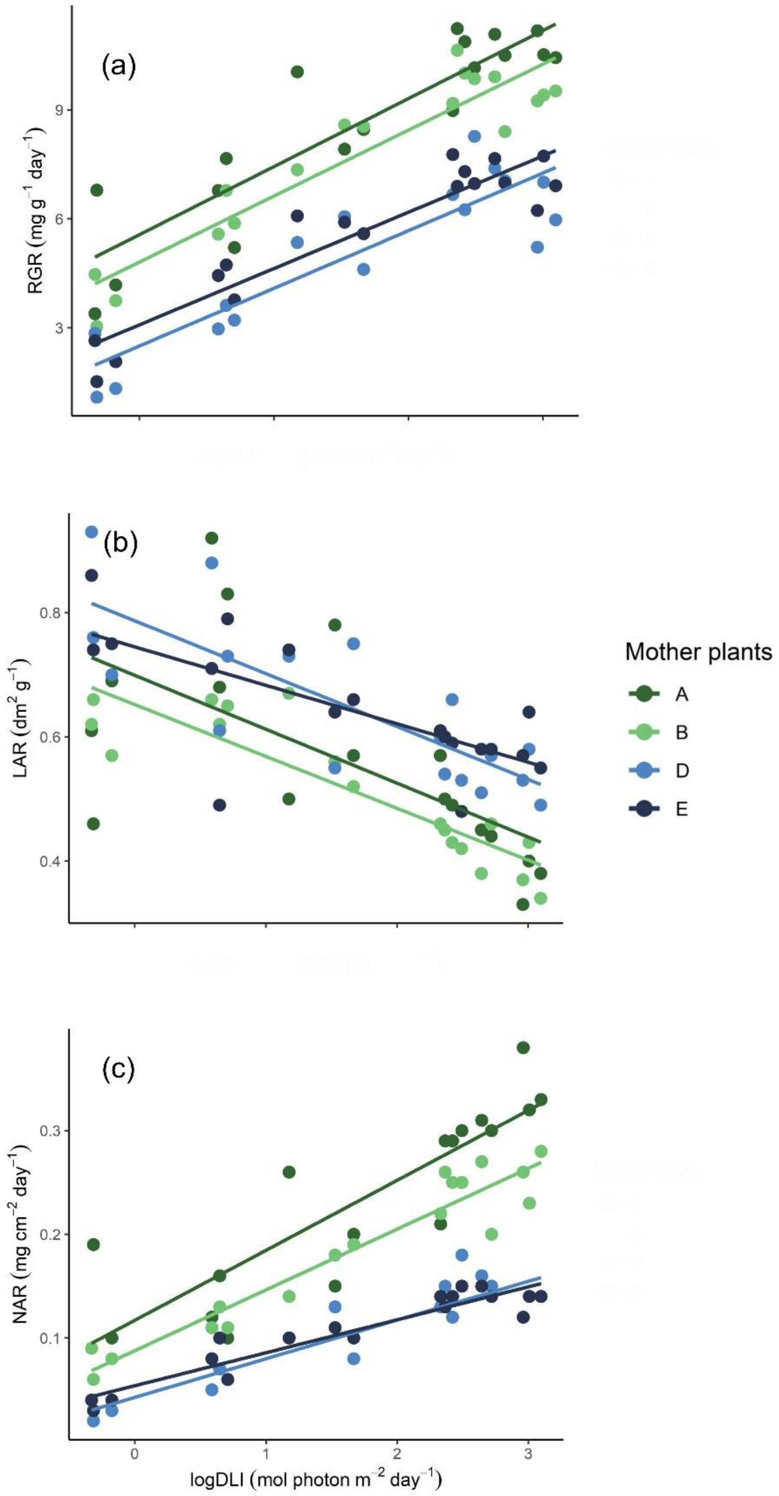

Fig. 3. Relationship between variables on a whole-plant scale and photosynthetically active radiation (PAR) for *E. edulis* progenies of four mother plants. **a** Relative growth rate (RGR). **b** Leaf area ratio (LAR). **c** Net assimilation rate (NAR).

At leaf scale, there was no the same pattern found for whole-plant scale variables. For A_{max}, α, Fv/fm and PI_{ABS} there was no effect of M_P, the response being influenced only by the availability of light (Table 3 and Fig. 4). Regardless of the M_P, there was a significant increase in A_{max} as the availability of light increased, with the highest A_{max} values found in environments with the highest availability of light (Fig. 4a). As for α, Fv/Fm and PI_{ABS}, we observed the opposite trend, where the lowest values for these variables were found in environments with greater availability of light (Fig. 4b, c and d). For other variables (R_d, LCP, LSP and φEo) there was an effect of both M_P and light (Table 3), however when making the pairwise comparisons between the different M_P, we observed that there was no pattern that grouped the progenies in relation its origin (Table 4). However, we observed a tendency for the progenies to have the highest values of LCP, LSP and R_d in environments with greater availability of light whereas the opposite relationship was found for φEo (Fig. 5)

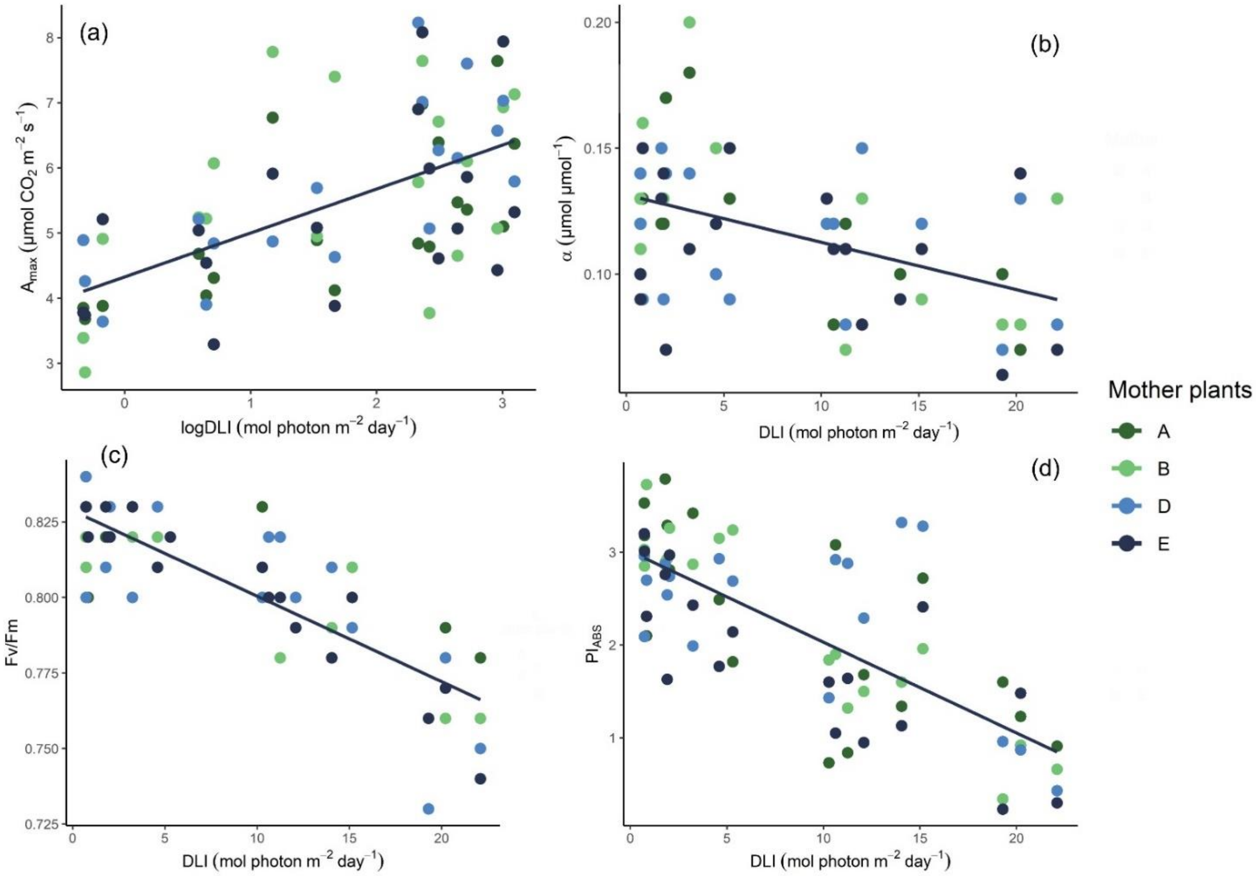

Fig. 4. Relationship between variables on a leaf scale and photosynthetically active radiation (PAR) for *E. edulis* progenies of four mother plants. **a** Maximum gross photosynthesis rate in saturating light (Amax). **b** Apparent quantum yield (α). **c** Potential quantum efficiency of photosystem II (Fv/Fm). **d** Performance index (PI_{ABS}).

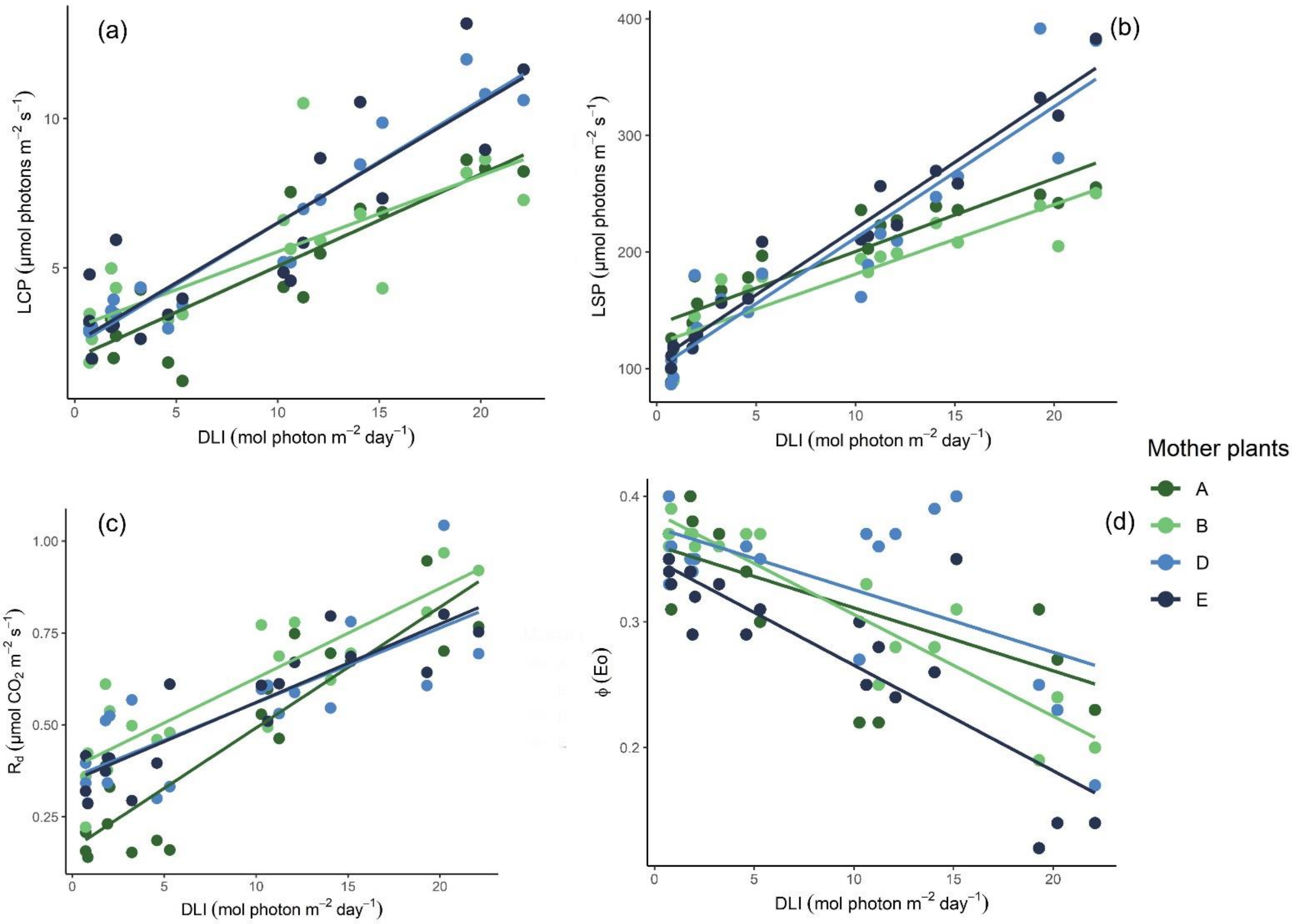

Fig. 5. Relationship between variables on a leaf scale and photosynthetically active radiation (PAR) for *E. edulis* progenies of four mother plants. **a** Light compensation point (LCP). **b** Light saturation point (LSP). **c** Dark respiration rate (Rd). **d** Probability that an absorbed photon moves an electron further than QA^{-} (φEo).

The whole-plant compensation point WPLCP values were on average 3 times higher for MPD and MPE when compared to MPA and MPB. We observed that although there was a little overlap between the confidence intervals, the variation in this interval was higher for the MPD and MPE (Table 5).

Table 5. Whole-plant compensation point (WLCP) values for *E. edulis* progenies of four mother plants and their respective confidence intervals (95%).

Mother plants	WLCP	Confidence intervals
A	0.05	0.01-0.18
B	0.07	0.03-0.18
D	0.20	0.08-0.52
E	0.13	0.09-0.30

4. Discussion

Our results indicate that *E. edulis* progenies from two forest fragments inserted in landscapes with different levels of deforestation are distinct from each other in relation to the genetic and physiological aspects analyzed. Contrary to our hypothesis that there is a genetic difference between the progenies and that these differences influence aspects of carbon balance at the leaf (organ) and whole plant (organism) scales, some genetic diversity indices (Na, f) do not differed between progenies (Santos et al., 2015; Santos et al., 2016).” and “In addition, the hypothesis that progenies from a forest fragment inserted in a more forested landscape will have a greater capacity to adjust to the light gradient under semi-controlled conditions, was partially accepted since progenies from these forest fragments showed a greater acclimation capacity to the light levels presenting higher growth rates and vigor.

Deforestation and habitat loss influences the genetic diversity of plant species (Young et al., 1996; Frankham, 2005; Lowe et al., 2005). Although there was no difference between the indices of genetic diversity, we observed fewer exclusive alleles in the progenies of the fragment inserted in the landscape with the lowest forest cover. We believe that these alleles can be easily lost in more deforested landscapes due to *E. edulis* populations are facing their habitat reduced. Additionally they are influenced by all microclimate changes that influence their survival in these forest fragments. Thus, as the new alleles represent an important mechanism for populations to adapt to environmental changes over generations, forest fragments inserted in more deforested landscapes can induce these populations decrease their surviving probability in adverse environmental conditions.

In this study, we report a strong genetic differentiation between the progenies from the two forest fragments, considering the analysis of genetic structure and the relatedness among progenies. This genetic differentiation between *E. edulis* progenies are probably reflecting the recent forest loss in studied region (Rocha, 2006). In a previous study conducted with the same species in southern Bahia, Santos et al. (2015) reported a change in the pattern of gene pool between the juvenile and adult stages, explaining it as a consequence of forest loss at landscape scale. Assessing the pattern of relatedness within each forest fragment, we observed a large number of groups in the forest fragment inserted in most deforested landscape with higher pollen donor individuals compared to more forested landscape. This result is probably related to the large displacement of pollinators searching for food resources less deforested landscape. It would be expected that the most deforested landscape would have less resource availability, compelling pollinators to move for long distance, and consequently helping to increase the admixture of pollen donors (Morante et al., 2015) This hypothesis could explain the low relatedness found between progenies from mother plants sampled in forest fragment inserted in highly forested landscape.

There are several environmental factors acting to shape the ecological processes in tropical forests. Among them, the light radiation is the variable exerting the greatest influence on ecophysiological behavior of plants (Chazdon and Fetcher, 1984; Valladares and Niinemets, 2008), mainly for palm trees that in most of them regenerate in the forest understory (Chazdon, 1986). The ability of plants to respond to the increase or decrease in PAR is related to adjustments in photosynthetic machinery (leaf scale), and to interactions between morphological and physiological characteristics (whole-plant scale) (Givnish, 1988; Claussen, 1996; Poorter, 1999; Rozendaal et al., 2006; Valladares and Niinemets, 2008). We observed that in the same way that there was a separation between the genetic materials of the two sampled landscape contrasting in terms of forest cover.

There was also a pattern for the variables in whole-plant scale. Progenies from mother plants sampled in a forest fragment inserted in more forested landscape, with a smallest canopy openness, and consequently favorable microclimate conditions, had highest RGR values. The RGR represents the increase in growth per unit of biomass and time (Hoffmann and Poorter, 2002; Alameda and Villar, 2009). Higher RGR values have some ecological advantages since rapid growth results in faster occupation of space within the forest, which can be advantageous in competitive situations (Grime and Hunt, 1975; Poorter and Remkes, 1990). This pattern was also observed for NAR as observed for other tropical species (Costa et al., 2019; Portela et al., 2019). The NAR can be a good indicator of the photosynthesis rate per unit of leaf area (Poorter, 2001) and species with high net assimilation rates, similar to our findings in the progenies from mother plants sampled in a forest fragment inserted in a landscape with the largest forest cover probably have a better potential for competitiveness due to light, a crucial factor for seedling regeneration (Poorter and Arets, 2003). This is particularly important for *E. edulis* progenies, which are generally found in more shaded environments in the forest understory (Cerqueira et al., 2021). The inverse pattern observed for LAR corroborates that to survive in shaded environments of the forest understory, shade-tolerant species increase LAR as a strategy to increase carbon gain, through a greater interception of light per unit leaf area (Poorter, 1999). Thus, for the growth variables, considering the whole-plant scale, we observe the response of a plant that is tolerant to shade, and with better responses in relation to the light availability for progenies from mother plants of fragments with greater quantity of forest in its surroundings.

Shade tolerance is related to the ability to maintain a positive carbon balance under low levels of light radiation (Gratani, 2014). According to the hypothesis of net carbon gain (Givnish, 1988), any characteristic that improves the efficiency of the use of light tends to be present in species tolerant to shade. Low respiratory rates and a lower light compensation point, in addition to greater biomass allocation to the aerial part are typical characteristics of shade tolerant species (Valladares and Niinemets, 2008), as we found for *E. edulis* progenies when subjected to low DLI values. Analyzing the variables at leaf scale, we noticed that there was no determined separation between the progenies in relation to the mother plant's environment, as found for the variables of the whole-plant scale. However, *E. edulis* progenies were influenced by the light availability for all of these variables.

The ability to acclimatize to contrasting light environments is particularly important for rainforest tropical species because juvenile plants growing in the forest understory are prone to undergo photoinhibition of photosynthesis under high light that increases through the formation of medium to large gaps (Lovelock et al., 1994; Leakey et al., 2003a; Leakey et al., 2003b; Leakey, 2005). This increase in light can cause chronic photoinhibition by compromising the reaction centers of photosystem II (PSII) (Quevedo-Rojas et al. 2018; Miyata et al. 2015). A parameter that has been used as an indicator of stress factor is the Fv/Fm ratio (Maxwell and Johnson, 2000; Pollastrini et al., 2014), where values below 0.75 can indicate photoinhibitory damage (Björkman and Demmig, 1987), decreasing efficiency of the photosynthetic process. In addition to Fv/Fm, other parameters that are gaining prominence as they include the efficiency of absorption, capture and transfer of excitation energy by PSII, are PI_{ABS} and φEo, which is also an indicative of loss of photochemical efficiency (Thach et al., 2007).

Previous studies have shown that *E. edulis* regeneration can benefit from openness as from medium gaps, since transferred to environments with greater DLI, there was a higher growth rate. Thus, sunflecks were essential to maintain a positive carbon balance for young plants of this palm (Nakazono et al., 2001; Lavinsky et al., 2014). Although the values of A_{max} have showed a tendency to increase environments with greater DLI, we noticed a marked reduction, both in Fv/Fm, PI_{ABS}, and φEo in these environments. These reductions, even though are not enough to severely inhibit photosynthesis, deserves attention in the scenario of continuous deforestation in the AF, which can further accentuate the changes in the understory microclimate, especially in relation to the light incidence.

Several studies showed that shade tolerance patterns cannot be predicted only at the leaf scale (Kitajima, 1994; Küppers, 1994; Lusk and Jorgensen, 2013). Although photosynthetic processes are of fundamental importance, the net carbon balance per unit of biomass at the whole-plant scale also determines the success of survival in the forest understory (Givnish, 1988). Thus, another methodology used to predict the ability of juvenile plants to survive and grow in the forest understory is the whole-plant scale light compensation point (WPLCP). As a measure that estimates shade tolerance, the WPLCP is assessed as the intercept of the relationship between RGR and DLI (Baltzer and Thomas, 2007). From this, the minimum DLI required to maintain a positive carbon balance can be indicated (Lusk and Jorgensen, 2013). We observed relatively low values regardless of the maternal environment of the mother plants that gave rise to *E. edulis* progenies (0.05 a 0.20 mol photons m^{-2} dia^{-1}). Higher values were found when analyzing shade tolerant temperate climate forest trees, about 0.9 mol photons m^{-2} day^{-1} (Baltzer and Thomas, 2007), or even for *Cariniana legalis*, a native species that also regenerates in the AF understory (Fagundes et al., 2021), about 0.18 mol photons m^{-2} day^{-1}. However, we observed low values of WPLCP for progenies from mother plants developed in forest fragment inserted in more forested landscape when compared to the less forested ones. We then suggest that the lower WPLCP value is evidence of the influence of maternal environment on progeny shade tolerance.

The low values of WPLCP found for the *E. edulis* progenies corroborate that this is a species that regenerates in the forest understory and maintains a positive carbon balance, even at very low levels of DLI. Thus, the landscape context is relevant for the establishment of *E. edulis* in forest fragments, and the maintenance or restoration of forests surrounding these fragments is recommended in species conservation actions. In addition, based on leaf and whole-plant scale analyzes, we observed a high plasticity of *E. edulis* to acclimatize both in dense shade (nearly 0.7 mol photons m^{-2} day^{-1}) and in environments that would be medium to large gaps.

E. edulis is an important source of food for a large number of birds and mammals, having a fundamental ecological role in the conservation of AF fragments (Galetti et al., 2013). In addition, its fruits have high levels of antioxidant compounds, being used to produce medicines, cosmetics and even pulp and juice from them (Schulz et al., 2016). Thus, *E. edulis* is one of the largest non-timber forest products in the AF (Silva-Matos, 1999). All these characteristics make this species a great option for restoration actions for degraded areas, mainly because it attracts several animals with its fruits, besides its ability to generate a source of income for the communities with its sustainable exploitation. From a practical point of view, our study shows that populations with a low number of exclusive alleles in forest fragments inserted in more deforested landscapes should be monitored in long term. Conservation actions should be taken, as the introduction of progenies from the forest fragments inserted in more forested landscapes, with alternative genotypes and alleles, to raise the levels of genetic diversity, and thus avoid the collapse of these populations in fragments with low number of adult and juvenile individuals (Leal, 2019). These actions can reduce future levels of inbreeding and provide better adaptive conditions for these populations to survive mainly in the current scenario of degradation of AF, besides the imminent climate changes. Also, mother plants from forest fragments inserted in landscapes with high forest cover are a desirable source of fruits and seeds to be used in forest restoration programs due to, as demonstrated in our study, their progenies have great vigor, revealed by the growth parameters, as well as a good capacity to adjust to light availability of rainforest understories. Additionally, continuous monitoring of progenies regenerated in these fragments is necessary in the current scenario of climate change and uninterrupted anthropic interference in their habitat.

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Supplementary material

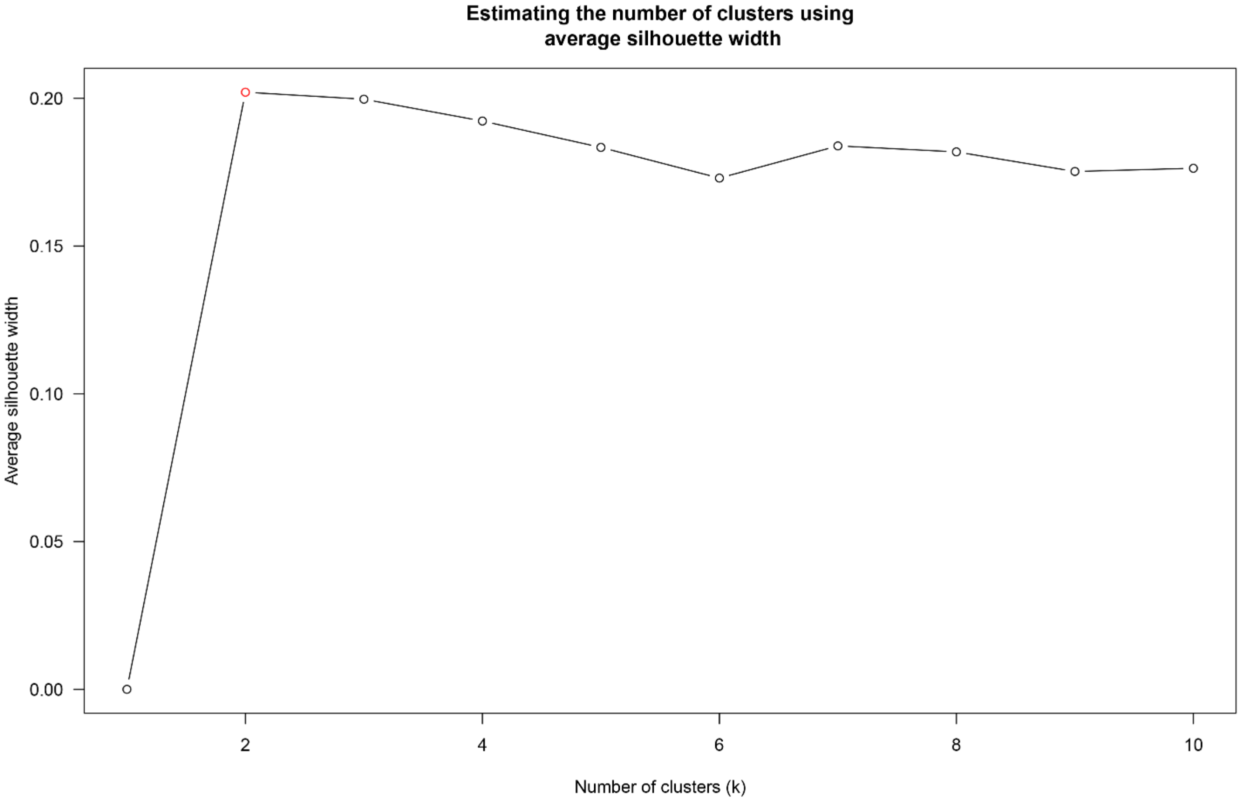

Fig. S1. Estimation of the number of groups, using the average method for the number of K populations in all progenies of *E. edulis* of the six mother plants sampled in forest fragment 1 and 2. The red dot indicates the most likely number of groups (K = 2).

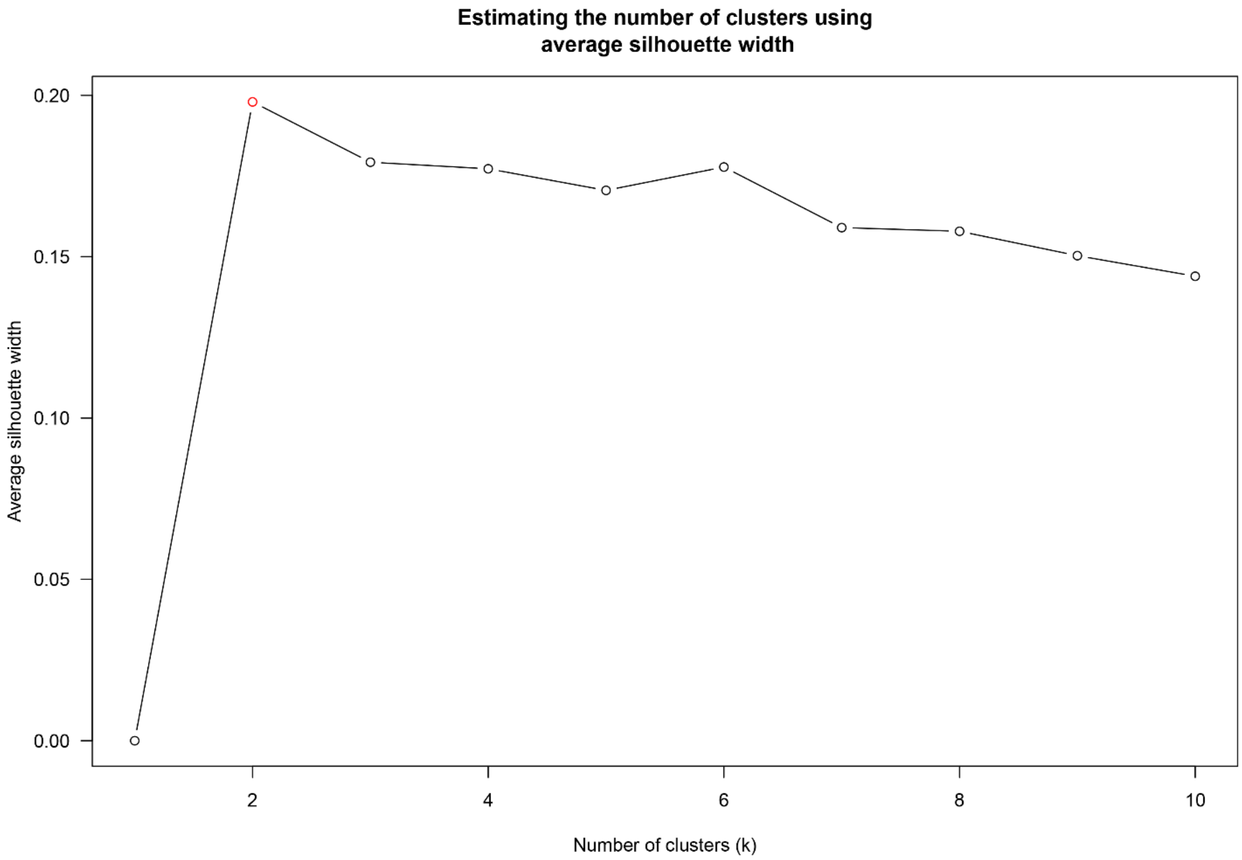

Fig. S2. Estimation of the number of groups, using the average method for the number of K populations in30 progenies of *E. edulis* of the mother plants sampled in forest fragment 1. The red dot indicates the most likely number of groups (K = 2).

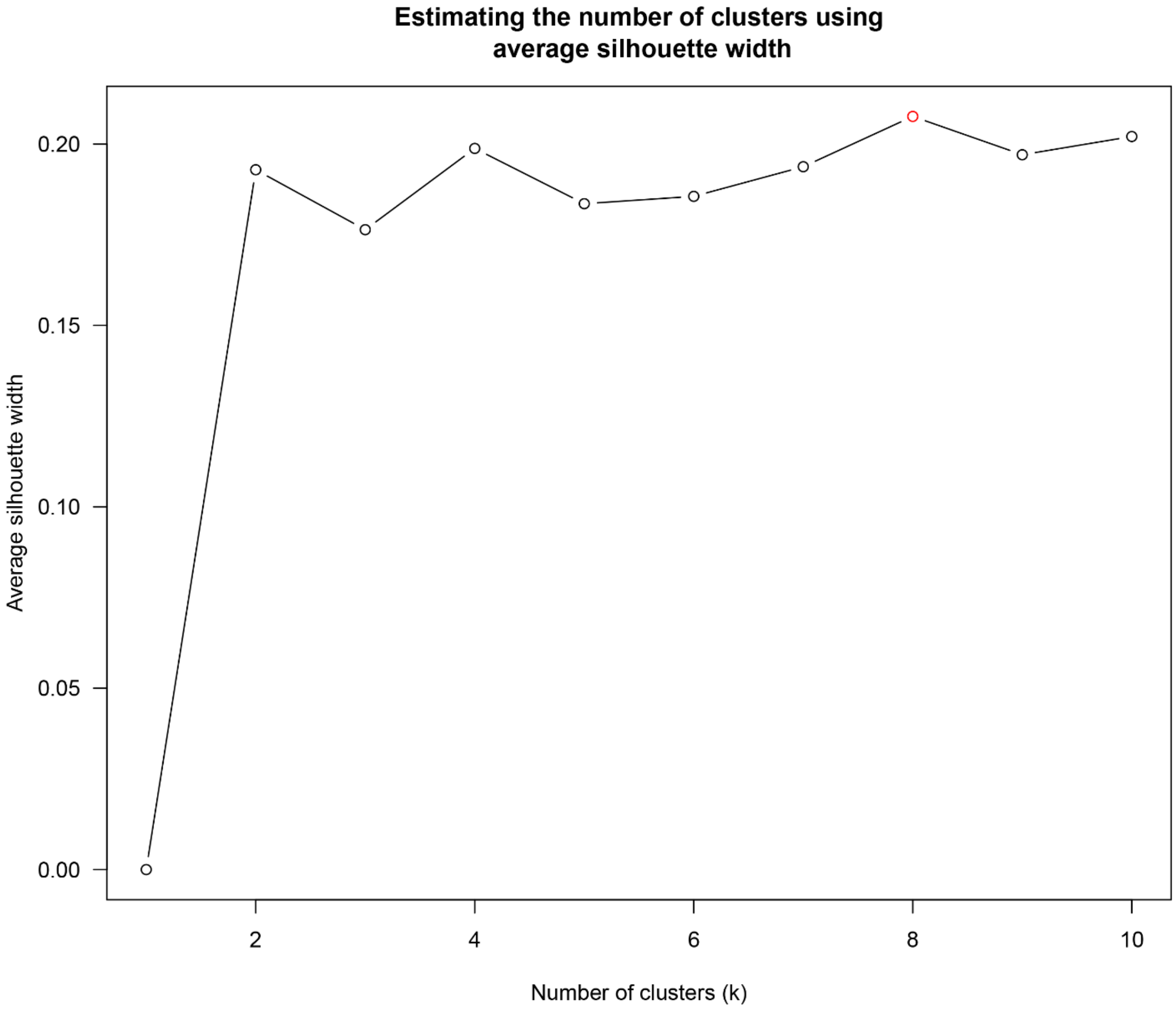

Fig. S3. Estimation of the number of groups, using the average method for the number of K populations in 30 progenies of *E. edulis* of the mother plants sampled in forest fragment 2. The red dot indicates the most likely number of groups (K = 2).

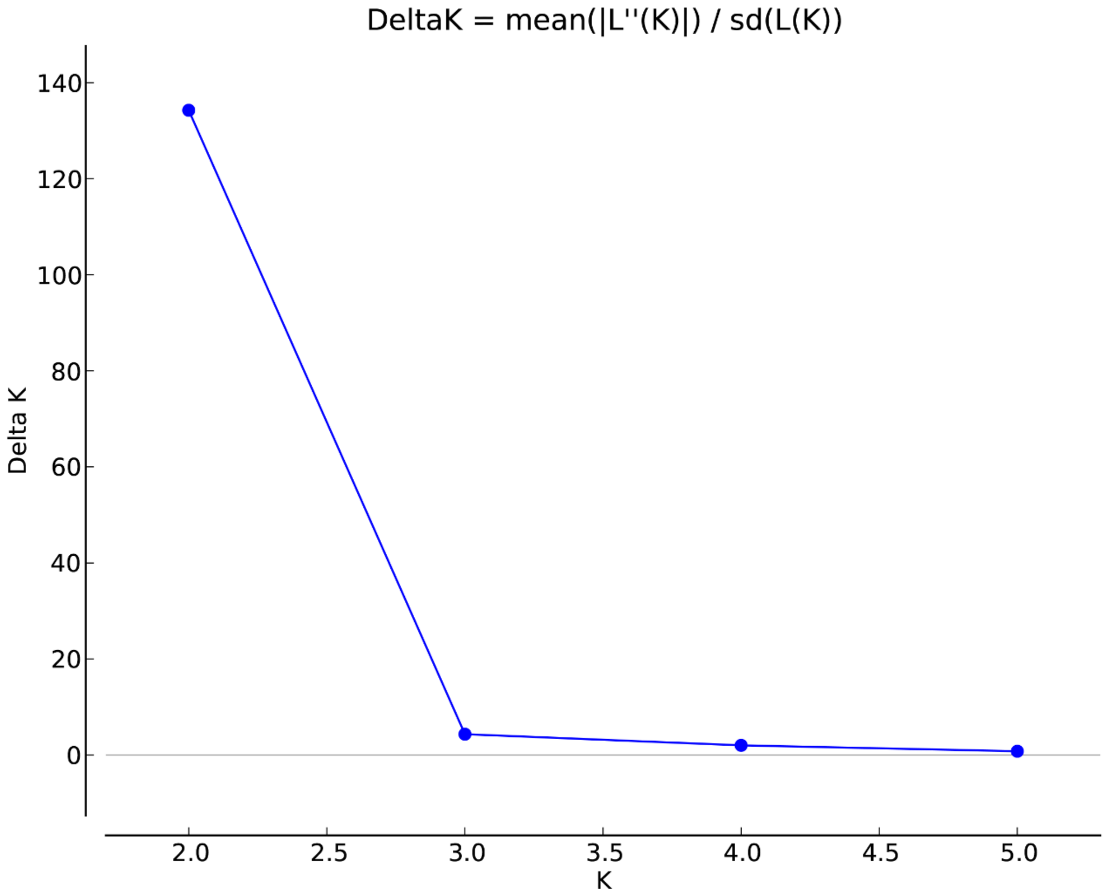

Fig. S4. Variation of the second order of the average values of maximum likelihood for the number of populations K in 60 progenies of *E. edulis* of the six mother plants sampled in forest fragment 1 and 2.

CONCLUSÃO GERAL

Os resultados obtidos com o desenvolvimento dessa tese contribuem para o avanço do conhecimento sobre a produção científica das espécies de palmeiras nativas da Mata Atlântica. Além disso, são trazidas novas evidências sobre a capacidade de aclimatação à perda de habitat e disponibilidade de luz de uma das palmeiras que se encontra ameaçada e possui fundamental importância para o funcionamento desse bioma, o palmito juçara (*E. edulis*).

A partir da revisão sistemática com abordagem cenciométrica realizada no primeiro capítulo foi possível perceber a relevância que espécies de *Euterpe* sp., *Acrocomia* spp. e *Syagrus* spp. possuem na quantidade de publicações. As espécies dos gêneros *Desmoncus* spp., *Geonoma* spp. e *Trithrinax* sp. merecem mais atenção em pesquisas futuras por apresentarem o menor número de publicações, principalmente para investigar processos relacionados como suas propriedades bioquímicas, seu uso e aspectos relacionados à genética. A espécie de palmeira mais estudada, *E. edulis*, ainda carece de estudos interdisciplinares que possam auxiliar na conservação dessa espécie ameaçada de extinção. Os estudos realizados para grande parte das palmeiras ainda são escassos, principalmente para algumas áreas de estudo, como a produção e manejo por comunidades locais, que podem ser o ponto de partida para descobrir e estimular o uso de produtos florestais não madeireiros. Assim, com base no primeiro capítulo pode-se revelar a existência de vieses geográficos e de áreas de conhecimento nas palmeiras nativas da Mata Atlântica, onde a porção sul da Mata Atlântica foi amplamente amostrada em comparação com a porção nordeste, o que merece a devida atenção para investigações futuras.

Com base na investigação realizada no segundo capítulo constatou-se que as plantas jovens de *E. edulis* ocorrem predominantemente em áreas mais sombreadas nos fragmentos florestais. Além disso, essa palmeira conseguiu aclimatar seis dos nove atributos foliares analisados (área foliar, massa foliar específica, índice de clorofila, concentração de nitrogênio, magnésio e fósforo) em relação a um gradiente de perda de floresta na paisagem. A maioria desses atributos foliares foram afetados tanto pelas características locais (abertura de dossel) quanto da paisagem (cobertura florestal). É provável que a falta de variação nas características relacionadas à proteção contra a herbivoria (dureza e espessura foliar) possa limitar o estabelecimento de indivíduos jovens dessa espécie em paisagens altamente desmatadas. Os resultados desse capítulo forneceram novas evidências que tanto a paisagem quanto o contexto local afetam os atributos foliares de jovens de *E. edulis*, levando a ajustes bioquímicos, químicos e morfológicos.

Por fim, no terceiro capítulo com uma abordagem interdisciplinar, foi demonstrado que as progênies provenientes de matrizes de fragmentos florestais inseridos em paisagens mais desmatadas possuem menor número de alelos e devem ser monitoradas a longo prazo. Ações de conservação devem ser realizadas, como a introdução de mudas originadas dos fragmentos inseridos em paisagens mais florestadas, com genótipos contendo maior número de alelos para aumentar a diversidade genética dessas populações nos fragmentos onde há baixo número de indivíduos adultos e jovens. Essas ações podem reduzir os níveis futuros de endogamia e fornecer melhores condições adaptativas para que essas populações sobrevivam principalmente no atual cenário de degradação da Mata Atlântica, aliado às iminentes mudanças climáticas. Além disso, as matrizes de fragmentos inseridos em paisagens com alta cobertura florestal são uma fonte potencial de frutos e sementes para serem utilizadas em programas de restauração florestal. Conforme demonstrado nesse estudo, essas progênies tiveram maior vigor, demonstrado pelas variáveis de crescimento, bem como maior capacidade de se ajustar à ampla variação na disponibilidade de luz. O monitoramento contínuo das progênies que se regeneram nesses fragmentos é necessário no cenário atual de mudanças climáticas e interferência antrópica ininterrupta em seu habitat.