FUNCTIONAL ECOLOGY AND CONSERVATION OF PALMS

EDITED BY: Gerardo Avalos, Thaise Emilio, Silvia Alvarez-Clare and
Kelly M. Andersen

PUBLISHED IN: Frontiers in Forests and Global Change and
Frontiers in Ecology and Evolution

frontiers Research Topics

ISSN 1664-8714
ISBN 978-2-8325-0440-6
DOI 10.3389/978-2-8325-0440-6

About Frontiers

Frontiers is more than just an open-access publisher of scholarly articles: it is a pioneering approach to the world of academia, radically improving the way scholarly research is managed. The grand vision of Frontiers is a world where all people have an equal opportunity to seek, share and generate knowledge. Frontiers provides immediate and permanent online open access to all its publications, but this alone is not enough to realize our grand goals.

Frontiers Journal Series

The Frontiers Journal Series is a multi-tier and interdisciplinary set of open-access, online journals, promising a paradigm shift from the current review, selection and dissemination processes in academic publishing. All Frontiers journals are driven by researchers for researchers; therefore, they constitute a service to the scholarly community. At the same time, the Frontiers Journal Series operates on a revolutionary invention, the tiered publishing system, initially addressing specific communities of scholars, and gradually climbing up to broader public understanding, thus serving the interests of the lay society, too.

Dedication to Quality

Each Frontiers article is a landmark of the highest quality, thanks to genuinely collaborative interactions between authors and review editors, who include some of the world's best academicians. Research must be certified by peers before entering a stream of knowledge that may eventually reach the public - and shape society; therefore, Frontiers only applies the most rigorous and unbiased reviews.
Frontiers revolutionizes research publishing by freely delivering the most outstanding research, evaluated with no bias from both the academic and social point of view.
By applying the most advanced information technologies, Frontiers is catapulting scholarly publishing into a new generation.

What are Frontiers Research Topics?

Frontiers Research Topics are very popular trademarks of the Frontiers Journals Series: they are collections of at least ten articles, all centered on a particular subject. With their unique mix of varied contributions from Original Research to Review Articles, Frontiers Research Topics unify the most influential researchers, the latest key findings and historical advances in a hot research area! Find out more on how to host your own Frontiers Research Topic or contribute to one as an author by contacting the Frontiers Editorial Office: frontiersin.org/about/contact

FUNCTIONAL ECOLOGY AND CONSERVATION OF PALMS

Topic Editors:
Gerardo Avalos, University of Costa Rica, Costa Rica
Thaise Emilio, State University of Campinas, Brazil
Silvia Alvarez-Clare, Morton Arboretum, United States
Kelly M. Andersen, Nanyang Technological University, Singapore

Citation: Avalos, G., Emilio, T., Alvarez-Clare, S., Andersen, K. M., eds. (2022). Functional Ecology and Conservation of Palms. Lausanne: Frontiers Media SA. doi: 10.3389/978-2-8325-0440-6

Table of Contents

frontiers | Frontiers in Forests and Global Change

TYPE Editorial
PUBLISHED 26 September 2022
DOI 10.3389/ffgc.2022.1021784

Editorial: Functional ecology and conservation of palms

Gerardo Avalos[1,2]*, Thaise Emilio[3], Kelly M. Andersen[4] and Silvia Alvarez-Clare[5]

[1]Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica, [2]The School for Field Studies, Center for Sustainable Development Studies, Beverly, MA, United States, [3]Plant Biology Department, Biology Institute, State University of Campinas, Campinas, Brazil, [4]Nanyang Technological University, Singapore, Singapore, [5]Morton Arboretum, Lisle, IL, United States

KEYWORDS

functional traits, palm ecology, leaf economic spectrum, palm *ex-situ* conservation, living palm collections, trait-based ecology, trait evolution

EDITED AND REVIEWED BY
Heather R. McCarthy,
University of Oklahoma, United States

*CORRESPONDENCE
Gerardo Avalos
gerardo.avalos@ucr.ac.cr

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

RECEIVED 17 August 2022
ACCEPTED 05 September 2022
PUBLISHED 26 September 2022

CITATION
Avalos G, Emilio T, Andersen KM and Alvarez-Clare S (2022) Editorial: Functional ecology and conservation of palms.
Front. For. Glob. Change 5:1021784.
doi: 10.3389/ffgc.2022.1021784

Editorial on the Research Topic
Functional ecology and conservation of palms

With more than 2,600 species and 181 genera, palms (Arecaceae) are one of the most diverse and widely distributed plant families in tropical environments (Baker and Dransfield, 2016). Although they make up a modest portion of the above-ground biomass in most neotropical forests (DeWalt and Chave, 2004), their contribution increases in places where palms are dominant (Muscarella et al., 2020). In the Amazon forests, palms are hyperdominant elements (ter Steege et al., 2013). Their sheer abundance secures them a key role in forest function and forest structure (Boukili and Chazdon, 2017).

Palms provide food for a wide variety of animal species (Onstein et al., 2017), including key resources for frugivores, which in turn disperse canopy trees that store most of the carbon in mature forests (Bello et al., 2015). Many human groups value palms and use them as raw material for building, food, drink, clothing, fuel, and medicine (Sylvester et al., 2012).

Palms tissues stretch the limits of plant cells to reach tree-like heights while preserving mechanical stability and long-term function using only apical meristems (Tomlinson, 2006). Little is known about the functional mechanisms governing palms' adaptation to environmental gradients, despite their ecological significance and distinctive morphological and physiological structure. Here, we summarize the functional role of palms from a variety of perspectives, which concentrate on the analysis of functional traits and their influence on adaptation to environmental gradients. Contributions are grouped into the analysis of functional traits and conservation issues.

How functional traits influence palm distribution and performance

Five articles analyzed how functional traits influence adaptation to environmental gradients, successional stages, hydrological conditions, differences in rainfall and nutrients, and habitat fragmentation. Functional trait analysis in palms is fragmentary and biased toward the most common species. The articles compiled here make significant contributions, but more remains to be done. Future studies should examine the ontogenetic, intraspecific, and geographic variation influencing the adaptive value of these traits.

The work by Lauder et al. is the first to analyze simultaneously the effect of successional stage on palm diversity, species and functional trait composition using an altitudinal gradient. Secondary forests were less diverse than mature forests and had less shade-tolerant species. With increasing elevation there was a decrease in juvenile abundance and changes in adult species composition. Sensitive adult species were increasingly confined to small fragments of mature forests which are essential to the long-term maintenance of species diversity and functional diversity.

Emilio et al. analyzed intraspecific variation (and co-variation) in seven leaf functional traits in 14 palm species distributed along a hydro-topographic gradient in central Amazonia. Most studies in tropical plants look at average values of functional traits per species. The role of intraspecific variation in adaptation to environmental gradients is little understood in general, and nearly unknown for palms. Intraspecific variation accounted for 23–74% of the total variation, with significant species effects. Intraspecific variation was unrelated to height above the nearest drainage. Palm species showed well-defined hydrological niches, but large intraspecific variation did not contribute to individual adjustment to the hydrological gradient.

Portela et al. combined functional traits with palm demography using *Astrocaryum aculeatissimum*, *Euterpe edulis*, and *Geonoma schottiana* within the context of habitat fragmentation. The population growth of *A. aculeatissimum* was stable in small and large fragments. *E. edulis* showed a decline in population growth in large fragments due to intense seed predation by monkeys but had stable lambda in smaller fragments. *G. schottiana* had stable population growth in large fragments but declined in smaller fragments. Functional traits showed that *G. schottiana* is a shade-adapted species, whereas *E. edulis* and *A. aculeatissimum* are habitat generalists; the first is affected by fragment size, the second is not. Differences in functional performance were linked to demographic variation.

Trujillo et al. used soil data to explore trait-environment relationships among palm communities in western Amazonia. They linked functional traits to soil gradients and forest types. They found significant trait-environment relationships. Palms with large leaves and fruits, and acaulescent and erect stems, were associated with fertile soils, while palms with unarmed leaves were associated with non-inundated forests. Functional traits varied with soil gradients on a regional scale following soil fertility.

Collins et al. used two specialist (*Chamaedorea tepejilote* and *Geonoma congesta*) and two generalist species (*Geonoma cuneata* var. cuneata and *Chamaedorea pinnatifrons*), to measure seedling performance in a shade house and in a field transplant experiment among soil types varying in nutrient availability to test how species distribution were correlated with soil phosphorus and rainfall. In the shade house, leaf functional traits changed with species rather than with soil nutrients, whereas biomass allocation and relative growth rate were determined by species-soil interactions. In the transplant experiment, survival was related to dry season rainfall. Seedling performance was determined by species-specific responses to soil nutrient and rainfall. While soil nutrients influence biomass allocation, dry season rainfall influences both specialist and generalist seedling survival and therefore their distributions along the nutrient and moisture gradient.

Avalos et al. advance our understanding of allometric relations in palms, a functional group critical for improving carbon stocks estimates in tropical forests. They presented allometric models for estimating total carbon content and aboveground carbon (AGC) using seven of the most common neotropical palm species. This analysis improves carbon stocks estimates in tropical forests. The general palm model estimating total carbon content accounted for 92% of the variation across species. The model estimating AGC showed a 91% fit, and was compared with two other models used to estimate carbon content: Goodman et al. (2013)'s and Chave et al. (2014)'s. All three converged on the estimation of AGC. It is crucial to include more palm species, a wider size range, a greater sample size, and more geographic areas to increase the accuracy of allometric models.

Carrete et al. show that palm-parrot biotic interactions are mediated by their traits. They combined field data, the literature, and citizen science to identify 1,189 interactions between 135 parrots and 107 palm species. Of these, 427 were unique parrot-palm interacting pairs. Pure antagonistic interactions were less common (5%) than mutualistic ones (89%). After controlling for phylogeny, the size of consumed seeds and parrot body mass were positively correlated. Seed dispersal distances varied among palm species, with larger parrots dispersing seeds at greater distances. Social behavior, predation, food availability, and seasonality may affect the nature of these interactions.

Palm conservation

Elshibli and Korpelainen examine the genetic diversity of the endangered palm *M. argun* of the Nubian desert where the harsh field conditions preclude the collection of data on the conservation status and genetic variation of this species. The seasonal river floodplains, essential for the survival of this palm, are disappearing due to climate change. The authors report low genetic diversity and lack of intergenerational genetic diversity. Seed collection from genetically diverse populations for *ex-situ* gene banks could prevent species extinction in this case.

Griffith et al. examine the role of botanical gardens in palm conservation. Living palm collections are essential for the ex-situ survival of many species that are endangered or extirpated from the wild. The authors highlight effective ex-situ conservation programs, whose value increase when genetic diversity is managed. This could guide restoration projects through collaborative research between botanical gardens. More than half (1,380 of 2,566 known species) of the world's palm species are grown in botanical gardens. Promoting palm conservation involves collection, cultivation, communication, and collaboration.

Author contributions

GA proposed the Research Topic. All authors looked for contributors and editors and served as editors and reviewers.

Acknowledgments

We thank all the contributors to this special issue as well as the researchers who served as editors and reviewers for their valuable input. We thank the editorial department of Frontiers in Forest and Global Change for their patience and guidance throughout the process.

Conflict of interest

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

Publisher's note

References

Baker, W. J., and Dransfield, J. (2016). Beyond Genera Palmarum: progress and prospects in palm systematics. *Bot. J. Linn. Soc.* 182, 207–233. doi: 10.1111/boj.12401

Bello, C., Galetti, M., Pizo, M. A., Magnago, L. F. S., Rocha, M. F., Lima, R. A., et al. (2015). Defaunation affects carbon storage in tropical forests. *Sci. Adv.* 1, e1501105. doi: 10.1126/sciadv.1501105

Boukili, V. K., and Chazdon, R. L. (2017). Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. *Perspect. Plant Ecol. Evol. Syst.* 24, 37–47. doi: 10.1016/j.ppees.2016.11.003

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M., Delitti, W., et al. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Change Biol.* 20, 3177–3190. doi: 10.1111/gcb.12629

DeWalt, S. J., and Chave, J. (2004). Structure and biomass of four lowland Neotropical forests. *Biotropica* 36, 7–19. doi: 10.1111/j.1744-7429.2004.tb00291.x

Goodman, R., Phillips, O. L., Torres, D., Freitas, L., Tapia-Cortese, S., Monteagudo, A., et al. (2013). Amazon palm biomass and allometry. *Forest Ecol. Manage.* 310, 994–1004. doi: 10.1016/j.foreco.2013.09.045

Muscarella, R., Emilio, T., Phillips, O. L., Lewis, S. L., Slik, F., Baker, W. J., et al. (2020). The global abundance of tree palms. *Glob. Ecol. Biogeogr.* 29, 1495–1514. doi: 10.1111/geb.13123

Onstein, R. E., Baker, W. J., Couvreur, T. L., Faurby, S., Svenning, J. C., and Kissling, W. D. (2017). Frugivory-related traits promote speciation of tropical palms. *Nat. Ecol. Evol.* 1, 1903–1911. doi: 10.1038/s41559-017-0348-7

Sylvester, O., Avalos, G., and Chávez-Fernández, N. (2012). Notes on the ethnobotany of Costa Rica's palms. *Palms.* 56, 190–201.

ter Steege, H., Pitman, N. C. A., Sabatier, D., Baraloto, C., Salomão, R. P., Guevara, J. E., et al. (2013). Hyperdominance in the Amazonian tree flora. *Science* 342, 325–342. doi: 10.1126/science.1243092

Tomlinson, P. B. (2006). The uniqueness of palms. *Bot. J. Linn Soc.* 151, 5–14. doi: 10.1111/j.1095-8339.2006.00520.x

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 23 July 2021
doi: 10.3389/fevo.2021.687188

Genetic Diversity and Population Structure of *Medemia argun* (Mart.) Wurttenb. ex H.Wendl. Based on Genome-Wide Markers

Sakina Elshibli* and Helena Korpelainen

Department of Agricultural Sciences, Viikki Plant Science Centre, University of Helsinki, Helsinki, Finland

Medemia argun is a wild, dioecious palm, adapted to the harsh arid environment of the Nubian Desert in Sudan and southern Egypt. There is a concern about its conservation status, since little is known about its distribution, abundance, and genetic variation. *M. argun* grows on the floodplains of seasonal rivers (wadis). The continuing loss of suitable habitats in the Nubian Desert is threatening the survival of this species. We analyzed the genetic diversity, population genetic structure, and occurrence of *M. argun* populations to foster the development of conservation strategies for *M. argun*. Genotyping-by-sequencing (GBS) analyses were performed using a whole-genome profiling service. We found an overall low genetic diversity and moderate genetic structuring based on 40 single-nucleotide polymorphisms (SNPs) and 9,866 SilicoDArT markers. The expected heterozygosity of the total population (H_T) equaled 0.036 and 0.127, and genetic differentiation among populations/groups (F_{ST}) was 0.052 and 0.092, based on SNP and SilicoDArT markers, respectively. Bayesian clustering analyses defined five genetic clusters that did not display any ancestral gene flow among each other. Based on SilicoDArT markers, the results of the analysis of molecular variance (AMOVA) confirmed the previously observed genetic differentiation among generation groups (23%; $p < 0.01$). Pairwise F_{ST} values indicated a genetic gap between old and young individuals. The observed low genetic diversity and its loss among generation groups, even under the detected high gene flow, show genetically vulnerable *M. argun* populations in the Nubian Desert in Sudan. To enrich and maintain genetic variability in these populations, conservation plans are required, including collection of seed material from genetically diverse populations and development of *ex situ* gene banks.

Keywords: *Medemia argun*, genetic diversity, Sudan, Nubian Desert, SNP markers, SilicoDArT markers, conservation

OPEN ACCESS

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

Reviewed by:
Mohamed Abdelaal,
Mansoura University, Egypt
Rakesh Bhutiani,
Gurukul Kangri Vishwavidyalaya, India

***Correspondence:**
Sakina Elshibli
sakina.elshibli@helsinki.fi

Specialty section:
This article was submitted to
Biogeography and Macroecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: 29 March 2021
Accepted: 21 June 2021
Published: 23 July 2021

Citation:
Elshibli S and Korpelainen H
(2021) Genetic Diversity and
Population Structure of Medemia
argun (Mart.) Wurttenb. ex H.Wendl.
Based on Genome-Wide Markers.
Front. Ecol. Evol. 9:687188.
doi: 10.3389/fevo.2021.687188

INTRODUCTION

The open-habitat palm (*Medemia argun*) is a dioecious species native to Sudan (Broun and Massey, 1929; Andrews, 1956) and adapted to harsh arid environments. Currently, its distribution is limited to the Nubian Desert of Sudan (**Figure 1A**), where the palm grows on the floodplains of seasonal rivers (wadis), including southern Egyptian oases (Ibrahim and Baker, 2009;

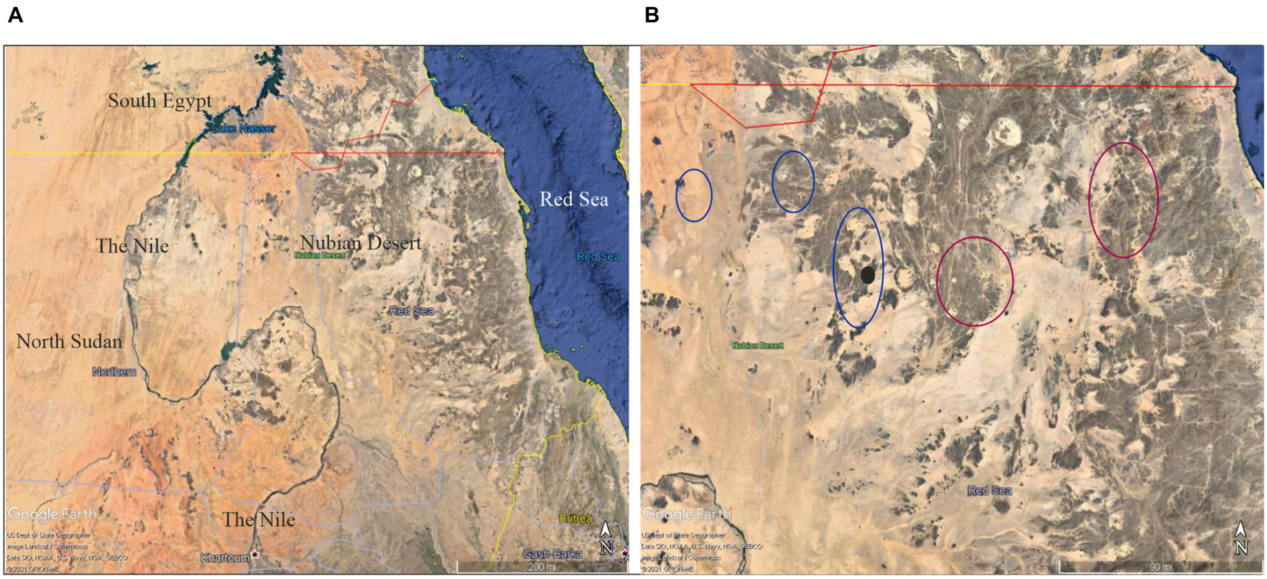


FIGURE 1 | (A) Google Earth view (15°00′–24°00′N, 38°00′–39°00′E) of the geographic location of the Nubian Desert in Sudan. **(B)** Sketched distribution of *M. argun* in the Nubian Desert in Sudan: blue circles indicate the main locations reviewed and updated by Cosiaux et al. (2020) using Google Maps; purple circles indicate previously unreported locations described by local travelers; the black circle indicates the location of the population sampled in this study.

Elshibli and Korpelainen, 2018). Little is known on the distribution, abundance, and genetic variation of *M. argun*, which has previously been listed by the International Union for Conservation of Nature's (IUCN) Red List as a critically endangered (IUCN, 1998), and very recently as a vulnerable species. The latter assessment was proposed by Cosiaux et al. (2020) based on the number of individuals deduced from satellite imagery (Google Earth and Bing Maps; **Figure 1B**). Based on these satellite images, Cosiaux et al. (2020) counted all visible individuals and estimated that the total number of *M. argun* palms in Sudan is 7,370 compared to the previous estimate of about 1,000 (Gibbons and Spanner, 1999). The occurrence of 31 scattered *M. argun* individuals in southern Egypt (Ibrahim and Baker, 2009) represents a marginal population. In Sudan, *M. argun* has been reported to exist only in the Nubian Desert (Ali and Idris, 2016).

The Nubian Desert is located in the eastern region of the Sahara Desert, covering an area of about 400,000 km^2 in northeastern Sudan and northern Eritrea between the Nile and the Red Sea (**Figure 1A**). Here, the average annual rainfall is around 75 mm, which indicates extreme and threatening drought conditions for plant and animal life (Florenzano et al., 2016). This region is arid and has rocky mountains and sand dunes, and hundreds of valleys with annual rivers (wadis) that dry up before reaching the Nile. Hence, the Nubian Desert is a remote and rugged area.

The Nubian Desert is the main habitat of *M. argun*. However, until the 1990s, *M. argun* palms were rarely seen and even considered to be extinct (Gibbons and Spanner, 1996). Gold mining has been done in northern Sudan since the times of the Kingdoms of Kush and Meroe in Nubia (∼700 BC; Klemm and Klemm, 2013), but present-day gold mining has increased by both companies and locals (Salih, 1999; Maliński, 2017), with negative effects on *M. argun* populations. In addition, the Nubian Desert is facing increasing aridity due to climate change (Blach-Overgaard et al., 2015). All these factors pose further threats to the extant range of *M. argun* and may possibly lead to increasingly fragmented habitats and populations. Concrete knowledge of the genetic resources, genetic differentiation, and population dynamics of *M. argun* is a prerequisite for reliable conservation planning and protection measures. This information can be obtained through assessing genetic diversity and population genetic structure to define the impacts of habitat fragmentation and loss on population fragmentation, fitness and adaptability, as well as to plan sound conservation and management strategies (Ellstrand and Elam, 1993; Frankham et al., 2002).

To our knowledge, the only DNA-based population genetic study conducted on *M. argun* (Elshibli and Korpelainen, 2018) involved the development and use of chloroplast microsatellite markers (cpSSR). Although a limited number of cpSSR markers were used, the results showed the incidence of genetic erosion among *M. argun* generations but raised questions about the level of genetic diversity, differentiation, and gene flow based on information of the nuclear genome. Elshibli and Korpelainen (2018) suggested analyzing seed dispersal within the network of temporal flood waters, since this factor affects the survival and genetic structure of *M. argun* in Sudan. Mountain ranges shaping the valleys and watercourses in the Nubian Desert may be the only natural barriers of gene flow. Accordingly, our hypothesis is that the isolated, fragmented populations are genetically distinct with unique alleles.

In angiosperms, chloroplast genomes are maternally inherited and, hence, chloroplast DNA markers are effective tools to estimate the contribution of seeds or pollen to gene flow, influencing the population genetic structure of subsequent generations (Ennos, 1994; Petit et al., 2005; Nistelberger et al., 2015). In addition, different types of DNA markers showing different rates of evolutionary changes and modes of genomic inheritance (i.e., uniparental and biparental) have been used to reveal historical relationships and the evolution of plant species (Jansen et al., 2007). Genotyping-by-sequencing analyses (GBS) are a widely applied approach, facilitating the discovery of a large set of genome-wide markers [single-nucleotide polymorphisms (SNPs) and SilicoDArT markers]; they have been increasingly adapted to a wide range of applications in plant genetics and genomics (Andrews et al., 2016; Korinsak et al., 2019; Hall et al., 2020; Nadeem et al., 2021**).**

The first objective of this study was to investigate the level of genetic diversity and population genetic structure of *M. argun* in the Nubian Desert of Sudan based on the nuclear genome using SNP and SilicoDArT markers. Our second aim was to compare the amount and pattern of genetic variability between SNP and SilicoDArT markers, and the previously used cpSSR markers (Elshibli and Korpelainen, 2018), for the same plant material. The third objective was to estimate the contribution of seeds and pollen to gene flow in the studied populations.

MATERIALS AND METHODS

Plant Material and Collection Sites

In November 2014, we conducted a field expedition looking for *M. argun* palms to sample them within the area described by Gibbons and Spanner (1996), although there was no previous data on the exact locations. Due to the harsh nature of the Nubian Desert, and to avoid getting lost, we hired two guides, who were local trade travelers aware of continuous, dense *M. argun* populations. Within a 2-day drive, we reached two sites of *M. argun* palms scattered along a diverging valley, part of the Wadi Gabgaba tributary system. The distance to reach the two sites was 7 km, while based on coordinates, the distance from site 1 (20°48′6.7″N, 34°25′29″E) to site 2 (20°49′2.3″N, 34°23′28″E) equaled 3.65 km. **Figure 2** shows Google Earth-based views of the two collection sites and the distribution pattern of *M. argun* individuals. The two sites were characterized by a very dry environment, creeping sand dunes, and few shrubs, as well as abundance of bitter cucumber (*Citrullus colocynthis*). The two sites were separated by a series of mountains. Leaf samples were collected from 51 *M. argun* individuals from the two sites and visually categorized into three age classes (young, middle-age, and old palms). Age class categories were considered as representing different generations. The three age classes were distinct groups among all sampled *M. argun* palms: the trunk height of all old palms was above 5 m, middle-age palms between 3 and 4 m, and young palms < 1 m (**Figure 3**). **Supplementary Table 1** shows the list of 51 samples, each with an identity code, assigned to site 1 or 2 and to the age category young, middle-age, and old. The collected samples included 19 young, 26 middle-age, and six old trees. Site 1 samples included 19 individuals with all three age class categories, and site 2 samples included 32 individuals representing young and middle-age class categories.

DNA Preparation

The DNA utilized in this study corresponds to the same sampled material used in Elshibli and Korpelainen (2018). Total genomic DNA was extracted from dry leaves using the E.Z.N.A.^{TM} SP Plant Mini Kit (Omega Bio-Tek, Norcross, GA, United States) following the manufacturer's instructions. The DNA quality was checked using a NanoDrop Spectrophotometer (Thermo Fisher Scientific^{TM}, Waltham, MA, United States) and further confirmed on 0.8% agarose gels. DNA samples were adjusted to a concentration of 50 ng/μl; 20 μl of each DNA sample was placed into a fully skirted 96-well PCR plate, packed, and shipped for genotyping.

Genotyping at the DArTseq Platform and Data Filtering

GBS were conducted using a whole-genome profiling service provided by Diversity Arrays Technology Pty Ltd. (Canberra, ACT, Australia). Diversity Arrays Technology (DArT) is one of the methodological concepts that generate multi-locus genome-wide markers and has a wide range of applications, including marker discovery, genotyping, and genetic diversity characterization (Jaccoud et al., 2001; Kilian et al., 2012). The DArTseq technology combines the DArT complexity reduction method and next-generation sequencing approaches (Sansaloni et al., 2011; Kilian et al., 2012). Complexity reduction was applied to select a defined fraction of genomic fragments in *M. argun* samples, named "representations," which were then pooled to create a "gene pool representation" and used for cloning and library construction.

Several enzyme combinations were tested for complexity reduction and the discovery of genomic fragments. DNA samples were exposed to digestion–ligation reactions using restriction enzymes, namely, Pstl in combination with Sphl, with the addition of barcoded adaptors corresponding to the overhangs of the two restriction enzymes. Two microliters of the digestion/ligation reaction were amplified with primers required for Illumina DNA sequencing. The *Pst*I–*Sph*I mixed fragments were amplified using the following PCR program: denaturation at 94°C for 1 min followed by 30 cycles of denaturation at 94°C for 20 s, annealing at 58°C for 30 s, elongation at 72°C for 45 s, and a final extension at 72°C for 7 min.

Amplicons from each sample of the 96-well plate were pooled and exposed to c-Bot (Illumina) bridge PCR and then sequenced using Illumina HiSeq 2500 for 77 cycles. The in-house marker-calling algorithm DArTsoft14 was used to extract two types of markers, SilicoDArT and SNP, as well as metadata for final marker selection and statistical analyses. Two samples (OS1-2 and MS1-7; **Supplementary Table 1**) failed due to a poor DNA quality.

Initially, we obtained 348 SNPs and 28,184 binary SilicoDArT markers. The qualities of both types of markers were determined by a set of parameters, including reproducibility and call rate percentages, while other parameters were based on the type

FIGURE 2 | Google Earth views of the collection site 1 (20°48′6.7″N, 34°25′29″E) and site 2 (20°49′2.3″N, 34°23′28″E) showing mountain ranges and the pattern of the distribution of *M. argun* individuals. The black small dots are *M. argun* palms.

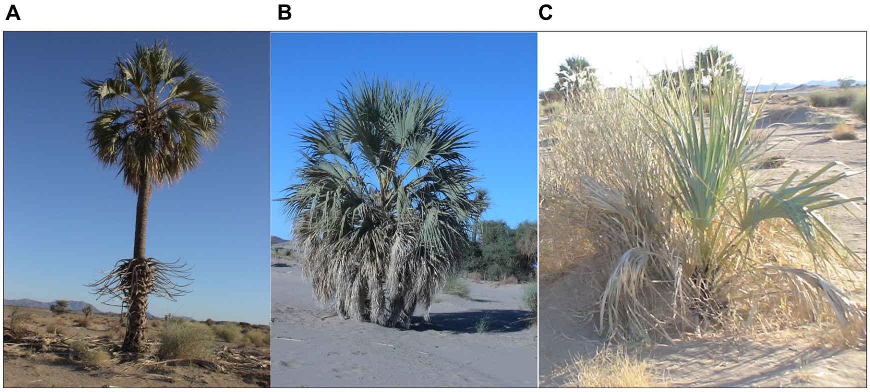


FIGURE 3 | Examples of the age classes: **(A)** old, **(B)** middle-age, and **(C)** young.

of marker. SNP markers were first filtered for all secondary and monomorphic loci. In addition, SNP data were filtered for call rate at the threshold of 0.95; the threshold of reproducibility was set at 0.99. All SNP loci were checked for significant (alpha = 0.001) departures from the Hardy–Weinberg equilibrium (HWE; Bonferroni corrected), but all of them were found to follow HWE. SilicoDArT markers were filtered for monomorphic loci, and call rate was set at the threshold of 0.95, while the minimum value of reproducibility was 0.99. Filtered data were used for subsequent diversity and genetic structuring analyses. Data filtering was performed using the R 4.0.2 (R Core Team, 2020) package DARTR (Gruber et al., 2018).

Data Analyses

Genetic Diversity

Data filtering retained 40 SNP and 9,866 SilicoDArT markers for 49 *M. argun* individuals. Frequency distributions of polymorphism information content (PIC) values were computed for both marker types. For the whole set of *M. argun* samples and for both SNP and silicoDArT data, various genetic diversity indices were computed using the package DARTR. Diversity indices included the average expected heterozygosity of the subpopulations/groups (H_S), the expected heterozygosity of the total population (H_T), the corrected H_T (H_{TP}), and the total genetic diversity among populations D_{ST} and corrected D_{ST} (D_{STP}). In addition, the fixation index (F_{ST}) and corrected F_{ST} (F_{STP}) as well as the inbreeding coefficient (F_{IS}) were computed (Nei, 1987).

Relatedness and Population Structure

Principal coordinate analyses (PCoA) were applied to investigate genetic relationships among individuals from different sites and generation groups using the package DARTR. For both SNP and SilicoDArT markers, Euclidean distance matrices were generated based on allele frequencies, and the corresponding unrooted neighbor-joining trees were constructed using the package DARTR. Based on Euclidean distance matrices, we tested the relationship between SilicoDArT and SNP markers, as determined by a Mantel test (Mantel, 1967) using 999 permutations.

Analyses of molecular variance (AMOVA; Excoffier et al., 1992) were conducted to determine, in a hierarchical manner, the contributions of among- and within-group variation to the total genetic variation of *M. argun* samples using GenAlEx 6.5 (Peakall and Smouse, 2012). The significance of the variance components was evaluated using 999 permutations.

Pair-wise genetic differentiation among groups of different generations and sites was estimated as pairwise F_{ST} values following Weir and Cockerham (1984) and using the package DARTR. In addition, the amount of gene flow (Nm) between gene pools was calculated based on F_{ST} estimates, $Nm = [(1/F_{ST}) - 1]/4$.

To find the best-fitting grouping of *M. argun* individuals, we used Bayesian methods implemented by the software BAPS 6.0 (Tang et al., 2009; Corander et al., 2013). Admixture analysis based on mixture clustering of individuals was chosen to estimate the K value that best explains the distribution of individual samples into different genetic clusters. The upper bound to the number of clusters was set to 20, and the input number of iterations was 50. A UPGMA tree (unweighted pair group method with arithmetic mean) was constructed based on the Kullback–Leibler divergence matrix as an output of mixture clustering of individuals. Based on the admixture results, we used the plot gene flow function of the BAPS software to estimate and plot the network of clusters.

Pollen and Seed Contributions to Gene Flow

We estimated the relative levels of gene flow contributions from seed and pollen migration by comparing nuclear DNA (SNP/SilicoDArT markers) differentiation detected in this study with chloroplast DNA differentiation previously analyzed by us (Elshibli and Korpelainen, 2018) for the same set of *M. argun* samples. Gene flow (Nm) based on cpSSR markers was calculated following McCauley (1995) as $Nm = (1/F_{STc} - 1)/2$, where F_{STc} is the population differentiation based on cpDNA. Gene flow (Nm) based on nuclear DNA was estimated according to Wright (1951) as $Nm = (1/F_{ST} - 1)/4$ (Ennos, 1994). The ratio of pollen to seed flow was calculated according to Ennos (1994), but see Freeland et al. (2012), with the following equation assuming that the chloroplast inheritance is strictly maternal:

$$\text{Pollen flow/seed flow} = [(1/F_{ST(b)} - 1) - 2(1/F_{ST(m)} - 1)]/(1/F_{ST(m)} - 1)$$

$F_{ST(b)}$ is the population differentiation calculated for biparentally inherited loci, i.e., SNP and SilicoDArT markers in this study. $F_{ST(m)}$ is the population differentiation calculated for maternally inherited cpDNA loci, i.e., cpSSR markers based on Elshibli and Korpelainen (2018).

Estimates of F_{ST} for cpDNA (cpSSR) were replaced by PhiPT values estimated for each group of generations and collection sites and were calculated using GenAlEx version 6.503 (Peakall and Smouse, 2006, 2012) for haploid microsatellites (see Elshibli and Korpelainen, 2018). For nuclear DNA, SNP, and SilicoDArT markers, we also used PhiPT values calculated with GenAlEx 6.5 (Peakall and Smouse, 2012) to make the comparisons between different markers more feasible. PhiPT values have been used to calculate gene flow (Nm) by GenAlEx 6.5 (Peakall and Smouse, 2012) as $Nm = [(1/PhiPT - 1]/4$.

RESULTS

A total of 40 SNP and 9,866 SilicoDArT markers obtained for 49 individuals were used to examine the amount and pattern of genetic variation in *M. argun*, representing two collection sites and three generation groups. The mean value of polymorphic information contents (PIC) was lower for SNP markers than for SilicoDArT markers and equaled 0.05 for SNPs and 0.15 for SilicoDArT markers. For SNP markers, values of 0.05 were most frequent, while values of 0.1 and 0.15 were least frequent; for SilicoDArT markers, values of less than 0.05 and of 0.15 were most frequent, while values of 0.4–0.5 were least frequent (**Figure 4**).

Genetic Diversity

The SNP markers showed a lower total genetic diversity, and a lower genetic diversity and genetic differentiation among groups compared to SilicoDArt markers. The H_T, D_{ST}, and F_{ST} values were 0.036 (H_{TP} = 0.037), 0.002 (D_{STP} = 0.003), and 0.052

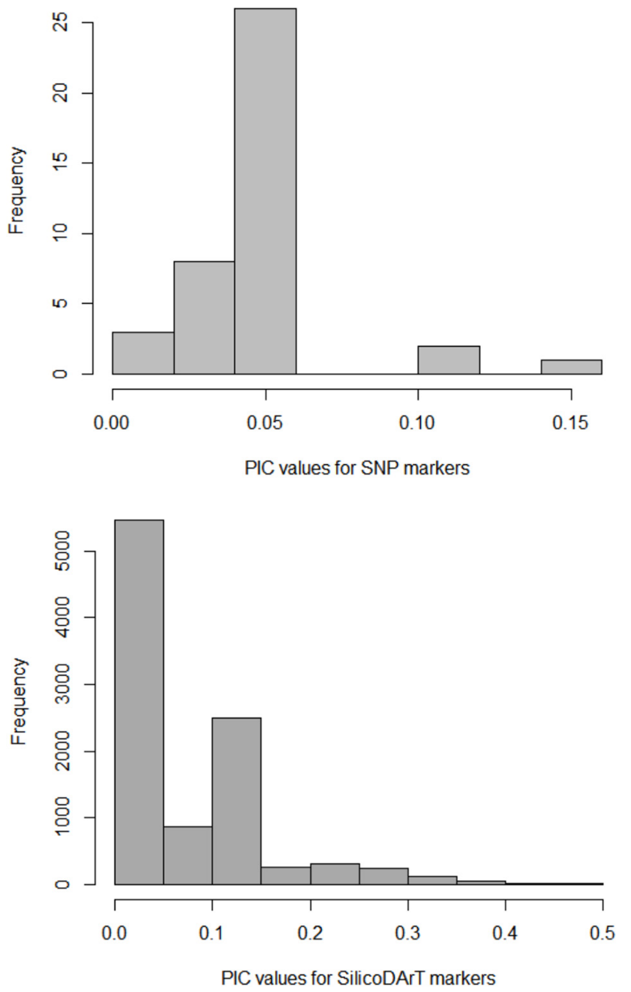


FIGURE 4 | Frequency distribution of polymorphic information contents (PIC) values for SNP and SilicoDArT markers.

(F_{STP} = 0.076) for SNPs, respectively, and 0.127 (H_{TP} = 0.133), 0.012 (D_{STP} = 0.018), and 0.092 (F_{STP} = 0.133) for SilicoDArt markers, respectively. The average expected heterozygosity of the subpopulations/groups (Hs) was 0.034 for SNP data and 0.115 for SilicoDArT markers. The mean observed heterozygosity (H_O) was 0.035 for SNP markers and 0.176 for SilicoDArT markers.

Relatedness and Population Structure

The PCoA conducted for the *M. argun* population showed that the total amount of genetic variation explained by the first three principal coordinates was 49.8% (22.3, 15.5, and 12% for each coordinate, respectively) for SNP markers and 72% (37.3, 20.5, and 14.2%, respectively) for SilicoDArT markers. Based on SNP markers, there was no specific distribution pattern among *M. argun* individuals in relation to generation groups (**Figure 5A1**) or collection sites (**Figure 5A2**). However, based on SilicoDArT markers, there was notable substructuring of individuals among generation groups (**Figure 5B1**) and slight substructuring among collection sites (**Figure 5B2**).

Based on SilicoDArT markers (**Figure 5B1**), the old individuals (numbers 3–6) appeared to be distributed distantly along PCo1, while young individuals were grouped at the intersection of PCo1 and 3. The middle-age individuals were distributed along PCo3 showing some substructuring pattern. Yet, there is some degree of overlapping among individuals representing different generation groups. Overlapping individuals include mostly young ones, but also the old individual number 6 and a subgroup of middle-age palms located on the upper side near the intersection of PCo1 and 3.

The cluster displayed by the neighbor-joining (NJ) cluster analysis (**Figure 6**) confirmed the patterns displayed by PCoA for both types of markers. No specific pattern was observed for SNP markers (**Figure 6A**). The clearer clustering based on SilicoDArT markers grouped *M. argun* genotypes into five clusters (**Figure 6B**). Cluster 1 (at the bottom) included two middle-age palms collected from site 2, while Cluster 2 included a group of middle-age palms collected from site 2 and one old palm from site 1. All genotypes within Cluster 3 are middle-age palms from site 1, Cluster 4 included four old palms from

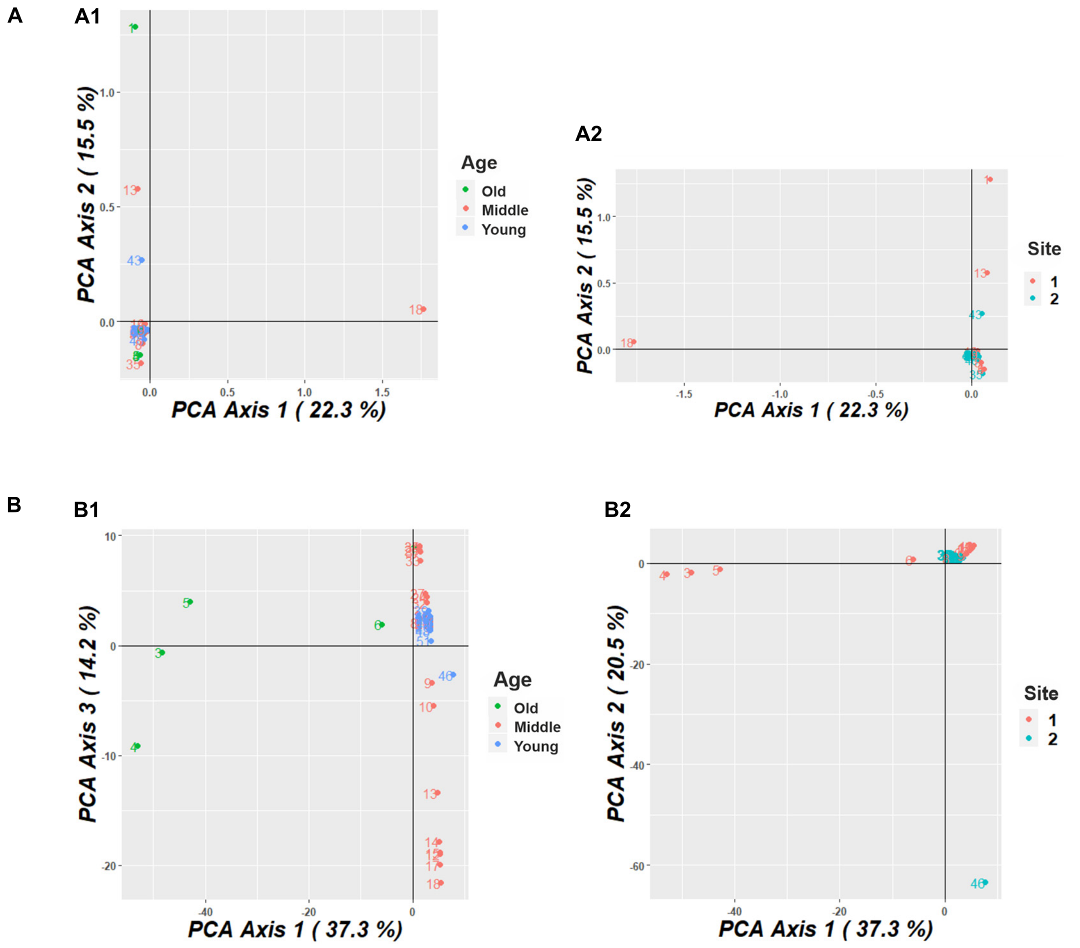


FIGURE 5 | (A) Principal coordinate analysis (PCoA) plot, based on SNP markers, showing the distribution of *M. argun* samples from **(A1)** three generations (old, middle-age, and young) and **(A2)** two collection sites in Sudan. **(B)** Principal coordinate analysis (PCoA) plot, based on SilicoDArT markers, showing the distribution of *M. argun* samples from **(B1)** three generations and **(B2)** two collection sites.

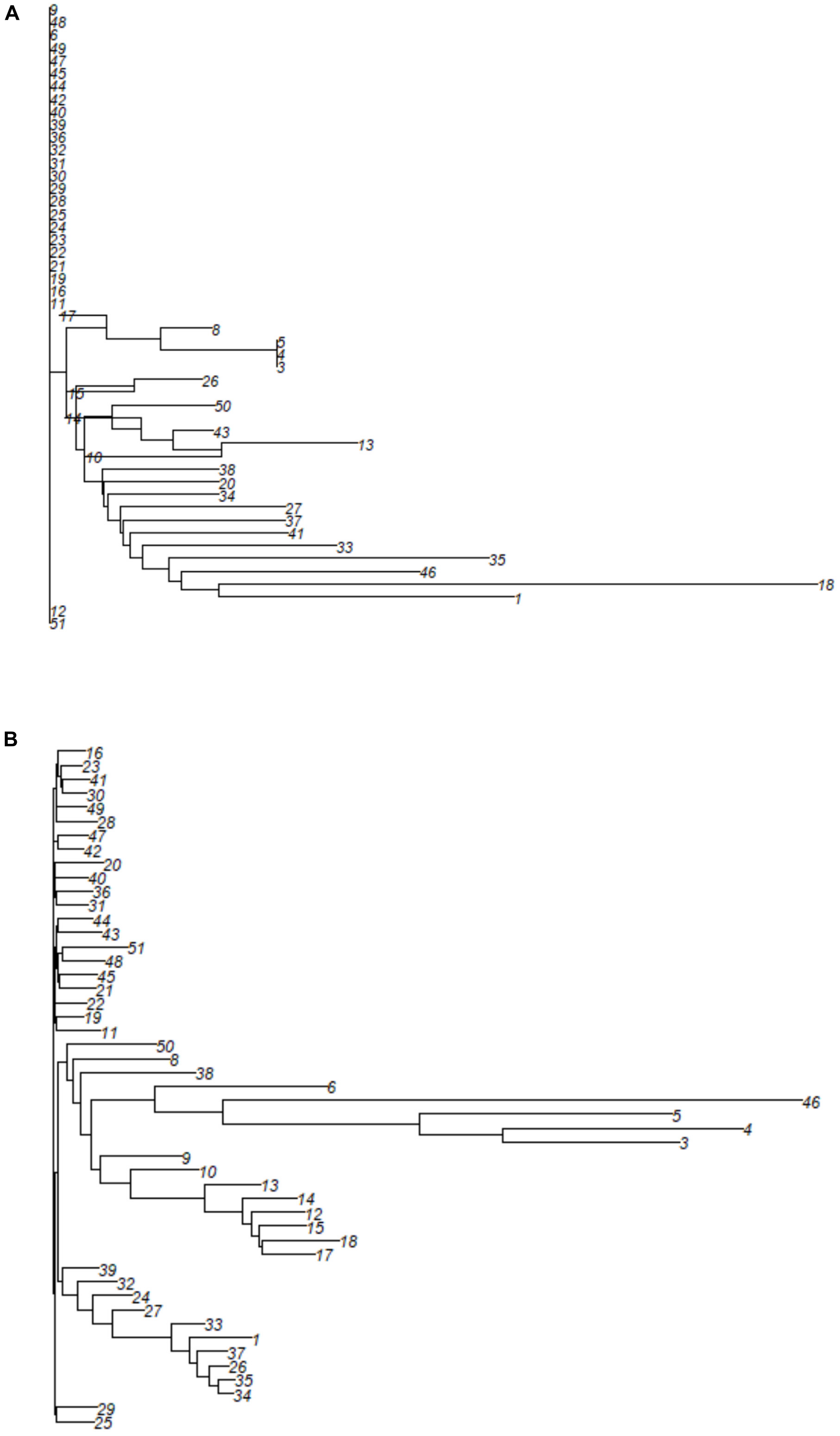


FIGURE 6 | A neighbor-joining cluster analysis based on **(A)** SNP and **(B)** SilicoDArT markers to group 49 *M. argun* individuals. For information on collection sites and generation categories, see the corresponding individual numbers in **Supplementary Table 1**.

site 1 and one young individual from site 2, and Cluster 5 is a mixture of middle-age palms from sites 1 and 2 and most young palms from site 2. All individuals in Cluster 5 (at the top) show no definite grouping. A positive correlation was found ($r = 0.396$, $p < 0.01$) between SNP- and SilicoDArT-based Euclidean distance matrices, as determined by the Mantel test.

TABLE 1 | Analyses of molecular variance (AMOVA) conducted for 49 *Medemia argun* samples based on SNP and SilicoDArT markers, including three age classes (generations) and two collection sites.

Source of variation	df	SS	Variance	Amount of variation	Stat		*p* value	*p* alpha
SNP markers								
Among generations	2	11.064	0.033	1%				
Within generations	46	232.855	5.062	99%	PhiPT	0.007	0.279	$p > 0.05$
Among sites	1	6.485	0.065	1%				
Within sites	47	237.434	5.052	99%	PhiPT	0.013	0.141	$p > 0.05$
SilicoDArT markers								
Among generations	2	9.160	0.262	23%				
Within generations	46	39.575	0.860	77%	PhiPT	0.234	0.008	$p < 0.01$
Among sites	1	259.150	0.000	0%				
Within sites	47	21,774.156	463.280	100%	PhiPT	0.020	0.854	$p > 0.05$

Based on SNP markers, most variation was within generations and sites, while variation among generations and sites was not significant (1%; $p > 0.05$, **Table 1**). Based on SilicoDArT markers, genetic variation among generations was 23% (PhiPT, $p < 0.01$), while 100% of variation was present within collection sites (PhiPT, $p > 0.05$, **Table 1**).

Based on SNP markers, the pairwise F_{ST} values equaled 0.109 ($p < 0.05$) between old and middle-age palms, and 0.177 ($p < 0.01$) between old and young palms with gene flow (Nm) equaling 2.044 and 1.162, respectively, while no differentiation was found between young and middle-age palms (**Table 2**). The pairwise F_{ST} value between the two collection sites was 0.025 ($p < 0.01$), and Nm was 9.75 (**Table 2**). The pairwise differentiation (F_{ST}) revealed by SilicoDArT markers was higher than that revealed by SNP markers, especially between old and middle-age palms (0.554; $p < 0.01$), and old and young ones (0.491; $p < 0.01$), which indicated limited gene flow. Considering generation groups, the lowest F_{ST} values were found between middle-age and young palms (**Table 2**). The pairwise F_{ST} value between the two sites was 0.121 ($p < 0.01$).

We used a Bayesian analysis to determine the number of genetic groups (K value). We found that $K = 5$ best explains the genetic structure of the *M. argun* samples (**Figure 7A**). Cluster 1 included one young individual from site 1 (YS1–40), Cluster 2 included one middle-age individual from site 1 (MS1–11), Cluster 3 included one young individual from site 2 (YS2–20), Cluster 4 included one old individual from site 1 (OS1–1), and Cluster 5 included 45 individuals belonging to different generations from both sites. Based on the admixture analysis, the revealed gene flow network (**Figure 7B**) showed that there is no ancestral intercluster gene flow between these five genetic groups. A similar clustering pattern was observed in the UPGMA tree constructed based on the divergence matrix, determined by the BAPS analysis (**Supplementary Figure 1**).

TABLE 2 | Pairwise F_{ST} values and gene flow (Nm) based on SNP and SilicoDArT markers for generations and collection sites.

	F_{ST}	Nm
SNP markers		
Old vs. middle-age	0.109 ($p < 0.05$)	2.044
Old vs. young	0.177 ($p < 0.01$)	1.162
Middle-age vs. young	0	UNDEF
Site 1 vs. Site 2	0.025 ($p < 0.01$)	9.75
SilicoDArT markers		
Old vs. middle-age	0.554 ($p < 0.01$)	0.201
Old vs. young	0.491 ($p < 0.01$)	0.259
Middle-age vs. young	0.043 ($p < 0.01$)	5.564
Site 1 vs. Site 2	0.121 ($p < 0.01$)	1.816

Pollen and Seed Contributions to Gene Flow

As discovered by Elshibli and Korpelainen (2018) based on cpSSR markers, the PhiPT value equaled 0.398 ($p < 0.001$) for generations/age classes and 0.116 ($p < 0.028$) for collection sites. We used these previous cpSSR marker results and the nuclear marker results from this study (PhiPT values; **Table 1**) to estimate the ratio of pollen and seed flow between different generations and collection sites. Based on SNP markers, the results revealed high pollen flow compared to seed flow, about 140 times for generation groups (ratio = 139.86) and about eight times for collection sites (ratio = 7.96). Based on SilicoDArT markers, pollen flow was about four times compared to seed flow for collection sites (ratio = 4.43), but seed flow was higher than pollen flow for generation groups (ratio = 0.16).

DISCUSSION

Although lower diversities were observed for SNP markers compared to SilicoDArT markers, the overall diversity shows comparable trends for both marker types, as elucidated by the moderate positive correlation revealed by the Mantel test. The genetic diversity level is explained by the PIC values (**Figure 4**), which describe the degree of polymorphism at each locus (Botstein et al., 1980). The average PIC values in this study were less than 0.25 for both marker types, which indicates a low level of polymorphism (Botstein et al., 1980) in the sampled population. Similarly, a low degree of genetic variation was previously observed in *M. argun* based on chloroplast DNA

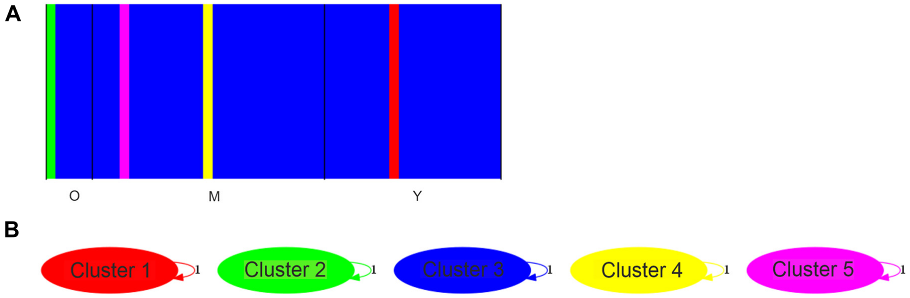


FIGURE 7 | (A) Bar plot from the Bayesian clustering analysis of individuals from three generations of *M. argun*; O assigned for old, M for middle-age, and Y for young individuals. Bar plot for a *K* = 5 model based on SNP markers. **(B)** A gene flow network identified for the five clusters (*K* = 5) as obtained by BAPS based on SNP markers. Weighted arrows indicate relative average amounts of ancestry coming from the source cluster but present now among individuals assigned to the target cluster. However, no gene flow was detected. Cluster 1 = individual YS2–40, Cluster 2 = individual MS1–11, Cluster 3 = individual YS2–20, Cluster 4 = individual OS1–1, and Cluster 5 includes other 45 individuals belonging to different generations from both sites.

markers (Elshibli and Korpelainen, 2018). On the other hand, data on tropical forest palm species indicate high expected heterozygosities (0.787 in *Euterpe edulis*, Novello et al., 2018; and 0.66 in *Euterpe precatoria*, Ramos et al., 2021). Overall, a wide range of PIC values were reported for other palm species, for example, based on SNP markers, in oil palm *Elaeis guineensis*, ranging from 0.223 to 0.375 (Ong et al., 2015), and from 0.066 to 0.375 (Pootakham et al., 2013). However, higher gene diversities were reported for other palm species; for example, the mean PIC value for the American oil palm (*Elaeis oleifera*) germplasm bank, including 553 samples from six geographic regions, collected in the Amazon rainforest in Brazil, was 0.355 (based on SNP markers, Pereira et al., 2020). Based on microsatellite markers, Ang et al. (2011) reported higher PIC values ranging from 0.491 to 0.932 (average 0.771) for the endangered and endemic palm *Johannesteijsmannia lanceolata*, sampled from the Angsi Reserve Forest in Malaysia. These high levels of diversities can be a result of biodiversity protection and management in the case of Angsi Forest Reserve and the wide coverage of diverse material collected in the case of the germplasm bank.

In this study, AMOVA showed less structuring among collection sites and generation groups than previously reported based on cpSSR markers (12 and 40%, respectively, Elshibli and Korpelainen, 2018). Different levels of genetic differentiation have been reported among natural populations of other palm species. For example, based on microsatellite markers, very low genetic differentiation was reported among natural populations of adult neotropical palms *Oenocarpus bataua* in a recently fragmented landscape and in a continuous forest in Ecuador (1.76%, Browne et al., 2015). Vardareli et al. (2019) reported lower genetic differentiation among six populations of the relict endemic *Phoenix theophrasti* in Turkey. The F_{ST} value was 0.34, and gene flow (Nm = 0.49) was very high within one generation among the six populations when compared to gene flow in *M. argun* based on SilicoDArT markers (old vs. younger individuals, **Table 2**). In *M. argun*, the gene flow (Nm) between the two sampled sites is high, while genetic differentiation based on F_{ST} values was significant among old and younger palm groups (**Table 2**), which confirmed the previously observed loss of genetic variation in *M. argun* palms among descending generations (Elshibli and Korpelainen, 2018).

For both marker types, the level of gene exchange was highest between young and middle-age palms as indicated by F_{ST} values (**Table 2**). Relatively similar genetic patterns among generations have been reported in a natural population of *Pinus sylvestris*, when comparing old (100 years) and middle-age trees (40–80 years) (F_{ST} = 0.129), and middle-age trees and seedlings (1–3 years old, F_{ST} = 0.037) (Wojnicka-Półtorak et al., 2017). The pairwise F_{ST} values between the two collection sites of both marker types were lower than found, for instance, among natural populations of endangered *Hopea hainanensis* trees (F_{ST} = 0.23) in tropical rainforest ecosystems (Wang et al., 2020).

da Silva Carvalho et al. (2015) found that variation in genetic diversity among 16 sites of seedlings in a tropical palm

FIGURE 8 | Google Earth view showing an example of *M. argun* habitat and the network of seasonal watercourses (the geographic coordinates: 20°59′34.96″N, 34° 40′00.20″E).

(*E. edulis*) in a human-modified rainforest was best explained by historical effective population sizes, while genetic differentiation is most likely influenced by recent changes caused by habitat loss and fragmentation. In agreement, Melo et al. (2018) reported that historical demography and environmental changes shaped the distribution and evolutionary success of the Amazonian palm (*Mauritia flexuosa*). These conclusions may explain the differences in the observed and reported levels of genetic differentiation and gene flow among different palm species including *M. argun*. Different trends were also observed among

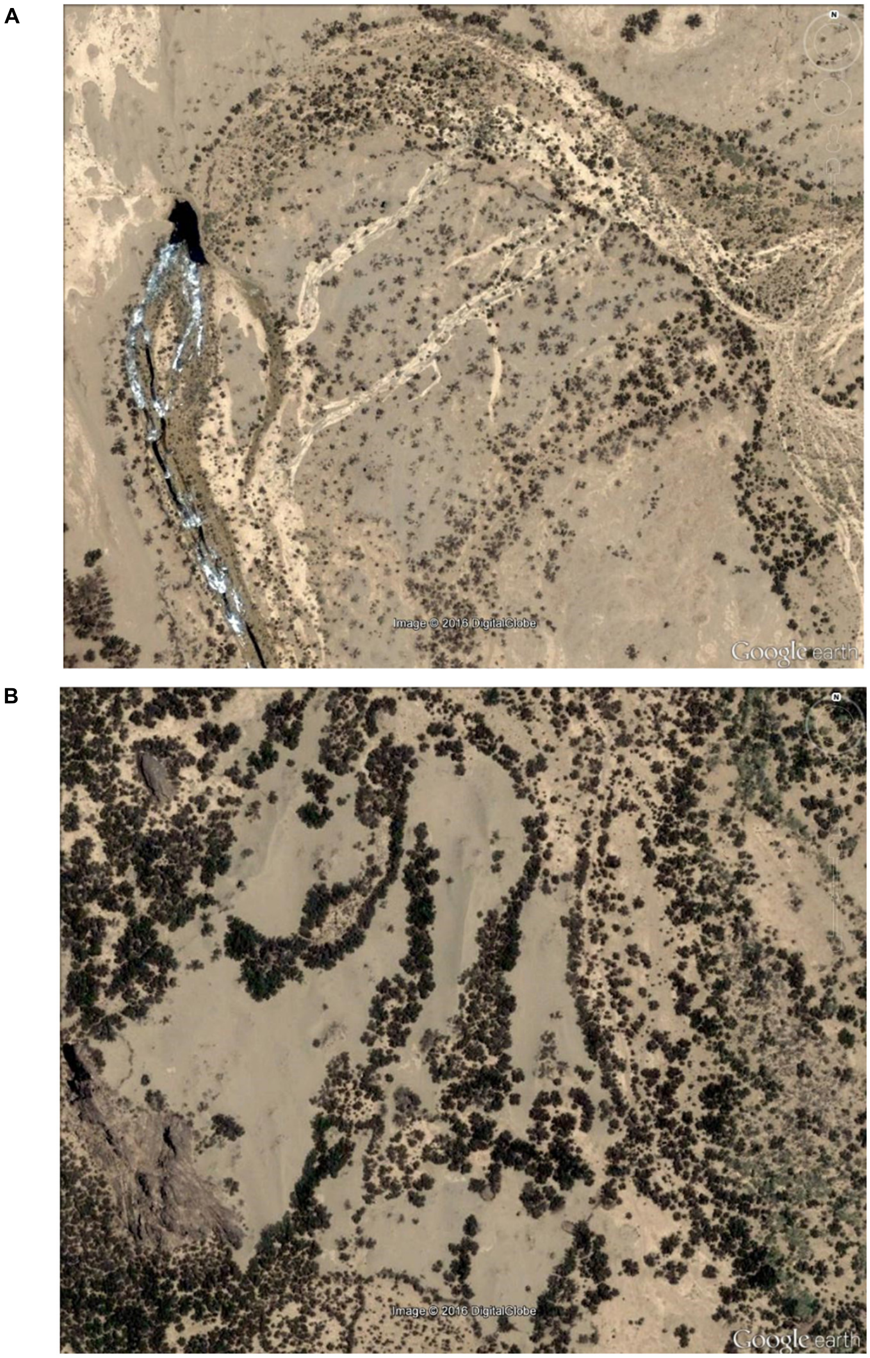


FIGURE 9 | Google Earth view of new populations of *M. argun*, as described by local trade travelers. The network of watercourses shapes their distribution. **(A)** In the image, *M. argun* palms with a flowing river in the location (the geographic coordinates: 21°28′49.66″N, 36° 05′47.65″E). **(B)** Dense populations of *M. argun*. The two different shades of color indicate the presence of tree species other than palms in the same location, as also told by travelers (the geographic coordinates: 21°30′35.43″N, 36°05′18.53″E).

natural stands of species other than palms. For example, Dadjo et al. (2020) found only 0.86% genetic differentiation among sites in *Garcinia kola* (Heckel), which is an extensively utilized tree, and Wojnicka-Półtorak et al. (2017) reported 13% genetic differentiation among age classes in natural populations of *P. sylvestris*.

The pattern of genetic structure (**Table 1**) as well as the presence of extensive gene flow (**Table 2**) between collection sites showed that these two sites do not possess as distinct subpopulations as expected. Some valleys may receive seeds from a network of small tributaries that bring different genetic materials from more distant stands of *M. argun* (for example, see **Figure 8**), which can lead to the observed coexistence of genetically distant individuals. The presence of such individuals within a population can explain the low level of genetic diversity, suggesting a founder effect in small populations due to few, new seeds being brought to new locations during rainy seasons. To gain deeper insights into the genetic processes of *M. argun*, it would be important to locate and study denser and more continuous populations of this palm species.

Based on the Sudan 1:250,000 Scale Survey Map (Maṣlaḥat Al-Misāḥah, 1909) and Google Earth map searches, we found previously unknown dense and continuous ranges of *M. argun* (**Figure 9** and **Supplementary Figures 2–4**). These populations are located in the region from East (21°00′–21°33′N, 35°50′–36°19′E; **Figure 1B**) and through the Kiau Valley, around the Abu Dueim Mountain to Khor Abu Dueim, and they expand westward to Gabgaba Valley. Some names of the surroundings are indicative of the long historical existence of *M. argun* populations in the area. In addition, we found another unreported population of *M. argun* in the northwestern part of the Sahara within Sudan (**Figure 10**). The existence of these populations is very important for the sustainability of this species and is highly relevant for future research. Field visits to some of these populations are needed to precisely locate populations, to validate the proposed distribution based on Google Earth maps, and to collect samples with a wider coverage. Locating different populations and individuals as reference sources will facilitate research using remote sensing and analyses of Satellite Image Time Series, which will offer further opportunities for detecting and understanding spatial and temporal changes in *M. argun* populations and for determining the causes of these changes, with possibility for modeling and predicting future changes. Research combining work on population genetics, ecology, population dynamics, and demography would be a holistic approach that would help to define the conservation needs of *M. argun* in the long term.

The availability of cpSSR marker results (Elshibli and Korpelainen, 2018) enabled us to compare the genetic effects of different modes of dispersal by calculating the pollen to seed gene flow ratio, assuming that the chloroplast genome is maternally inherited (Ennos, 1994). The higher rate of pollen-mediated gene flow in *M. argun* compared to seed flow was notable when there was a high gene flow and no or very little genetic differentiation. This was the case for SNP markers for generation and site groups, and for SilicoDArT markers for site groups. The higher rate of seed-mediated gene flow compared to pollen flow was apparent when there was limited gene flow and considerable genetic differentiation. This was visible for generation groups based on SilicoDArT markers. A wide range of pollen to seed flow ratios have been reported among species; for example, pollen to seed gene flow ratios of 17 and five have been observed in oak populations across Europe (Gerber et al., 2014). Pollen to seed ratios of up to 10 have been reported in sweet vernal grass, as revealed by comparing AFLP (nuclear) and cpDNA data (Freeland et al., 2012). Based on 93 compiled studies comparing maternal, paternal, and nuclear DNA markers in seed plants, the median value of pollen/seed gene flow ratio estimates was 17 (Petit et al., 2005). Comparable very high pollen/seed flow ratios, as observed in our study (140 times), have been reported, in the hermaphroditic tropical tree *Corythophora alta* (200 times; Hamilton and Miller, 2002), and in wind-pollinated, animal-dispersed tree species (an average ratio nearly 150 times; García-Verdugo et al., 2010; reviewed by Freeland et al., 2012). Although most studies have reported the predominance of gene flow by pollen (e.g., Petit et al., 2005; Garot et al., 2019; Sujii et al., 2021), seed dispersal accounts for a large part of the total gene flow in 25 species (Petit et al., 2005). Genetic differentiation caused by limited seed dispersal (Elshibli and Korpelainen, 2018) is homogenized by strong gene flow caused by pollen [see Bai et al. (2014)]. Similarly, Sujii et al. (2021) have reported that spatially limited gene flow by seeds has been compensated by high gene flow through pollen in the neotropical legume tree, *Centrolobium tomentosum*. There is no information about pollinators of *M. argun* and seed dispersal agents other than watercourses, which pinpoint future areas of research.

FIGURE 10 | Google Earth view of a proposed new population of *M. argun* in the northwestern part of the Sahara within Sudan (the geographic coordinates: 21°57′37.31″N, 25°07′13.83″E).

This study highlights the benefits of employing both nuclear and cpDNA markers to analyze pollen- and seed-mediated gene flow in *M. argun*. Based on cpDNA markers, Elshibli and Korpelainen (2018) suggested a key role of seeds and the seasonal network of watercourses in determining the spatial genetic structure of *M. argun* populations. Based on nuclear markers analyzed in this study, the clustering pattern observed in Bayesian analyses, we confirm the existence of genetically distant individuals even under the observed high pollen/seed flow ratios. Elshibli and Korpelainen (2018) have designed a set of 49 cpSSR markers, of which seven were developed and applied, and the rest can be tested and used to provide further comparative analyses on *M. argun* populations.

The observed low genetic diversity in the sampled *M. argun* populations indicates the vulnerability of these populations to cope with the expected changes in the environmental conditions of the Nubian Desert due to climate change (Blach-Overgaard et al., 2015) and increased human impact as a result of growing mining activities (e.g., Klemm and Klemm, 2013). The detected loss of genetic diversity among generation groups proposes an increasing risk of extinction in *M. argun* populations because of a low adaptive capacity, and the accumulation of deleterious alleles and the consequent loss of fitness (Hedrick and Kalinowski, 2000). For example, Ali (2016) has reported observing dead *M. argun* palms in some valleys, which could be related to reduced adaptation to drought and/or diseases.

Knowledge of genetic diversity can be used as an indicator to predict population reduction and effective population sizes. Current and future declines are important IUCN criteria when assessing the conservation status of a species (IUCN Standards and Petitions Committee, 2019). Effective assessment practices and the development of conservation programs on *M. argun* would greatly benefit from comprehensive investigations on changes in temporal and spatial genetic variability within and among populations.

Although this study was performed under challenging conditions without resources for wider field expeditions, our results confirmed the existence of genetically vulnerable *M. argun* populations. To develop an effective conservation strategy for *M. argun* in the Nubian Desert in Sudan, we recommend a plan to (1) allocate funding for field research to map the distribution and abundance of the individuals in their natural habitat; (2) develop an *ex situ* conservation strategy by collecting seed material for experimentation and development of managed *M. argun* materials that could be utilized to increase genetic variability of threatened populations; (3) develop general and public awareness about the value of *M. argun*, especially among local and international gold miners; and (4) develop legislation to protect *M. argun* populations alongside gold mining activities.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://datadryad.org/stash and https://doi.org/10.5061/dryad.x95x69pht.

AUTHOR CONTRIBUTIONS

SE performed the fieldwork, prepared the material for sequencing, and analyzed the data. HK supervised the work. SE wrote the manuscript with contributions from HK. Both authors contributed to the article and approved the submitted version.

FUNDING

The University of Helsinki provided financial support for the research.

ACKNOWLEDGMENTS

We would like to thank Amal Elshibli for technical support on map-based surveys and for participating in the fieldwork.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.687188/full#supplementary-material

REFERENCES

Ali, O., and Idris, M. (2016). The contribution of environmental impact assessment studies to the flora biodiversity in Sudan. *J. Environ. Prot.* 7, 1707–1718. doi: 10.4236/jep.2016.712138

Ali, O. M. M. (2016). The argun palm, *Medemia argun*, in the Eastern Nubian Desert of Sudan. *Palms* 60, 145–153.

Andrews, F. W. (1956). *The Flowering Plants of the Sudan*. Scotland: T Buncle & Co. Ltd.

Andrews, K. R., Good, J. M., Miller, M. R., Luikart, G., and Hohenlohe, P. A. (2016). Harnessing the power of RADseq for ecological and evolutionary genomics. *Nat. Rev. Genet.* 17:81. doi: 10.1038/nrg.2015.28

Ang, C. C., Lee, S. L., Lee, C. T., Tnah, L. H., Zakaria, R. M., and Ng, C. C. (2011). Isolation and characterization of microsatellite loci in an endangered palm, *Johannesteijsmannia lanceolata* (Arecaceae). *Am. J. Bot.* 98, e117–e119. doi: 10.3732/ajb.1000494

Bai, W. N., Wang, W. T., and Zhang, D. Y. (2014). Contrasts between the phylogeographic patterns of chloroplast and nuclear DNA highlight a role for pollen-mediated gene flow in preventing population divergence in an East Asian temperate tree. *Mol. Phylogenet. Evol.* 81, 37–48. doi: 10.1016/j.ympev.2014.08.024

Blach-Overgaard, A., Balslev, H., Dransfield, J., Normand, S., and Svenning, J. (2015). Global-change vulnerability of a key plant resource, the African palms. *Sci. Rep.* 5:12611. doi: 10.1038/srep12611

Botstein, D., White, R. L., Skolnick, M., and Davis, R. W. (1980). Construction of a genetic linkage map in man using restriction fragment length polymorphisms. *Am. J. Hum. Genet.* 32:314.

Broun, A. F., and Massey, R. E. (1929). *Flora of the Sudan. Published with the Consent of the Sudan Government. Obtainable from the Sudanese Government Office*. Wellington House: Sudanese Government Office.

Browne, L., Ottewell, K., and Karubian, J. (2015). Short-term genetic consequences of habitat loss and fragmentation for the neotropical palm *Oenocarpus bataua*. *Heredity* 115, 389–395. doi: 10.1038/hdy.2015.35

Corander, J., Marttinen, P., Sirén, J., and Tang, J. (2013). *BAPS: Bayesian Analysis of Population Structure*. Available online at: http://web.abo.fi/fak/mnf/mate/jc/software/BAPS5manual.pdf (accessed October 15, 2020).

Cosiaux, A., Ibrahim, H., and Baker, W. J. (2020). *Medemia argun. IUCN Red List Threat. Species* 2020:e.T30401A2793256.

da Silva Carvalho, C., Ribeiro, M. C., Côrtes, M. C., Galetti, M., and Collevatti, R. G. (2015). Contemporary and historic factors influence differently genetic differentiation and diversity in a tropical palm. *Heredity* 115, 216–224. doi: 10.1038/hdy.2015.30

Dadjo, C., Nyende, A. B., Yao, N., Kiplangat, N., and Assogbadjo, A. E. (2020). Genome-wide genetic diversity and population structure of *Garcinia kola* (Heckel) in Benin using DArT-Seq technology. *PLoS One* 15:e0238984. doi: 10.1371/journal.pone.0238984

Ellstrand, N. C., and Elam, D. R. (1993). Population genetic consequences of small population size: implications for plant conservation. *Annu. Rev. Ecol. Syst.* 24, 217–242. doi: 10.1146/ANNUREV.ES.24.110193.001245

Elshibli, S., and Korpelainen, H. (2018). Genetic profiling of the critically endangered palm species *Medemia argun* using newly developed chloroplast DNA markers. *Plant Ecol. Div.* 11, 185–192. doi: 10.1080/17550874.2018.1455231

Ennos, R. (1994). Estimating the relative rates of pollen and seed migration among plant populations. *Heredity* 72, 250–259. doi: 10.1038/hdy.1994.35

Excoffier, L., Smouse, P. E., and Quattro, J. M. (1992). Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics* 131, 479–491. doi: 10.1093/genetics/131.2.479

Florenzano, A., Mercuri, A. M., Altunoz, M., and Garcea, E. A. (2016). Palynological evidence of cultural and environmental connections in Sudanese nubia during the early and middle Holocene. *Quat. Int.* 412, 65–80. doi: 10.1016/j.quaint.2016.01.001

Frankham, R., Ballou, J. D., and Briscoe, D. A. (2002). *Introduction to Conservation Genetics*. Cambridge: Cambridge University Press.

Freeland, J. R., Biss, P., and Silvertown, J. (2012). Contrasting patterns of pollen and seed flow influence the spatial genetic structure of sweet vernal grass (*Anthoxanthum odoratum*) populations. *Journal of Hered.* 103, 28–35. doi: 10.1093/jhered/esr111

García-Verdugo, C., Forrest, A. D., Fay, M. F., and Vargas, P. (2010). The relevance of gene flow in metapopulation dynamics of an oceanic island endemic, *Olea europaea* subsp. *guanchica*. *Evolution* 64, 3525–3536. doi: 10.1111/j.1558-5646.2010.01091.x

Garot, E., Joët, T., Combes, M. C., and Lashermes, P. (2019). Genetic diversity and population divergences of an indigenous tree (*Coffea mauritiana*) in Reunion Island: role of climatic and geographical factors. *Heredity* 122, 833–847. doi: 10.1038/s41437-018-0168-9

Gerber, S., Chadœuf, J., Gugerli, F., Lascoux, M., Buiteveld, J., Cottrell, J., et al. (2014). High rates of gene flow by pollen and seed in oak populations across Europe. *PloS One* 9:e85130. doi: 10.1371/journal.pone.0085130

Gibbons, M., and Spanner, T. W. (1996). *Medemia argun* lives! *Principes* 40, 65–74.

Gibbons, M., and Spanner, T. W. (1999). In the valleys of the Sudan: finding Medemia. *Palm J.* 149, 33–35.

Gruber, B., Unmackm, P. J., Berry, O. F., and Georges, A. (2018). dartr: an R package to facilitate analysis of SNP data generated from reduced representation genome sequencing. *Mol. Ecol. Resour.* 18, 691–699. doi: 10.1111/1755-0998.12745

Hall, D., Zhao, W., Wennström, U., Gull, B. A., and Wang, X. R. (2020). Parentage and relatedness reconstruction in *Pinus sylvestris* using genotyping-by-sequencing. *Heredity* 124, 633–646. doi: 10.1038/s41437-020-0302-3

Hamilton, M. B., and Miller, J. R. (2002). Comparing relative rates of pollen and seed gene flow in the island model using nuclear and organelle measures of population structure. *Genetics* 162, 1897–1909. doi: 10.1093/genetics/162.4.1897

Hedrick, P. W., and Kalinowski, S. T. (2000). Inbreeding depression in conservation biology. *Annu. Rev. Ecol. Syst.* 31, 139–162.

Ibrahim, H., and Baker, W. J. (2009). *Medemia argun*–past, present and future. *Palms* 53:9.

IUCN. (1998). *Medemia argun*. Available online at: http://www.iucnredlist.org/details/30401/0 (accessed July 13, 2015).

IUCN Standards and Petitions Committee. (2019). *Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Committee*. Available online at: http://www.iucnredlist.org/documents/RedListGuidelines.pdf (accessed May 15, 2021).

Jaccoud, D., Peng, K., Feinstein, D., and Kilian, A. (2001). Diversity arrays: a solid state technology for sequence information independent genotyping. *Nucleic Acids Res.* 29:e25.

Jansen, R. K., Cai, Z., Raubeson, L. A., Daniell, H., Depamphilis, C. W., Leebens-Mack, J., et al. (2007). Analysis of 81 genes from 64 plastid genomes resolves relationships in angiosperms and identifies genome-scale evolutionary patterns. *Proc. Natl. Acad. Sci.U.S.A.* 104, 19369–19374. doi: 10.1073/pnas.0709121104

Kilian, A., Wenzl, P., Huttner, E., Carling, J., Xia, L., Blois, H., et al. (2012). "Diversity arrays technology: a generic genome profiling technology on open platforms," in *Data Production and Analysis in Population Genomics*, eds F. Pompanon and A. Bonin (Totowa, NJ: Humana Press), 67–89. doi: 10.1007/978-1-61779-870-2_5

Klemm, R., and Klemm, D. (2013). *Gold and Gold Mining in Ancient Egypt and Nubia: Geoarchaeology of the Ancient Gold Mining Sites in the Egyptian and Sudanese Eastern Deserts*. Berlin: Springer Science & Business Media.

Korinsak, S., Tangphatsornruang, S., Pootakham, W., Wanchana, S., Plabpla, A., Jantasuriyarat, C., et al. (2019). Genome-wide association mapping of virulence gene in rice blast fungus *Magnaporthe oryzae* using a genotyping by sequencing approach. *Genomics* 111, 661–668. doi: 10.1016/j.ygeno.2018.05.011

Maliński, P. (2017). *Searching for Nubian Desert Gold with a Metal Detector*. Available online at: https://scholar.google.com/scholar?hl=fi&as_sdt=0%2C5&q=Malinski%2C+P.+%282017%29.+%C2%B4+Searching+for+Nubian+Desert+Gold+with+a+Metal+Detector.+Q22+Available+online+at%3A+http%3A%2F%2Fcyfrowaetnografia.pl%2FContent%2F6217%23page%3D124+%28accessed+December+06%2C+2020%29&btnG= (accessed December 06, 2020).

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Res.* 27(2 Pt 1), 209–220.

Maṣlaḥat Al-Misāḥah, S. (1909). *Sudan 1:250,000*. Available online at: https://www.loc.gov/item/87692353/ (accessed May 13, 2021).

McCauley, D. E. (1995). The use of chloroplast DNA polymorphism in studies of gene flow in plants. *Trends Ecol. Evol.* 10, 198–202. doi: 10.1016/s0169-5347(00)89052-7

Melo, W. A., Freitas, C. G., Bacon, C. D., and Collevatti, R. G. (2018). The road to evolutionary success: insights from the demographic history of an Amazonian palm. *Heredity* 121, 183–195. doi: 10.1038/s41437-018-0074-1

Nadeem, M. A., Guizado, S. J. V., Shahid, M. Q., Nawaz, M. A., Habyarimana, E., Erciṣli, S., et al. (2021). In-depth genetic diversity and population structure of endangered Peruvian Amazon rosewood germplasm using genotyping by sequencing (GBS) technology. *Forests* 12:197. doi: 10.3390/f12020197

Nei, M. (1987). *Molecular Evolutionary Genetics*. New York, NY: Columbia University Press.

Nistelberger, H. M., Byrne, M., Coates, D., and Roberts, J. D. (2015). Genetic drift drives evolution in the bird-pollinated, terrestrial island endemic *Grevillea georgeana* (Proteaceae). *Bot. J. Linn. Soc.* 178, 155–168. doi: 10.1111/boj.12270

Novello, M., Viana, J. P. G., Alves-Pereira, A., de Aguiar Silvestre, E., Nunes, H. F., Pinheiro, J. B., et al. (2018). Genetic conservation of a threatened Neotropical palm through community-management of fruits in agroforests and second-growth forests. *For. Ecol. Manag.* 407, 200–209. doi: 10.1016/j.foreco.2017.06.059

Ong, P. W., Maizura, I., Abdullah, N. A. P., Rafii, M. Y., Ooi, L. C. L., Low, E. T. L., et al. (2015). Development of SNP markers and their application for genetic diversity analysis in the oil palm (*Elaeis guineensis*). *Genet. Mol. Res.* 14, 12205–12216. doi: 10.4238/2015.October.9.9

Peakall, R., and Smouse, P. E. (2006). GENALEX 6: genetic analysis in excel. population genetic software for teaching and research. *Mol. Ecol. Notes* 6, 288–295. doi: 10.1111/j.1471-8286.2005.01155.x

Peakall, R., and Smouse, P. E. (2012). GenAlEx 6.5: genetic analysis in excel. population genetic software for teaching and research-an update. *Bioinformatics* 28, 2537–2539. doi: 10.1093/bioinformatics/bts460

Pereira, V. M., Filho, J. A. F., Leão, A. P., Vargas, L. H. G., de Farias, M. P., Rios, S. D. A., et al. (2020). American oil palm from Brazil: genetic diversity, population structure, and core collection. *Crop Sci.* 60, 3212–3227. doi: 10.1002/csc2.20276

Petit, R. J., Duminil, J., Fineschi, S., Hampe, A., Salvini, D., and Vendramin, G. G. (2005). Invited review: comparative organization of chloroplast, mitochondrial and nuclear diversity in plant populations. *Mol. Ecol.* 14, 689–701. doi: 10.1111/j.1365-294X.2004.02410.x

Pootakham, W., Uthaipaisanwong, P., Sangsrakru, D., Yoocha, T., Tragoonrung, S., and Tangphatsornruang, S. (2013). Development and characterization of single-nucleotide polymorphism markers from 454 transcriptome sequences in oil palm (*Elaeis guineensis*). *Plant Breed.* 132, 711–717. doi: 10.1111/pbr.12095

R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ramos, S. L. F., Dequigiovanni, G., Lopes, M. T. G., de Aguiar, A. V., Lopes, R., Veasey, E. A., et al. (2021). Genetic structure in populations of *Euterpe precatoria* Mart in the Brazilian Amazon. *Front. Ecol. Evol.* 8:603448. doi: 10.3389/fevo.2020.603448

Salih, A. M. (1999). *The Manasir of Northern Sudan: Land and People. A Riverain Society and Resource Scarcity*. Köln: Rüdiger Köppe Verlag.

Sansaloni, C., Petroli, C., Jaccoud, D., Carling, J., Detering, F., Grattapaglia, D., et al. (2011). Diversity arrays technology (DArT) and next-generation sequencing combined: genome-wide, high throughput, highly informative genotyping for molecular breeding of *Eucalyptus*. *BMC Proc.* 26(Suppl 7):54. doi: 10.1186/1753-6561-5-S7-P54

Sujii, P. S., Tambarussi, E. V., Grando, C., de Aguiar Silvestre, E., Viana, J. P. G., Brancalion, P. H., et al. (2021). High gene flow through pollen partially compensates spatial limited gene flow by seeds for a Neotropical tree in forest conservation and restoration areas. *Conserv. Genet.* 22, 383–396. doi: 10.1007/s10592-021-01344-3

Tang, J., Hanage, W. P., Fraser, C., and Corander, J. (2009). Identifying currents in the gene pool for bacterial populations using an integrative approach. *PLoS Comput. Biol.* 5:e1000455. doi: 10.1371/journal.pcbi.1000455

Vardareli, N., Doğaroğlu, T., Doğaç, E., Taşkın, V., and Taşkın, B. G. (2019). Genetic characterization of tertiary relict endemic *Phoenix theophrasti* populations in Turkey and phylogenetic relations of the species with other palm species revealed by SSR markers. *Plant Syst. Evol.* 305, 415–429.

Wang, C., Ma, X., Ren, M., and Tang, L. (2020). Genetic diversity and population structure in the endangered tree *Hopea hainanensis* (Dipterocarpaceae) on Hainan Island, China. *PLoS One* 15:e0241452. doi: 10.1371/journal.pone.0241452

Weir, B. S., and Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution* 38, 1358–1370. doi: 10.1111/j.1558-5646.1984.tb05657.x

Wojnicka-Półtorak, A., Celiński, K., and Chudzińska, E. (2017). Genetic differentiation between generations of *Pinus sylvestris* natural population: a case study from the last European primeval forest. *Aust. J. For. Sci*. 134, 261–280.

Wright, S. (1951). Fisher and Ford on" the sewall Wright effect". *Am. Sci.* 39, 452–479.

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

frontiers
in Forests and Global Change

ORIGINAL RESEARCH
published: 01 September 2021
doi: 10.3389/ffgc.2021.715266

Intraspecific Variation on Palm Leaf Traits of Co-occurring Species—Does Local Hydrology Play a Role?

Thaise Emilio[1]*, Havle Pereira Jr.[2] and Flávia R. C. Costa[3]*

[1] Programa Nacional de Pós-Doutorado (PNPD), Programa de Pós-Graduação em Ecologia, State University of Campinas (UNICAMP), Campinas, Brazil, [2] Programa de Pós-Graduação em Botânica, Instituto Nacional de Pesquisas da Amazonia (INPA), Manaus, Brazil, [3] Coordenação de Pesquisas em Biodiversidade, Instituto Nacional de Pesquisas da Amazonia (INPA), Manaus, Brazil

The study of plant species and trait distributions can provide answers to many of the ecological challenges of our times, from climate change to the biodiversity crisis. Although traits are classically measured at the species level, understanding intraspecific variation is necessary to determine the type of response species will have to climate change. Here we measured and analyzed seven leaf traits (leaf area—LA, specific leaf area—SLA, leaf thickness—LT, leaf dry mass content—LDMC, venation density—VD, stomata length—SL, and stomata density—SD) across 14 locally dominant palm species (10 individuals/species) distributed along hydro-topographic gradients (1.4–37 m of terrain height above nearest drainage) of a central Amazonian forest to disentangle the role of species identity, relatedness, and local hydrology on trait variation and covariation. Our results show that trait variation is not always larger between species than within species as expected. Intraspecific variation accounted for 23–74% of trait variation depending on the trait. Most of the variation happened at species level for SL, LA, LT, and SD but not for SLA, VD, and LDMC. For a third of the traits (LDMC, SLA, and SD), we found some evidence of phylogenetic inertia. This lack of independency among traits is confirmed by the maintenance of strong correlation among some of those traits after controlling for local environmental conditions. Intraspecific variation, however, was not related to height above nearest drainage for any of the traits. Most of the trait–environment relationships were species-specific. Therefore, the change in palm trait composition detected along topography, from higher community means of SLA and LA, lower LT, LDMC, SL, and SD in the wet valleys to opposite traits in drier plateaus, is mostly due to the turnover in species composition and relative abundance variation. We conclude these palm species have well-defined hydrological niches, but their large intraspecific variation in leaf traits does not contribute to the adjustment of individuals to the local hydrological conditions in this Amazonian forest.

Keywords: Amazon forest, climate change, hydrological niche, trait covariation, phylogenetic conservatism, community weighted mean, Arecaceae

Edited by:
Nick Smith,
Texas Tech University, United States

Reviewed by:
Kelsey R. Carter,
Los Alamos National Laboratory, United States
Eric J. Ward,
United States Geological Survey (USGS), United States

***Correspondence:**
Thaise Emilio
thaise.emilio@gmail.com
Flávia R. C. Costa
flaviacosta001@gmail.com

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

Received: *26 May 2021*
Accepted: *14 July 2021*
Published: *01 September 2021*

Citation:
Emilio T, Pereira H Jr and Costa FRC (2021) Intraspecific Variation on Palm Leaf Traits of Co-occurring Species—Does Local Hydrology Play a Role? Front. For. Glob. Change 4:715266. doi: 10.3389/ffgc.2021.715266

INTRODUCTION

In recent years, there has been increased interest in documenting and understanding patterns of trait intraspecific variation, and an emphasis in the importance of individual level traits to understand several ecological processes (Messier et al., 2010; Siefert et al., 2015). This is natural, since functional traits per definition are individual-level properties (Violle et al., 2007) and the individuals are the direct units of response to any environmental pressure, even if these later combine into higher levels. If traits vary considerably among individuals and, especially, if this variation is coupled to important environmental drivers, it needs to be incorporated into analyses and models to predict the responses of populations, communities, and ecosystems to environmental change (Albert et al., 2011). It has been frequently assumed that within-species variation is smaller than among species. This is exemplified by the large number of studies based on species means (e.g., Liu et al., 2021; Kelly et al., 2021) regardless of both theoretical background (Bolnick et al., 2011; Violle et al., 2012) and empirical evidence for intraspecific variation (e.g., Albert et al., 2011; Marenco et al., 2017; Osnas et al., 2018; Dong et al., 2020), pointing out that we still know little at which scales, life-forms, taxa and across which environmental gradients intraspecific variation is relevant to ecological processes. Moreover, there is a virtual lack of information on these patterns of intra to interspecific trait variation in palms, which have been suggested to be particularly susceptible to droughts (Eiserhardt et al., 2011; Esquivel-Muelbert et al., 2019; but see Emilio et al., 2019). Thus, understanding how much palm intraspecific trait variation is linked to hydrological gradients will help determine if species have the potential to adjust to new climatic conditions or will need to migrate to follow their climatic niches.

Climate seasonality is widely recognized as a driver of palm species distribution (Blach-Overgaard et al., 2010; Eiserhardt et al., 2011) and functional trait composition (Göldel et al., 2015) in large scales, but local hydrology is also strongly associated to floristic patterns in the local scale (review in Svenning, 2001; Vormisto et al., 2004; Costa et al., 2009). Local hydrology is mostly determined by topography. In the upper parts of topographic profiles the soil surface is vertically far from the water table, and plants depend more on precipitation for water supply; in the lower portions of the profile roots may be in direct contact with the water table seasonally or year-round (Fan et al., 2017). Filtering of functional traits by these varying hydrological conditions may be the basis of species composition changes along topographic gradients, as described for trees (Cosme et al., 2017; Oliveira et al., 2019). There is so far no study of this local hydrological filtering effect on palms, regardless of the many studies pointing to their clear turnover along topographic gradients. Understanding how local hydrology affects trait selection under the same macroclimate is critical to model and forecast the effects of climate change, since the interaction of plant traits and local hydrology modulates plant performance under extreme weather conditions (Estebán et al., 2021).

Local hydrology is an important ecological force driving community assembly (Silvertown et al., 1999, 2015) and is related with palm floristic variation (Costa et al., 2009; Schietti et al., 2014). Although local hydrological gradients may drive species selection, many species are generalists (Ruokolainen and Vormisto, 2000), or at least have wide niche breadths, raising the question of how they adjust to the varying soil moisture conditions. The basic expectation would be that palms have large plasticity or genetic variation (Melo et al., 2018), leading to large intraspecific variation coupled to the local hydrological variation. This has been much less examined so far, with studies showing either large intraspecific trait variation well coupled to hydro-topographic gradients (Schmitt et al., 2020) or small contribution of intraspecific variation (Cornwell and Ackerly, 2009). Again, there are no studies of intraspecific variation on palms regardless of the evidence for genetic variation from local to broad scales. Genotypic negative frequency-dependent selection has been shown to increase genetic diversity at local scales (Browne and Karubian, 2018). At large scales, genetic variation across species ranges has been detected in widespread palms (Gomes et al., 2011; Melo et al., 2018), suggesting that widespread palms may have enough genetic variation to adjust to varying environments.

In the other hand, palms could be expected to have lower plasticity in leaf traits than trees, given their lower architectural flexibility, as compared to dicotyledonous trees (Tomlinson, 1990, 2006). An example of a very conserved trait of palms is the evergreen stem-leaf apical continuum, which may limit the options to adjust to hydrological variation, as palms are not able to shed leaves in response to drought. Phylogenetic inertia and/or strong selective pressures on certain traits could also limit the capacity of intraspecific adjustment to environmental variation. For example, the well-known discrepancy in palm species richness between moist and wet habitats is more related to palms retaining traits of the ancestral biome than to differences in diversification rates between them (Cássia-Silva et al., 2019). Those potential constraints have not prevented palms from occupying a wide range of environments, from deserts to tropical forests (Dransfield et al., 2008), suggesting an ample adaptation capacity. At the same time, morphological (LMA), chemical (N and P contents), and physiological (assimilation and respiration rates) leaf traits were shown not to be conserved along the palm phylogeny, but to converge to similar values in different lineages as an adaptation to shaded conditions of forest understories (Ma et al., 2015). Thus, it is not yet clear what is the potential of palms for intraspecific adjustments to environmental variation, given their phylogenetic constraints.

Importantly, our limited understanding of trait variation is not restricted to the palm family. Although several studies have looked at intraspecific variation (e.g., Messier et al., 2010; Fajardo and Siefert, 2018; Fyllas et al., 2020), we are still unable to generalize from those results. Intrinsic and extrinsic processes operating from ecological to evolutionary timescales make understanding trait variation a complex task. As a consequence, the variance and shifts in trait–environment relationships among different evolutionary lineages may result simply from the broad phylogenetic contexts in which most studies are done, and thus obscure the understanding of the drivers of intraspecific variation (Cavender-Bares et al., 2020). This can be particularly problematic given that adaptations to new environments normally involve a combination of traits responding together to a range of selection pressures—not single traits and pressures (Reznick and Ghalambor, 2001).

Traits are unlikely to vary independently, and the set of traits (as phenotypes) may respond collectively to genetic and environmental factors (Armbruster and Schwaegerle, 1996). Traits can also show covariation that is not driven by the current environment but by the selection of optimal adaptative responses along their evolutionary histories. For example, stomata morphology may have evolved in angiosperms as response to a trade-off to maximize gas exchange while minimizing the fraction of epidermis covered by stomata (de Boer et al., 2016) and while we can hypothesize about the adaptative value of both traits separately, it is unlikely that they were selected independently. Different lineages may also have evolved alternative traits and trait combinations to respond to the same pressures (Marks and Lechowicz, 2006); thus, understanding drivers of intraspecific variation on traits requires understanding of how traits are phylogenetically constrained within lineages and the trait combinations that might be expressed in response to environmental variation. For example, in a tropical forest, most species are more likely to occur where their traits are closely related to local community weighted mean (CWM) values (Muscarella and Uriarte, 2016), but constraints to local functional variation act more strongly on multivariate phenotypes than on univariate traits. Hence, it is necessary to account for at least some of those sources of variation if we want to increase our ability to predict plastic plant responses to climate change (Nicotra et al., 2010).

To understand which traits are likely to show variation in palms, we first analyzed the sources of variation and covariation on leaf traits of co-occurring species. Then, we related trait variation at individual and community levels to local hydrological gradients. Specifically, we asked:

(1) *How much of leaf trait variation is due to (a) intraspecific variation and (b) phylogenetic conservatism?* We expect trait variation between species to be larger than trait variation within species. Models predict that individual traits whose values have a low dependence on the values of other traits will be more related to phylogeny than the integrative traits, which are more likely to be related to the environment (Marks, 2007) and therefore, show wider intraspecific variation. Here we evaluate this prediction by testing the phylogenetic signal for seven leaf traits and its relationship with intraspecific variation. If trait variation is phylogenetically constrained, we expect to observe lower intraspecific variation among lineages where close relatives are more similar in traits than expected by chance.

(2) *What is the role of trait covariation on intraspecific variation?* Traits that are related to each other can shift together as result of genetic constraints or due to intrinsic coordination in response to environmental pressures, with impact on intraspecific variation. If correlation among traits results from genetic constraints, trait covariation will be retained after controlling for trait–environment variation. In this case, intraspecific variation is expected to be low as trait combinations should be fixed. Alternatively, traits can be ecologically coordinated while structurally (or functionally) independent (Givnish, 1987). In this case, trait covariation is not intrinsic but the result of both traits being co-selected in each environment. Here, correlations among traits will disappear after controlling for the environmental effect and intraspecific variation is expected to be high if traits show plastic responses to the environment.

(3) *How does environment (local hydrology) affect (a) intraspecific and (b) community level variation on leaf traits*? If intraspecific variation is adaptative in relation to local hydrology, we expect trait variation to relate to the local hydrological gradient after controlling for species and other environmental gradients (hereafter local conditions). Alternatively, if intraspecific variation emerges independently from hydrological gradients—for example, as a result of trait covariation (*hypothesis question 2*), this relationship will not persist after controlling for species or other environmental effects. At the community level, we expect average community traits to be related to local hydrological gradients even when trait variation within species is decoupled from local hydrology variation, if selection is operating over multivariate phenotypes (*hypothesis question 2*) and those traits are not strongly phylogenetically constrained (*hypothesis question 1*). In this case, average community weighted traits will be the result of species turnover and abundance variation instead of trait responses to hydrological gradients within species.

MATERIALS AND METHODS

Study Site

The study was conducted at the Ducke Forest Reserve, a Long-Term Ecological Research (PELD) site with an area of 10,000 ha, located 26 km north of Manaus, Brazil (2° 55′ S, 59° 59′ W). Climate is moist tropical (“Am” tropical according to Köppen–Geiger classification), with a relative humidity of 75–86%, mean annual rainfall of 2,500 mm (over the last 53 y), and 1–2 dry months with <100 mm precipitation (Costa et al., 2020). The predominant vegetation is dense lowland forest, locally known as *terra-firme* forest. Topography is undulating with a dense drainage network, resulting in plateaus that are dissected by small streams and valleys, with an average height difference of about 30–40 m between valleys and plateaus (Chauvel et al., 1987). In the valleys, the water table is around 0–2 m deep year-round (Hodnett et al., 1997), while in plateaus and hillslopes, the water table is below 30 m (Cuartas et al., 2012). Clay content is higher in the plateaus and sand content is higher in the valleys (Luizão et al., 2004). The soils are acidic and poor in phosphorus, calcium, magnesium, sodium, and potassium, and in general the aluminum content is high (Chauvel et al., 1987). We refer to the combination of all those environmental characteristics and their consequences (e.g., forest dynamics) as local conditions.

A grid of trails covering 8 × 8 km gives access to 72 permanent plots 1 km apart from each other (Magnusson et al., 2005). Plots are 250 m long, with this long axis aligned with the elevation contour to minimize variation on soil properties and hydrology. We selected 14 plots covering the hydrological gradient for the collection of data on functional characteristics (cf. **Supplementary Figure 1**). Species abundance data came from 72–250 × 4 m plots sampled by Jean Louis Guillaumet (see Costa et al., 2009) and made available in the data repository of the Brazilian Biodiversity Research Program (PPBio, please see section "Data Availability Statement").

Collection of Leaf Trait Data

We collected data on the leaf traits of 10 individuals per species, for the 14 most abundant species in the area (Costa et al., 2009; **Supplementary Table 1**). Individuals were selected along the plots to cover the full range of hydrological conditions occupied by each species (**Supplementary Figure 1**). For understory palms, we selected only adult individuals, who were recognized by the presence of reproductive structures. For the canopy species, the selection was made based on individuals 3–12 m height. Canopy height in those forests is around 25–30 m height; sampling was performed avoiding forest gaps and other light patches. Thus, all individuals (regardless been from canopy or understory species) were sampled under the same average understory light conditions. We collected from each individual showing evidence of healthy growth, i.e., growing apical meristem and at least three green intact leaves, one healthy leaf (without or with minimum visually detectable fungi, lichens, herbivory marks, or deformities), to represent the optimal state of the organ. Whenever possible, we standardized out sampling to collect the second or third leaf of the plant, which represents a fully expanded mature dark green leaf, in order to minimize the effect of leaf age on the measured traits. A summary of collected samples, including plant height, is available (**Supplementary Table 1**).

In the laboratory, we separated six leaflets (two from the base, two from the middle, and two from the apex of the leaf), three of which were used for anatomical measurements and three for morpho-anatomical measurements. The values of each anatomical and morpho-anatomical characteristics of each individual were then calculated as the average of the three leaflets representing the base, middle, and apex of the leaves. Individuals of *Bactris hirta* and *Geonoma aspidiifolia* had entire or semi-entire leaf blades, so the entire blade was weighed and scanned, and we made only one measurement of thickness and one anatomical cut per leaf of those species. On these leaflets, we measured the thickness with a micrometer (between the central rib and the margin) and the area (scanned and quantified with the ImageJ software, Rasband (1997–2008), available at: http://rsb.info.nih.gov/ij) according to the protocol of Perez-Harguindeguy et al. (2013). After these measurements, leaflets were dried at 65°C for 72 h, and weighed with an accuracy of 0.0001 g. All the leaflets of each leaf were weighed to obtain fresh weight.

We cut a square centimeter between the border and the central rib of the three other leaflets to quantify the anatomical structures. These pieces were fixed for 72 h in FAA solution (formaldehyde, glacial acetic acid, and alcohol). After this period, one of the pieces was prepared for visualization of veins (with diaphanization in 2% sodium hypochlorite) and another immersed in Franklin's solution 1:1 (glacial acetic acid and hydrogen peroxide) for dissociation of the epidermis and visualization of stomata. Subsequently, both samples were clarified in sodium hypochlorite 5%, dehydrated in an alcoholic series (25–95%), and stained with safranin (Kraus and Arduin, 1997), and the slides were mounted for measurements.

The dry matter content (LDMC, mg g^{-1}) was calculated by the ratio of the sum of the fresh weights to the sum of the dry weights of the three leaflets per individual. Specific leaf area (SLA, cm^2 g^{-1}) was calculated by the sum of the areas of the three leaflets divided by the sum of their dry weight. To estimate the total light-absorbing surface of the leaves, we measured and weighted a single leaflet and then scaled up by converting the summed weight of all leaflets to area (Renninger and Phillips, 2011).

The vein density (mm^2) was measured in three images per leaflet, with 40× magnification, using the Leaf Gui software (Price, 2012, available at: http://www.leafgui.org/). Stomata density was measured in three images per leaflet, at 20× magnification. The size of the stomata, estimated here by the length of the guard cells (μm), was also calculated from the average of three images from each leaflet, recorded at a 40× magnification. The images were analyzed using the ImageJ software.

Environmental Data

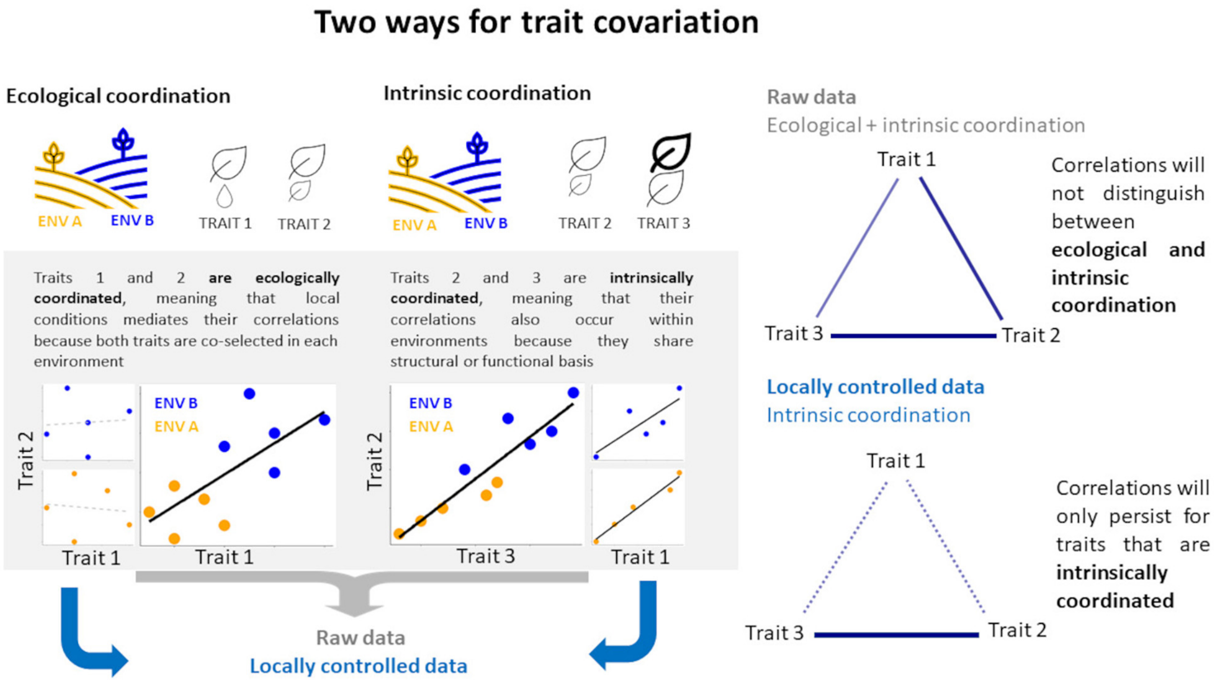
The local hydrology was represented by the vertical distance of the terrain surface to the nearest drainage (HAND, Height Above Nearest Drainage; Rennó et al., 2008) at the plot level. HAND (m) is an estimate of the soil water drainage capacity, with low values indicating terrain close to the water table, and high values are terrains with greater vertical distance to the water table. The HAND values were obtained from Schietti et al. (2014). Local hydrology, determined by changes in topography and highly associated to soil texture, is the major gradient structuring community composition in this area (Costa et al., 2009, 2015; Schietti et al., 2014).

Data Analysis

Variation Partitioning

To understand how much of the leaf trait variation is due to intraspecific variation (**Question 1a**), we performed a variance component analysis using linear mixed models (LMM), in which we partitioned trait variance between species and local conditions. To estimate the components of trait variance, we fitted an intercept-only linear mixed model, where random differences from group to group are modeled as a group dependent intercept (Snijders and Bosker, 2011) as in the equation below:

$$T = 1 + (1|s) + (1|p) + R \quad (1)$$



Traits 1 and 2 are **ecologically coordinated,** meaning that local conditions mediates their correlations because both traits are co-selected in each environment

Traits 2 and 3 are **intrinsically coordinated,** meaning that their correlations also occur within environments because they share structural or functional basis

Correlations will not distinguish between **ecological and intrinsic coordination**

Correlations will only persist for traits that are **intrinsically coordinated**

FIGURE 1 | Diagram showing two ways for trait covariation. In this hypothetical example, a single species is distributed along two local environmental conditions (ENV A = orange, ENV B = blue) and three traits are measured (Trait 1, Trait 2, and Trait 3) along the gradients in ENV A and ENV B. Correlations among traits occur for Trait 1 vs. Trait 2 and for Trait 2 vs. Trait 3 when data from both environmental conditions are pooled together (large plots, left-hand side). However, correlations may be stronger, weaker, or non-existent when the effect of environment is controlled (small plots, left-hand side). Therefore, we will only be able to discriminate between ecological and intrinsic coordination when comparing correlations based on raw data with correlations based on locally controlled data.

where each trait (T) was measured from an individual that belongs to a species(s) found in a plot (p) with specific local conditions. Here we implemented the model with plots representing the spatial variation on local conditions given by the environment, e.g., topography, soil, and hydrology (Nakagawa and Schielzeth, 2010; Harrison et al., 2018). Then, we estimate the among-species and among-plot variance in our trait of interest from the comparison of the observed variance within and between species and plots. This model also allows the estimation of the residual variance term (R, here the amount of variation that is not explained by species or plots) which includes both natural within-species variability not related to plot variation, and any measurement error. All parameters were estimated by the residual maximum likelihood (REML) method with the lme4 library (Bates et al., 2015).

Total explained variance was calculated by pooling among-species (s), among-plots(p), and residual (R) variance together. Variance was then partitioned among the three components in relation to the total with s% representing the amount of variation explained by species, p% representing the amount of variation explained by plot, and R% representing the unexplained variation. Intraspecific variation was calculated from pooling together p% and R%. Using mixed models for variance partitioning is advantageous when considering numerous species or sites because of increased estimation accuracy, as it does not use as many degrees of freedom as ANOVA (Harrison et al., 2018).

Phylogenetic Signal

To understand how much of leaf trait variation is due to phylogenetic conservatism (**Question 1b**), the presence of a phylogenetic signal (i.e., is the tendency of related species to resemble one another) was tested for each trait using two most commonly used indexes, Pagel's lambda (Pagel, 1999) and Bloomberg's K (Blomberg et al., 2003). Pagel's lambda (λ) is a scaling parameter for the correlations of traits between species relative to the expected under a Brownian motion model of evolution. The value of λ approximates (i) zero when the relationship between species traits departs from the expected under Brownian motion (i.e., traits are changing along evolution independently of phylogeny) and (ii) one when the relationship between species traits approaches the expected under Brownian motion (i.e., tend toward phylogenetic conservation). Bloomberg's K is a scaled ratio of the variance among species traits over the contrast's variance. The value of Bloomberg's K approximates (i) zero when related species have traits more similar than expected from their phylogenetic relationships, (ii) one when the relationship between species traits approaches the expected under Brownian motion, and (iii) exceed one when related species traits are less similar than expected by their phylogenetic relationships. Analysis of simulated data shows that Pagel's lambda performs better when traits follow the Brownian motion model of evolution and Bloomberg's K when there are changes in evolutionary rates along time (Münkemüller et al., 2012); thus, their combined use should cover both possibilities.

Phylogenetic data were obtained from a published species level palm phylogeny (Faurby et al., 2016). Simple mean trait values per species were used for phylogenetic signal tests over 1,000 posterior distribution equally probable phylogenetic trees from Faurby et al. (2016).

Trait Covariation

The role of trait covariation on intraspecific variation (**Question 2**) was examined using correlation matrices among traits. Specifically, we tested the hypothesis of trait coordination constraints on intraspecific variation by partitioning the coordinated response of multiple traits to local conditions (ecological coordination) from trait covariation that is decoupled from local conditions (intrinsic coordination). The rational for this approach is the expectation that when we control for the local conditions on trait variation, the trait covariations resulting from local conditions co-selection will disappear while trait covariation that is independent from local conditions will persist (**Figure 1**). We implemented this by comparing the correlations based on mean trait values per species calculated from the original sampled (raw) data to the correlation calculated from species random intercepts, which here represents differences among species excluding the environmental conditions given by the plot-effect (see section "Variation Partitioning"). Significant associations among traits were graphically represented using trait covariation networks for models based on raw data and environmentally controlled data given by the R package *qgraph* (Epskamp et al., 2012).

Trait–Environment Relationships

To evaluate the role of local hydrology on intraspecific variation on leaf traits (**Question 3a**), we tested the effect of local hydrology (HAND) on the intraspecific trait variation by expanding the LMM model used before to include HAND as a fixed factor, and species and site as random intercepts. The site effect considers any spatial or unmeasured environmental effects on trait variation. Then, to determine the effect of HAND in the community level trait values (**Question 3b**), we regressed plot CWM against HAND. Community weighted means of the 72 plots for which we have relative abundances were calculated with the formula:

$$CWM = \sum_{k=1}^{n_j} w_{k,j} \times T_{kj} \tag{2}$$

where **w** = relative abundance; **j** = species; **k** = plot; and **T** = mean species trait.

RESULTS

How Much of Leaf Trait Variation Is Due to Intraspecific Variation? Within vs. Between Species Trait Variation

Within-species leaf trait variation was not always smaller than between-species variation (**Supplementary Table 2**). SL, LA, SD, and LT were the traits with larger proportion (>50%) of variation explained by species identity than by intraspecific variation. VD and LDMC had less than 50% of variation explained by species identity, and thus a larger contribution of within-species variation. Species identity explained between 26 and 77% of the variance on leaf traits. Intraspecific variation was between 22 and 73% with local environmental conditions explaining between 1 and 11% and unexplained (residual) variation accounting for 19–71%. The decreasing in the proportion of variance explained by species identity was mirrored by an increase in the residuals, and not by an increased amount of variation explained by local conditions (**Figure 2**).

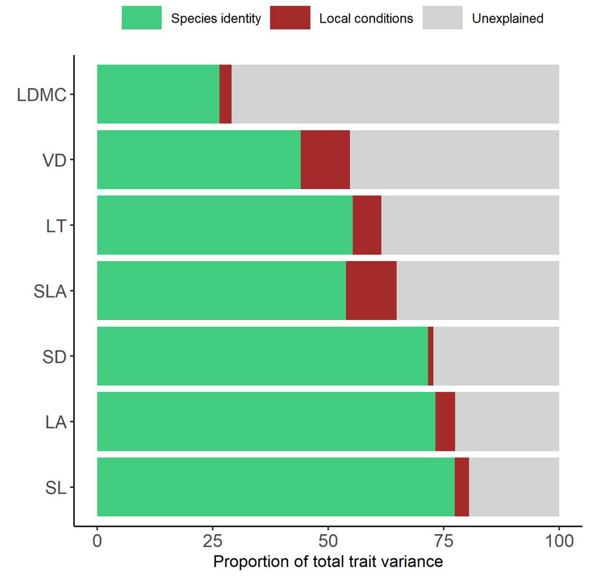


FIGURE 2 | Partitioning of variance for each leaf trait into local conditions (plot), species identity and unexplained (residual). Leaf traits are sorted from low to high unexplained variation. LDMC, leaf dry mass content; VD, venation density; LT, leaf thickness; SLA, specific leaf area; SD, stomata density; LA, leaf area; SL, stomata length.

How Much of Leaf Trait Variation Is Due to Phylogenetic Conservatism? Phylogenetic Variation

Our results show evidence of phylogenetic conservatism in the leaf traits of co-occurring palm species for only a third of traits (**Table 1**). In most of the phylogenetic trees, leaf trait values varied as much within close related species than among distant ones (**Supplementary Figure 2**). Pagels's lambda was above the threshold of statistical significance ($p < 0.05$) for all phylogenetic trees while Bloomberg's K was above this threshold for most of them. We found evidence of trait conservatism in 74% of the phylogenetic trees for SD, 27% for SL, and 22% for LDMC. For VD and LT, we found phylogenetic signal for less than 5% of the 1,000 equally probable phylogenetic trees, while for LA and SLA, we found for none. Phylogenetic signal was not correlated to trait intraspecific variation ($r = 0.06$, $p = 0.895$, **Supplementary Figure 3**).

TABLE 1 | Phylogenetic signal of the palm leaf functional traits, across the phylogeny of the local community.

Leaf trait	Pagel's λ		Bloomberg's K	
	Percentage trees with $p < 0.05$ (%)	Mean	Percentage trees with $p < 0.05$ (%)	Mean
LDMC	3	0.442	**22**	0.640
VD	ns	0.012	1	0.470
LT	ns	0.003	3	0.453
SLA	ns	0.000	ns	0.327
SD	ns	0.742	**74**	0.654
LA	ns	0.278	ns	0.449
SL	ns	0.168	**27**	0.553

Leaf traits are sorted from low to high unexplained variation.
LDMC, leaf dry mass content; VD, venation density; LT, leaf thickness; SLA, specific leaf area; SD, stomata density; LA, leaf area; SL, stomata length. Percentage of trees with p-value < 0.05 is calculated from 1000 equally probable phylogenetic trees for palm family.
Values in bold denote when more of 5% of the trees returned a statistic below this threshold and ns when none of them.

What Is the Role of Trait Covariation on Intraspecific Variation? Among Traits Relationships

The simple correlations between traits were between 0.19 and 0.57 among all comparisons (**Supplementary Figure 4**). LA, SD, VD, and SLA were positively correlated to each other and negatively correlated to LT. SL was negatively correlated to all other traits, but LT. Trait covariation relationships changed when we control for trait–environment relationships (**Figure 3**). The only correlations that remained significant were among SLA, VD, and LT in one cluster, and among SL and LA in another. Correlations between VD and other traits nearly doubled after controlling for environmental effects, as well between SLA and LT. Correlations between LA and SD changed little.

How Does Environment (Local Hydrology) Affect Intraspecific and Community Level Variation of Leaf Traits? Trait–Environment Relationships

Height above nearest drainage explained almost no intraspecific variation on palm leaf traits on the models controlling for species and local conditions (**Table 2**), meaning that, on average, the observed intraspecific variation was not associated with the variation in the hydrological condition. Some species, however, did show a trend of intraspecific variation of some traits (e.g., VD and SL for *Bactris hirta*) aligned to the environmental variation, although most of these trends tend to be weak (**Figure 4**). The lack of a concerted response of intraspecific variation across all species to the environment is given not only by weak within-species effects but also by opposed trends across species, e.g., leaf thickness of *Astrocaryum tucuma* increased with HAND while that of *Bactris hirta* decreased (**Figure 4**). At the community level, most traits' CWM changed along HAND (**Table 3**). SLA and LA decreased, while LT, SD, and VD increased with HAND (**Figure 4**).

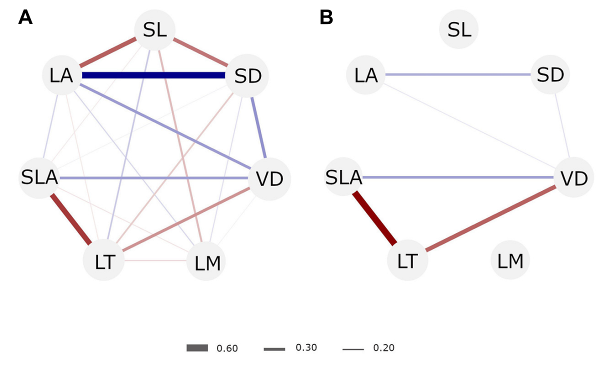


FIGURE 3 | Correlation between leaf traits **(A)** based on raw trait data and **(B)** based on the proportion of phenotypic variation attributed to the species effect (s%) that excludes the plot(environmental)-effect (see **Figure 1** and section "Materials and Methods" for details). Positive correlations are denoted in blue tones and negative correlations in red tones. Correlation strengths are represented by line thickness. Only correlations with *p*-value below the threshold of 0.05 are shown. SL, stomata length; SD, stomata density; VD, venation density; LM, leaf dry mass content; LT, leaf thickness; SLA, specific leaf area; LA, leaf area.

DISCUSSION

In this study, we addressed the patterns of intra to interspecific variation in leaf traits of locally dominant palm species, and its relationships to local hydrology, in a moist forest of central Amazonia. We found that: (1) traits vary widely within species; (2) most traits do not have phylogenetic signal at the studied mesoscale (10 × 10 km); (3) correlations among traits were mostly due to intrinsic species constraints, i.e., few of the evaluated traits are free to respond to the environment independently from others; (4) intraspecific trait variation was not associated to the hydrological gradient in a coherent form across all species; and (5) even though species showed low intraspecific adjustment to hydrology, community-averaged traits closely tracked hydrological changes.

Our results show that, even in a local scale, the palm leaf traits have large amounts of intraspecific variation. Within-species variation was mostly not related to the variation in local hydrological conditions across species. Although some combinations of species and traits did show trends of variation aligned to the environment, we did not find the trait variation along the main environmental gradient driving community composition changes to be consistent. Studies comparing contributions of intra vs. interspecific variation to the changes of trait values along environmental gradients have shown consistently higher contributions of interspecific than the intraspecific component, on either trees or herbs, and across different vegetation types and spatial scales (Cornwell and Ackerly, 2009; Jung et al., 2010; Kichenin et al., 2013; Siefert et al., 2014; Luo et al., 2016). Here we suggest that the same is true for the palm life-form, even though the exceptionally low contribution of the intraspecific component recorded in this study is new.

TABLE 2 | Results of linear mixed models including height above nearest drainage (HAND) as fixed factor and species and local conditions (plot) as random intercepts.

	(Intercept)			**Hand**			**Marginal R^2/conditional R^2**
	Estimates	***CI***	***p***	**Estimates**	***CI***	***p***	
LDMC	427.78	398.50–457.07	**<0.001**	0.44	–0.73 to 1.62	0.459	0.004/0.283
VD	15.82	12.29–19.35	**<0.001**	–0.05	–0.17 to 0.08	0.461	0.006/0.546
LT	0.15	0.11–0.19	**<0.001**	0	–0.00 to 0.00	0.158	0.013/0.622
SLA	270.36	194.25–346.47	**<0.001**	–0.55	–3.03 to 1.93	0.666	0.002/0.655
SD	12.33	9.70–14.97	**<0.001**	–0.04	–0.09 to 0.01	0.145	0.006/0.729
LA	2.88	1.19–4.57	**<0.001**	0.01	–0.03 to 0.05	0.736	0.001/0.781
SL	56.1	50.19–62.02	**<0.001**	–0.07	–0.20 to 0.05	0.224	0.005/0.804

Leaf traits are sorted from low to high unexplained variation.
LDMC, leaf dry mass content; VD, venation density; LT, leaf thickness; SLA, specific leaf area; SD, stomata density; LA, leaf area; SL, stomata length.
Values in bold denotes p-value below the threshold of 0.05.

We did not detect strong phylogenetic conservatism in the examined traits at this local scale that could suggest limited capacity of change in trait values. This may result from the combination between our focus on the local scale—where genetic distinction among populations is less likely to be relevant—and a single monophyletic lineage, therefore restricting the number of alternative traits and combinations that might have evolved in response to the same pressures. These results are in agreement with the lack of phylogenetic conservatism of leaf traits in 80 species widely distributed among the major palm clades (Ma et al., 2015). Most of the evolutionary divergences in traits of our studied palms occurred within genus or family levels, and there is strong segregation of congeneric or confamilial species along the hydrological gradient (**Supplementary Figure 1**). At the same time, we observed substantial intraspecific variation in the examined leaf traits, indicating that indeed these species have the potential to express variation in traits. Therefore, it is not phylogenetic inertia that limits the intraspecific adjustment of trait values to the hydrological gradient.

It is not clear if palms have an intrinsically lower capacity for environmental adjustment of the anatomical and morphological leaf traits such as those studied here, in comparison with other life-forms, or other factors may be responsible for the observed patterns. One possibility is that the low seasonality (∼2 dry months) of the studied forest could decrease the plant-perceived local hydrological differences, even if they are striking to us (e.g., Hodnett et al., 1997), and not demand intraspecific adjustments. This, however, would be at odds with the strong palm species turnover along this gradient (Costa et al., 2009) and the strong adjustment to similar gradients observed in Guiana trees subjected to the same seasonality (Schmitt et al., 2020). Intraspecific adjustments may, otherwise, be occurring in physiological traits, below-ground traits, or even at the whole organism level (e.g., above- to belowground ratios, stem to leaf area ratios, fine root to leaf area ratios, etc.). Seasonal hypoxic or anoxic soil conditions in the valleys should demand adjustments in the metabolism and usually require special structures such as aerenchyma, lenticels, or physiological adjustments (Parent et al., 2008). These adjustments may not be linked to the traits examined here, and thus we cannot conclude that no intraspecific adjustments to the hydrological gradient are occurring, but only that not in the leaf morpho-anatomical traits we studied.

Intraspecific variation, however, was not associated with the hydrological gradient in our study area in a coherent form across all species. Although it is possible that intraspecific variation in palm leaves results from unmeasured environmental variables, the relatively small amount of variation explained by plots within-species suggests that conditions that vary at plot scale (e.g., soil characteristics and canopy openness) are unlikely to be related to the observed variation. It is interesting to note that in our study area, the hydrological conditions covary with soil fertility, with a tendency for lower fertility toward bottomlands. Although this correlation may be a confounding factor, the direction of trait selection we observed at the community level is more compatible with selection by the hydrological than by the fertility gradient. For example, we observed higher values of SLA and lower values of LDMC where soils are very wet but poorer, which is the opposite of the expected based on fertility. Therefore, the patterns of trait variation observed here are more likely to be linked to changes in local hydrological conditions than the other known dominant gradients. Examining how contrasting selection forces (as exemplified here) could also be contributing to increase intraspecific variation may be an interesting line of investigation for next studies.

Differences in leaf age and microenvironment conditions could explain some of the intraspecific variation observed. Although we have controlled in our sampling for leaf age and forest stratum, the longevity of palm leaves in forest understory varies between 2 and 9 years (Henderson, 2002). During this time, the microenvironmental conditions in forest understory (especially light conditions) may change adding an uncontrolled source of variation at the individual level. Other microenvironmental conditions of relevance for palms are topography, soil, and litter distribution (Svenning, 2001). In this study, we controlled by soil and topographic variation sampling in plots that follow topographic contour in order to minimize local soil variation (Magnusson et al., 2005). Litter variation was not controlled in this study. Litter depth shows temporal and spatial variation in our study area (Rodrigues and Costa, 2012) but is unlikely

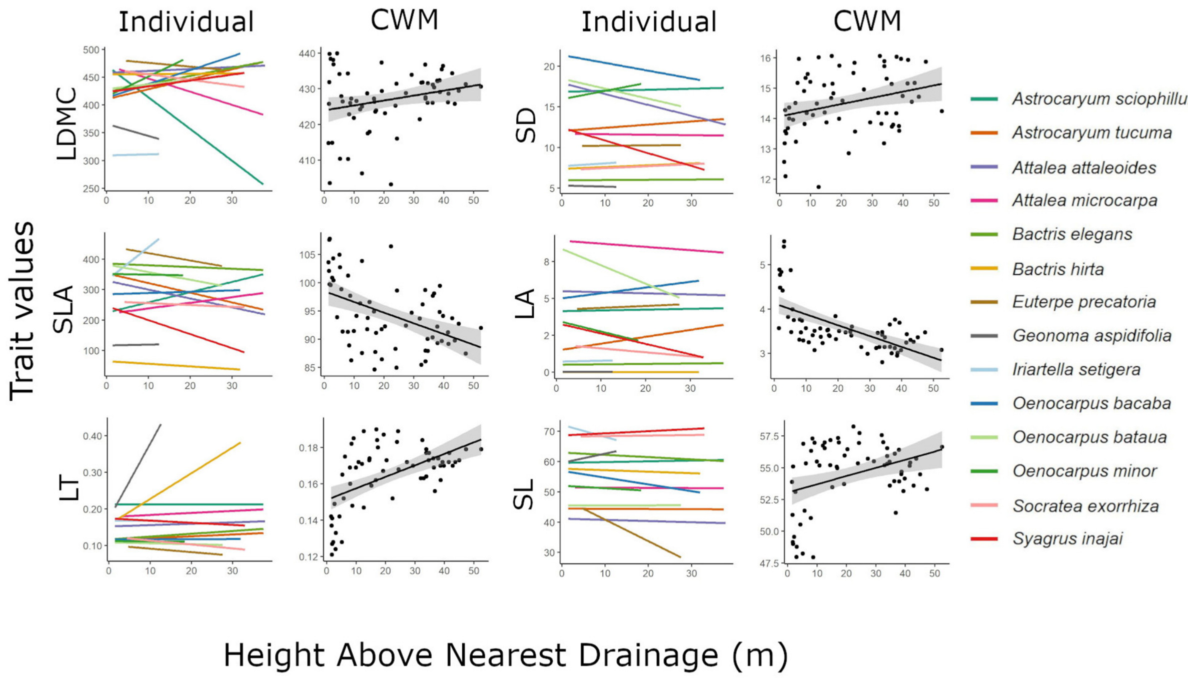


FIGURE 4 | Individual and community weighted mean (CWM) trait variation along height above nearest drainage gradient. Only relations with *p*-value below the threshold of 0.05 for CWM models (**Table 3**) are shown. LDMC, leaf dry mass content; VD, venation density; LT, leaf thickness; SLA, specific leaf area; SD, stomata density; LA, leaf area; SL, stomata length.

TABLE 3 | Standardized beta coefficients for relationships between the community weighted mean of seven leaf traits (Trait CWM) and the local hydrology, represented by height above nearest drainage (HAND).

Trait CWM	b_{std}	R^2
LDMC	0.25*	0.06
VD	ns	ns
LT	0.54***	0.29
SLA	−0.47***	0.22
SD	0.30*	0.08
LA	−0.62***	0.39
SL	0.36**	0.13

Leaf traits are sorted from low to high unexplained variation.
LDMC, leaf dry mass content; VD, venation density; LT, leaf thickness; SLA, specific leaf area; SD, stomata density; LA, leaf area; SL, stomata length.
****For p-value <0.001, **for p-value <0.01, *for p-value <0.05, and ns for p-values above the threshold of 0.05.*

to affect any of the traits measured here, at least not directly. We believe the care taken during the sampling was compatible with the microenvironment variation observed in the field and we do not expect it to have an important impact on our conclusions. However, microenvironmental variation experienced in scales of few meters or along the leaf lifespan should account for some of the intraspecific variation observed here.

Another reason why intraspecific variation of single traits may not be linked to environmental variation is the existence of structural constraints to variation, when one trait is not free to vary because it is structurally bounded to other traits. A single axis of trade-offs between leaf traits has been the dominant idea regarding trait coordination (Wright et al., 2004). More recently, one study has shown that the same traits can be either coupled or decoupled in the same species, depending on the environmental conditions (Ramırez-Valiente et al., 2020). Much of the controversy about trait covariation arises from the confusion between trait coordination or trait co-selection. Trait coordination arises from inevitable trade-offs between one trait and others. Trait co-selection, on the other hand, will be the result of two traits being selected simultaneously by environmental conditions. In our study, we show that a large part of trait covariation in palm leaves happens independently of the environmental variation, suggesting a major role of intrinsic trait coordination in trait variation patterns, but very little co-selection by environment.

A previous study (Muscarella and Uriarte, 2016) has provided empirical evidence that species are more likely to occur where some of their traits have values closer to the CWM, but other traits diverge from that; reinforcing the idea that selection may be operating over a multivariate trait space. We observed a community-level change in trait values along the hydrological gradient that was given mostly by the turnover of species, with little contribution of intraspecific changes. Several of the community-wide functional changes along the topo-hydrological gradient reflect the same pattern of acquisitive strategies associated to the wetter valleys switching to more conservative strategies toward the plateaus observed for trees in this same forest (Cosme et al., 2017), other Amazonian forests (Fontes et al., 2020; Schmitt et al., 2020), and other biomes (Cornwell and Ackerly, 2009). Together, our findings that even within a monophyletic lineage, shifts in trait–environment relationships are common suggest that trait–environment relationships at the community level are the result mainly of shifts in community composition and relative species abundances. This means that while CWM can be informative of the functional strategies in place for some traits, this is more likely to reflect the co-selection of traits along a common environmental gradient than single trait–environment relationships. Our results and proposition echo the findings of previous studies showing the decoupling between functional traits in tropical rain forests (e.g., Baraloto et al., 2010). Therefore, we need to be cautious when inferring ecological strategies from single traits without accounting for covariation of traits. Future work should evaluate phenotype performance along other gradients and traits.

Together our findings expand the current knowledge on trait variation to show that leaf traits can be widely variable within species, tightly coordinated to each other and at the same time, this variation can be independent from local environmental conditions. An additional practical implication of this finding is that sampling along hydrological gradients for those traits may be simplified as, at least in this situation, intraspecific variation is not driven by local hydrological gradients. Our study contributes to disentangle different sources of leaf variation by combining the study of trait variation and covariation in an environmentally and phylogenetically controlled framework. Although we found some evidence of phylogenetic conservatism in leaf traits, this is unlikely to be the main constraint to trait variation since phylogenetic signal is not related to the amount of intraspecific variance in this study. Alternatively, we observed large amounts (56–81%) of trait covariation that could be either generating or constraining interspecific variation on palm leaf traits, which requires further investigation. Finally, we conclude that although within-species variation in the examined traits is large, it does not contribute to the adjustment of individuals to the local hydrological conditions in this Amazonian forest. Therefore, species may need to migrate to follow their hydrological niches as climate changes. Species can also use other routes of adjustment and new traits, especially drought resistance traits, should be investigated.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

TE and FC conceptualized the study. TE and HP collected the data under the supervision of FC. TE, FC, and HP analyzed the data. TE and FC drafted the manuscript with contributions from HP. All authors contributed to the article and approved the submitted version.

FUNDING

This study was supported by the CAPES Science Without Borders Project (078/2013) and CNPq Grants (441282/2016-4, 403764/2012-2, and 558244/2009-2) that funded the Central Amazon Long-Term Ecological Project, whose plots were used for this study. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES)—Finance Code 001 to TE.

ACKNOWLEDGMENTS

We thank Elisângela Rocha, Jackeline Milagros, Magno Plinck, and Talitha Ferreira for assistance during fieldwork and the Agroforestry Botany Laboratory of the Federal University of Amazonas where part of the sample processing was carried out. We are grateful to Maria Gracimar Pacheco for lab support and guidance on anatomical measurements. TE thanks Demetrius Martins for the valuable discussion on the analysis of trait covariation and Fabricio Baccaro for his comments on the early version of this manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2021.715266/full#supplementary-material

REFERENCES

Albert, C. H., Grassein, F., Schurr, F. M., Vieilledent, G., and Violle, C. (2011). When and how should intraspecific variability be considered in trait-based plant ecology? *Perspect. Plant Ecol. Evol. Syst.* 13, 217–225. doi: 10.1016/j.ppees.2011.04.003

Armbruster, W. S., and Schwaegerle, K. E. (1996). Causes of covariation of phenotypic traits among populations. *J. Evol. Biol.* 9, 261–276. doi: 10.1046/j.1420-9101.1996.9030261.x

Baraloto, C., Timothy Paine, C. E., Poorter, L., Beauchene, J., Bonal, D., Domenach, A.-M., et al. (2010). Decoupled leaf and stem economics in rain forest trees. *Ecol. Lett.* 13, 1338–1347. doi: 10.1111/j.1461-0248.2010.01517.x

Bates, D., Mäechler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Statist. Softw.* 67, 1–48. doi: 10.18637/jss.v067.i01

Blach-Overgaard, A., Svenning, J. C., Dransfield, J., Greve, M., and Balslev, H. (2010). Determinants of palm species distributions across Africa: the relative roles of climate, non-climatic environmental factors, and spatial constraints. *Ecography* 33, 380–391. doi: 10.1111/j.1600-0587.2010.06273.x

Blomberg, S. P., Garland, T., and Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57, 717–745. doi: 10.1111/j.0014-3820.2003.tb00285.x

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., et al. (2011). Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26, 183–192. doi: 10.1016/j.tree.2011.01.009

Browne, L., and Karubian, J. (2018). Rare genotype advantage promotes survival and genetic diversity of a tropical palm. *New Phytol.* 218, 1658–1667. doi: 10.1111/nph.15107

Cássia-Silva, C., Freitas, C. G., Alves, D. M. C. C., Bacon, C. D., and Collevatti, R. G. (2019). Niche conservatism drives a global discrepancy in palm species richness between seasonally dry and moist habitats. *Glob. Ecol. Biogeogr.* 28, 814–825. doi: 10.1111/geb.12895

Cavender-Bares, J., Fontes, C. G., and Pinto-Ledezma, J. (2020). Open questions in understanding the adaptive significance of plant functional trait variation within a single lineage. *New Phytol.* 227, 659–663. doi: 10.1111/nph.16652

Chauvel, A., Lucas, Y., and Boulet, R. (1987). On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. *Experientia* 43, 234–241. doi: 10.1007/BF01945546

Cornwell, W. K., and Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecol. Monogr.* 79, 109–126. doi: 10.1890/07-1134.1

Cosme, L. H. M., Schietti, J., Costa, F. R. C., and Oliveira, R. S. (2017). The importance of hydraulic architecture to the distribution patterns of trees in a central Amazonian forest. *New Phytol.* 215, 113–125. doi: 10.1111/nph.14508

Costa, F. V., Costa, F. R., Magnusson, W. E., Franklin, E., Zuanon, J., Cintra, R., et al. (2015). Synthesis of the first 10 years of long-term ecological research in Amazonian Forest ecosystem-implications for conservation and management. *Natur. Conserv.* 13, 3–14. doi: 10.1016/j.ncon.2015.03.002

Costa, F. R. C., Guillaumet, J.-L., Lima, A. P., and Pereira, O. S. (2009). Gradients within gradients: the mesoscale distribution patterns of palms in a central amazonian forest. *J. Veg. Sci.* 20, 69–78. doi: 10.1111/j.1654-1103.2009.05314.x

Costa, F. R. C., Zuanon, J. A. S., Baccaro, F. B., de Almeida, J. S., Menger, J., Souza, J. L. P., et al. (2020). Effects of climate change on central amazonian forests: a two decades synthesis of monitoring tropical biodiversity. *Oecologia Aust.* 24, 317–335. doi: 10.4257/oeco.2020.2402.07

Cuartas, L. A., Tomasella, J., Nobre, A. D., Nobre, C. A., Hodnett, M. G., Waterloo, M. J., et al. (2012). Distributed hydrological modeling of a micro-scale rainforest watershed in Amazonia: Model evaluation and advances in calibration using the new HAND terrain model. *J. Hydrol.* 46, 15–27. doi: 10.1016/j.jhydrol.2011.12.047

de Boer, H. J., Price, C. A., Wagner-Cremer, F., Dekker, S. C., Franks, P. J., and Veneklaas, E. J. (2016). Optimal allocation of leaf epidermal area for gas exchange. *New Phytol.* 210, 1219–1228. doi: 10.1111/nph.13929

Dong, N., Prentice, I. C., Wright, I. J., Evans, B. J., Togashi, H. F., Caddy-Retalic, S., et al. (2020). Components of leaf-trait variation along environmental gradients. *New Phytol.* 228, 82–94. doi: 10.1111/nph.16558Dransfield

Dransfield, J., Uhl, N. W., Asmussen, C. B., Baker, W. J., Harley, M. M., and Lewis, C. E. (2008). *GENERA PALMARUM: The Evolution and Classification of Palms*. Kew: Kew Publishing, 732.

Eiserhardt, W. L., Svenning, J. C., Kissling, W. D., and Balslev, H. (2011). Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Ann. Bot.* 108, 1391–1416. doi: 10.1093/aob/mcr146

Emilio, T., Lamarque, L. J., Torres-Ruiz, J. M., King, A., Charrier, G., Burlett, R., et al. (2019). Embolism resistance in petioles and leaflets of palms. *Ann. Bot.* 124, 1173–1184. doi: 10.1093/aob/mcz104

Epskamp, S., Schmittmann, V. D., and Borsboom, D. (2012). qgraph: network visualizations of relationships in psychometric data. *J. Stat. Softw.* 48, 1–18.

Esquivel-Muelbert, A., Brienen, R. J. W., Baker, T. R., Dexter, K. G., Lewis, S. L., Feldpausch, T. R., et al. (2019). Compositional response of Amazon forests to climate change. *Glob. Chang. Biol.* 25, 39–56. doi: 10.1111/gcb.14413

Estebán, E. J. L. V., Castilho, C., Melgaço, K. L., and Costa, F. R. C. (2021). The other side of droughts: wet extremes and topography as buffers of drought negative effects in an Amazonian forest. *New Phytol.* 229, 1995–2006. doi: 10.1111/nph.17005

Fajardo, A., and Siefert, A. (2018). Intraspecific trait variation and the leaf economics spectrum across resource gradients and levels of organization. *Ecology* 99, 1024–1030. doi: 10.1002/ecy.2194

Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B., and Otero-Casal, C. (2017). Hydrologic regulation of plant rooting depth. *Proc. Natl. Acad. Sci. U.S.A.* 114, 10572–10577. doi: 10.1073/pnas.1712381114

Faurby, S., Eiserhardt, W. L., Baker, W. J., and Svenning, J. (2016). Molecular phylogenetics and evolution an all-evidence species-level supertree for the palms (Arecaceae). *Mol. Phylogenet. Evol.* 100, 57–69. doi: 10.1016/j.ympev.2016.03.002

Fontes, C. G., Fine, P. V. A., Wittmann, F., Bittencourt, P. R. L., Piedade, M. T. F., Higuchi, N., et al. (2020). Convergent evolution of tree hydraulic traits in Amazonian habitats: implications for community assemblage and vulnerability to drought. *New Phytol.* 228, 106–120. doi: 10.1111/nph.16675

Fyllas, N. M., Michelaki, C., Galanidis, A., Evangelou, E., Zaragoza-castells, J., Dimitrakopoulos, P. G., et al. (2020). Functional trait variation among and within species and plant functional types in mountainous Mediterranean forests. *Front. Plant Sci.* 11:212. doi: 10.3389/fpls.2020.00212

Givnish, T. J. (1987). Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytol.* 106, 131–160.

Göldel, B., Kissling, W. D., and Svenning, J. C. (2015). Geographical variation and environmental correlates of functional trait distributions in palms (Arecaceae) across the New World. *Bot. J. Linn. Soc.* 179, 602–617. doi: 10.1111/boj.12349

Gomes, L. R. P., Lopes, M. T. G., Bentes, J. L., da, S., Barros, W. S., Costa Neto, P., et al. (2011). Genetic diversity in natural populations of Buriti (*Mauritia flexuosa* L. f.). *Crop Breed. Appl. Biotechnol.* 11, 216–223. doi: 10.1590/s1984-70332011000300003

Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., et al. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* 6:e4794. doi: 10.7717/peerj.4794

Henderson, A. (2002). *Evolution and Ecology of Palms*. New York NY: New York Botanical Garden Press.

Hodnett, M. G., Vendrame, I., de, O., Marques Filho, A., Oyama, M. D., and Tomasella, J. (1997). Soil water storage and groundwater behaviour in a catenary sequence beneath forest in central Amazonia: I. Comparisons between plateau, slope and valley floor. *Hydrol. Earth Syst. Sci.* 1, 265–277. doi: 10.5194/hess-1-265-1997

Jung, V., Violle, C., Mondy, C., Hoffmann, L., and Muller, S. (2010). Intraspecific variability and trait-based community assembly. *J. Ecol.* 98, 1134–1140. doi: 10.1111/j.1365-2745.2010.01687.x

Kelly, R., Healy, K., Anand, M., Baudraz, M. E., Bahn, M., Cerabolini, B. E., et al. (2021). Climatic and evolutionary contexts are required to infer plant life history strategies from functional traits at a global scale. *Ecol. Lett.* 24, 970–983. doi: 10.1111/ele.13704

Kichenin, E., Wardle, D. A., Peltzer, D. A., Morse, C. W., and Freschet, G. T. (2013). Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. *Funct. Ecol.* 27, 1254–1261. doi: 10.1111/1365-2435.12116

Kraus, J. E., and Arduin, M. (1997). *Manual Básico de Métodos em Morfologia Vegetal*, Vol. 1. Rio de Janeiro: Edur, 198.

Liu, Q., Sterck, F. J., Zhang, J. L., Scheire, A., Konings, E., Cao, M., et al. (2021). Traits, strategies, and niches of liana species in a tropical seasonal rainforest. *Oecologia* 196, 499–514. doi: 10.1007/s00442-021-04937-4

Luizão, R. C. C., Luizão, F. J., Paiva, R. Q., Monteiro, T. F., Sousa, L. S., and Kruijt, B. (2004). Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest. *Glob. Chang. Biol.* 10, 592–600. doi: 10.1111/j.1529-8817.2003.00757.x

Luo, Y. H., Liu, J., Tan, S. L., Cadotte, M. W., Wang, Y. H., Xu, K., et al. (2016). Trait-based community assembly along an elevational gradient in subalpine forests: quantifying the roles of environmental factors in inter- and intraspecific variability. *PLoS One* 11:e0155749. doi: 10.1371/journal.pone.0155749

Ma, R.-Y., Zhang, J. L., Cavaleri, M. A., Sterck, F., Strijk, J. S., and Cao, K. F. (2015). Convergent evolution towards high net carbon gain efficiency contributes to the shade tolerance of palms (Arecaceae). *PLoS One* 10:e0140384. doi: 10.1371/journal.pone.0140384

Magnusson, W. E., Lima, A. P., Luizao, R., Costa, F. R. C., de Castilho, C. V., and Kinupp, V. F. (2005). RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research. *Biota Neotrop.* 5:bn01005022005.

Marenco, R. A., Camargo, M. A. B., Antezana-Vera, S. A., and Oliveira, M. F. (2017). Leaf trait plasticity in six forest tree species of central Amazonia. *Photosynthetica* 55, 679–688. doi: 10.1007/s11099-017-0703-6

Marks, C. O. (2007). The causes of variation in tree seedling traits: The roles of environmental selection versus chance. *Evolution* 61, 455–469. doi: 10.1111/j.1742-4658.2007.00021.x

Marks, C. O., and Lechowicz, M. J. (2006). Alternative designs and the evolution of functional diversity. *Am. Nat.* 167, 55–66. doi: 10.1086/498276

Melo, W. A., Freitas, C. G., and Bacon, C. D. (2018). The road to evolutionary success: insights from the demographic history of an Amazonian palm. *Heredity* 121, 183–195. doi: 10.1038/s41437-018-0074-1

Messier, J., McGill, B. J., and Lechowicz, M. J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecol. Lett.* 13, 838–848. doi: 10.1111/j.1461-0248.2010.01476.x

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., et al. (2012). How to measure and test phylogenetic signal. *Methods Ecol. Evol.* 3, 743–756. doi: 10.1111/j.2041-210X.2012.00196.x

Muscarella, R., and Uriarte, M. (2016). Do community-weighted mean functional traits reflect optimal strategies? *Proc. R. Soc. B* 283:20152434. doi: 10.1098/rspb.2015.2434

Nakagawa, S., and Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biol. Rev.* 85, 935–956. doi: 10.1111/j.1469-185X.2010.00141.x

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., et al. (2010). Plant phenotypic plasticity in a changing climate. *Trends Plant Sci.* 15, 684–692. doi: 10.1016/j.tplants.2010.09.008

Oliveira, R. S., Costa, F. R. C., Van Baalen, E., de Jonge, A., Bittencourt, P. R., Almanza, Y., et al. (2019). Embolism resistance drives the distribution of Amazonian rainforest tree species along hydro-topographic gradients. *New Phytol.* 221, 1457–1465. doi: 10.1111/nph.15463

Osnas, J. L. D., Katabuchi, M., Kitajima, K., Wright, S. J., Reich, P. B., Van Bael, S. A., et al. (2018). Divergent drivers of leaf trait variation within species, among species, and among functional groups. *Proc. Natl. Acad. Sci. U.S.A.* 115, 5480–5485. doi: 10.1073/pnas.180398911

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature* 401, 877–884.

Parent, C., Capelli, N., Berger, A., Crèvecoeur, M., and Dat, J. F. (2008). An overview of plant responses to soil waterlogging. *Plant Stress* 2, 20–27.

Perez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., et al. (2013). New Handbook for standardized measurment of plant functional traits worldwide. *Aust. J. Bot.* 61, 167–234. doi: 10.1071/BT12225

Price, C. A. (2012). "LEAF GUI: Analyzing the geometry of veins and areoles using image segmentation algorithms," in *High-Troughput Phenotyping in Plants. Methods in Molecular Biology (Methods and Protocols)*, Vol. 918, ed. J. Normanly (Totowa, NJ: Humana Press).

Ramırez-Valiente, J. A., López, R., Hipp, A. L., and Aranda, I. (2020). Correlated evolution of morphology, gas exchange, growth rates and hydraulics as a response to precipitation and temperature regimes in oaks (Quercus). *New Phytol.* 227, 794–809. doi: 10.1111/nph.16320

Rasband, W. S. (1997–2008). *ImageJ*. National Institutes of Health, Bethesda, Maryland, MA, United States. Available online at: https://imagej.nih.gov/ij/

Renninger, H. J., and Phillips, N. (2011). Hydraulic properties of fronds from palms of varying height and habitat. *Oecologia* 167, 925–935. doi: 10.1007/s00442-011-2038-5

Rennó, C. D., Nobre, A. D., Cuartas, L. A., Soares, J. V., Hodnett, M. G., Tomasella, J., et al. (2008). HAND, a new terrain descriptor using SRTM-DEM: mapping terra-firme rainforest environments in Amazonia. *Remote Sens. Environ.* 112, 3469–3481. doi: 10.1016/j.rse.2008.03.018

Reznick, D. N., and Ghalambor, C. K. (2001). "The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution," in *Microevolution Rate, Pattern, Process. Contemporary Issues in Genetics and Evolution*, Vol. 8, eds A. P. Hendry and M. T. Kinnison (Dordrecht: Springer). doi: 10.1007/978-94-010-0585-2_12

Rodrigues, F. R. O., and Costa, F. R. C. (2012). Litter as a filter of emergence for herbaceous seedlings and sporophytes in central Amazonia. *J. Trop. Ecol.* 28, 445–452. doi: 10.1017/S0266467412000491

Ruokolainen, K., and Vormisto, J. (2000). The most widespread Amazonian palms tend to be tall and habitat generalists. *Basic Appl. Ecol.* 1, 97–108. doi: 10.1078/1439-1791-00020

Schietti, J., Emilio, T., Rennó, C. D., Drucker, D. P., Costa, F. R. C., Nogueira, A., et al. (2014). Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. *Plant Ecol. Divers* 7, 241–253. doi: 10.1080/17550874.2013.783642

Schmitt, S., Hérault, B., Ducouret, É, Baranger, A., Tysklind, N., Heuertz, M., et al. (2020). Topography consistently drives intra- and inter-specific leaf trait variation within tree species complexes in a Neotropical forest. *Oikos* 129, 1521–1530. doi: 10.1111/oik.07488

Siefert, A., Fridley, J. D., and Ritchie, M. E. (2014). Community functional responses to soil and climate at multiple spatial scales: when does intraspecific variation matter? *PLoS One* 9:e111189. doi: 10.1371/journal.pone.0111189

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., et al. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecol. Lett.* 18, 1406–1419. doi: 10.1111/ele.12508

Silvertown, J., Araya, Y., and Gowing, D. (2015). Hydrological niches in terrestrial plant communities: a review. *J. Ecol.* 103, 93–108. doi: 10.1111/1365-2745.12332

Silvertown, J., Dodd, M. E., Gowing, D. J. G., and Mountford, J. O. (1999). Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature* 400, 61–63.

Snijders, T. A., and Bosker, R. J. (2011). *Multilevel Analysis: An Introduction to Basic and Advanced Multilevel Modeling*. London: Sage, 354.

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

Tomlinson, P. B. (1990). *The structural Biology of Palms*. Oxford: OxfordUniversity Press, 277.

Tomlinson, P. B. (2006). The uniqueness of palms. *Botan. J. Linn. Soc.* 151, 5–14. doi: 10.1111/j.1095-8339.2006.00520.x

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., et al. (2012). The return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.* 27, 244–252. doi: 10.1016/j.tree.2011.11.014

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

Vormisto, J., Tuomisto, H., and Oksanen, J. (2004). Palm distribution patterns in Amazonian rainforests: What is the role of topographic variation? *J. Veg. Sci.* 15:485.

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

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

frontiers
in Forests and Global Change

ORIGINAL RESEARCH
published: 24 September 2021
doi: 10.3389/ffgc.2021.723553

Palm Functional Traits, Soil Fertility and Hydrology Relationships in Western Amazonia

William Trujillo[1]*, *Carlos A. Rivera-Rondón*[2] *and Henrik Balslev*[3]

[1] Grupo Investigaciones Territoriales Para el Uso y Conservación de la Biodiversidad, Fundación Reserva Natural La Palmita, Centro de Investigación, Bogotá, Colombia, [2] UNESIS, Departamento de Biología, Pontificia Universidad Javeriana, Bogotá, Colombia, [3] Department of Biology, Ecoinformatic and Biodiversity, Aarhus University, Aarhus, Denmark

Quantification of multivariate trait spectra (or axes of specialization) make the definition of plant strategies more operational, which promotes trait-based theory of community assembly and the understanding of dynamics and functioning of ecosystems. We used field-quantified soil data to explore trait-environment relationships across palm communities in western Amazonia. We collected data from 116 palm species in 458 transects across four distinct forest types. We combined these data with trait records to relate local plant community trait composition to broad gradients in soil variables and forest types. There were significant trait-environment relationships across western Amazonia. Palms with large leaves and fruits, and palms with both growth forms (acaulescent/erect) were associated with fertile soils, while palms with unarmed leaves and stems were associated with non-inundated environments. These results suggest that the functional traits of palms vary consistently along soil gradients on a regional scale. This variation could be explained by the soil fertility and acidity + aluminum gradients, suggesting environmental filters related to resource availability and stressful environments, such as acid soils and soils with high aluminum content.

Keywords: floodplain, functional ecology, *terra firme*, soil properties, South America

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

Reviewed by:
Michael Kessler,
University of Zurich, Switzerland
Heidi Renninger,
Mississippi State University,
United States

Correspondence:
William Trujillo
williamtrujilloca@gmail.com

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

Received: *10 June 2021*
Accepted: *25 August 2021*
Published: *24 September 2021*

Citation:
Trujillo W, Rivera-Rondón CA and Balslev H (2021) Palm Functional Traits, Soil Fertility and Hydrology Relationships in Western Amazonia. Front. For. Glob. Change 4:723553. doi: 10.3389/ffgc.2021.723553

INTRODUCTION

The most functional plant traits reflect adaptations to environmental conditions found in their immediate proximity (Díaz et al., 2016). Life-history evolution has produced distinct plant strategies that are positioned along the fast–slow trait spectrum and leaf-height-seed strategy (Westoby, 1998). Given the important roles of soil microbes in both nutrient acquisition and plant disease, we should expect relationships between plant-soil feedbacks and the plant strategies traditionally linked with functional traits (Xi et al., 2021). Plant–soil feedbacks express how plants interact with soil microbes and soil biogeochemical and physical properties (Van der Putten et al., 2013). For example, plants can invest in traits that promote rapid growth (via nutrient acquisition) or in traits that provide defense against antagonists (Díaz et al., 2016). Plant height may indicate plant life span and competitive ability for light (Moles et al., 2009).

The relationship between soil types and local and regional-scale palm community composition in lowland rain forest has been attributed to differences in soil fertility (Vormisto et al., 2004; Andersen et al., 2010). In lowland tropical rain forests the exchangeable bases, phosphorus (P) and nitrogen (N) explain palms and tree distributions (Clark et al., 1995; Phillips et al., 2003; Tuomisto et al., 2003a,b, Andersen et al., 2010; Baribault et al., 2012; Condit et al., 2013). Macronutrients such as P may be the most important limiting nutrient to tree growth (Vitousek, 1984). In northwestern Amazonia, Cámara et al. (2017) found that macronutrients, especially exchangeable bases (Ca^{2+}, K^+, and Mg^{2+}) and P, emerged as more important than micronutrients in predicting species abundances in palm communities in non-inundated forests.

Studies of soil properties relative to plant traits have mostly focused on the importance of trait effect in driving soil properties and ecosystem functioning. Plant traits can influence soil microbial communities (Legay et al., 2014), soil abiotic properties (Reich, 2014), and nutrient cycling (Fortunel et al., 2009; Grigulis et al., 2013). Increasing plant functional trait diversity has been proposed as a potential mechanism to increase carbon allocation and storage below-ground (De Deyn et al., 2008). However, the relationship between soil properties and plant traits is bidirectional and have not been sufficiently incorporated into analyses that test for the importance of soil fertility as a driver of environmental filtering (Laughlin et al., 2015). Species and environmental conditions control community composition by selecting species with functional trait values that confer optimum fitness for those conditions (Keddy, 1992). Both structural and physiological leaf traits have been shown to correlate with soil nutrients at global scales (Maire et al., 2015). Plant traits can be rough proxies for ecosystem functioning and they respond to the biogeochemical and biophysical properties of ecosystems (Lavorel and Garnier, 2002; Wright et al., 2004).

Although plant-soil nutrient relationships have been studied extensively (see reviews by Chapin 1980, Aerts and Chapin 2000), the quantification of the response of traits through the nutrient gradient at different scales remains relatively unexplored (Ordoñez et al., 2009). Such quantitative knowledge is needed to advance our understanding of ecosystem functions, especially in the face of global change (Ordoñez et al., 2009). Here we investigated how palm traits are distributed in the forest types in western Amazonia and how they relate to soil properties. We hypothesized that the field-quantified environmental variables provide strong links with local trait composition.

MATERIALS AND METHODS

Study Area

On the largest spatial scale, Amazonia is characterized by a humid tropical climate with decreasing precipitation and increasing seasonality with increasing distance from the equator and toward the east (Silman, 2007). Soils in the western parts of the region have developed on Cenozoic sediments from the Andean orogeny, whereas soils in the east (e.g., on the Guyana shield) developed on Proterozoic crystalline bedrock (Sombroek, 2000). Within the western part of Amazonia (**Figure 1**), our 458 transects were sampled from four habitat types with 9–274 transects per habitat: non-inundated (Ninu) forest (274 transects: restinga 12, *terra firme* 233, and terrace 29), inundated forest (144 transects, floodplain), white-sand (9 transects), and pre-montane hills (PrH; 32 transects; Kristiansen et al., 2011; Eiserhardt et al., 2013; Balslev et al., 2019).

Data Collection

Palm Species Distribution and Abundance Across the Western Amazon

Collection of palm data on species presence/absence and abundance was carried out using a standardized transect methodology. Each transect was 5 × 500 m (0.25 ha) and divided into 100 subunits of 5 × 5 m. In each transect subunit (5 × 5 m), all individuals of palms were identified to the species level including seedlings, juveniles, subadults, and adults. A total of 458 transects (114.75 ha) with a total of 445,044 palm individuals were inventoried. Further details on the methodology can be found in Balslev et al. (2019).

Environmental Variables

In total, 11 soil variables were included in the analysis: pH, loss-on-ignition (loi, a proxy for organic matter content), aluminum concentration (Al^{3+}), potassium concentration (K^+), exchangeable acidity (acidity, H + Al), base saturation (BS), calcium concentration (Ca^{2+}), sodium concentration (Na^+), P concentration, effective cation exchange capacity (ECEC), and magnesium concentration (Mg^{2+}). Three soil samples were taken in each transect, one at each extreme and one in the center, and the three samples were averaged to obtain a single value per transect. The habitat type was registered in the transects (Forest Type; non-inundated = nin, Inundated = Inu, white sand = WhS, and premontane hills = PrH). More details about the units and variables can be obtained in Balslev et al. (2019).

Palm Functional Traits

The palm functional traits were obtained mainly from Kissling et al. (2019). We completed missing data with additional literature revision (Kahn and Ferreira, 1995; Borchsenius and Bernal, 1996; Henderson, 2000; Galeano and Bernal, 2010; Kahn and Millán, 2013). Thirteen functional traits were recorded for each palm species (**Table 1**). We used maximum fruit diameter as proxy for fruit size. In this study, fruit size was used as a proxy for the seed size, because several previous studies have demonstrated a positive correlation between fruit and seed size in fleshy-fruited plants, especially for single or few seeded fruits (Jordano, 2000).

Data Analysis

The continuous traits were categorized to show their distribution and frequencies among the forest types (**Table 1**). With the field data, three tables were constructed: matrix $Q_{(q \times m)}$ = 13 functional traits of 116 palm species (**Table 1**); matrix $R_{(n \times p)}$ = environmental variables of 458 transects; and matrix $L_{(n \times q)}$ = palm abundance in the 458 transects. Principal components analysis (PCA) was used to reduce the dimensionality of the environmental variables (11 soil variables) and to define the main variables that explain the variation among the sampled plots. A Fourth-Corner analysis (Dray et al., 2014) was used to evaluate the relationship of the species trait values with the environmental variables. Because there may be

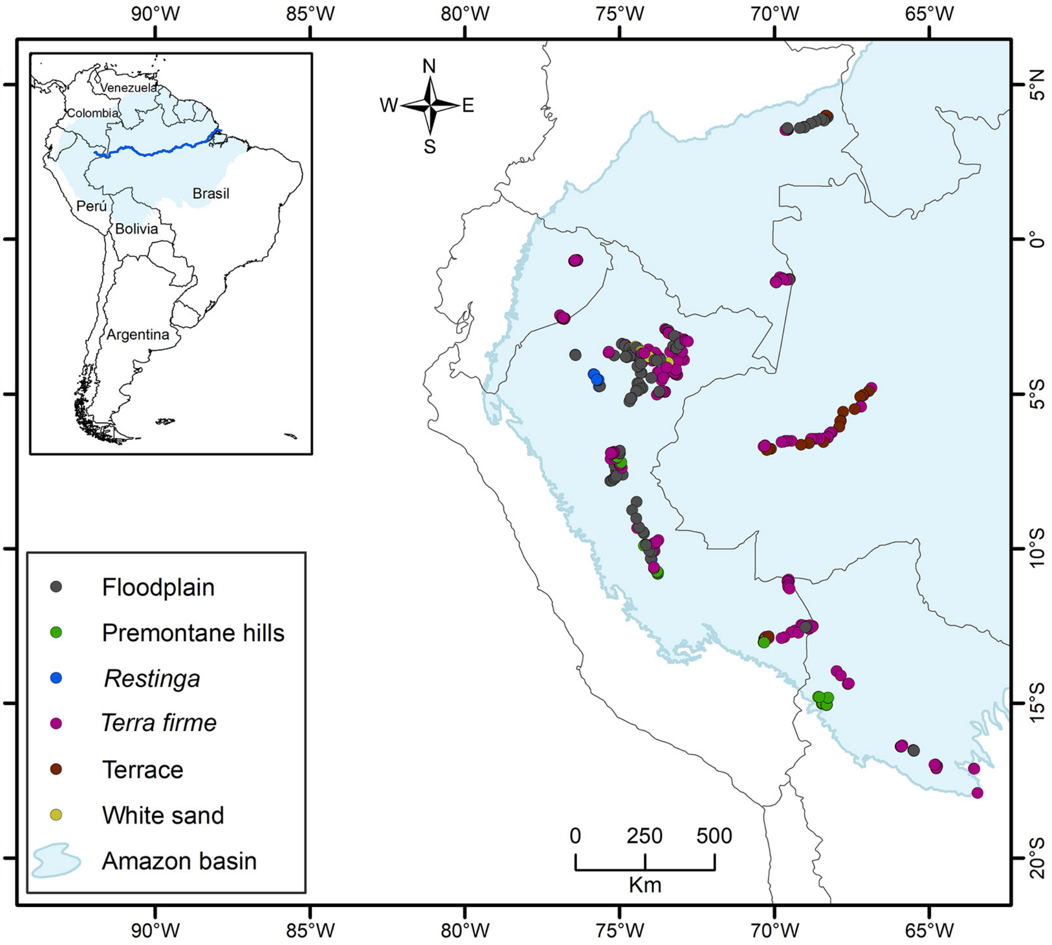


FIGURE 1 | Location of the 458 transects (500 × 5 m) sampled in the western Amazonia, with indication of the forest types. In the analysis in this paper the data from Restinga, Terra firme, and Terrace are combined into the category Non-flooded forests.

differences in the ecological responses of individuals according to their age, this analysis was carried out only using the data of adults (90,561 individuals). The Fourth-corner analysis tests the individual trait-environment relationship (Dray et al., 2014). We used the Model 6, which performs two separate tests using models 2 and 4 and to combine the results by keeping the higher *p* value produced by the two permutation tests. The model 2 permutes the n samples (i.e., rows of *R* or *L*) and model 4 permutes the p species (i.e., rows of *Q* or columns of *L*). The Model 6 has the advantage of limiting the level of the type I error (Dray et al., 2014). Statistical analyses were carried out using R statistical software (R Core Team, 2016) and the *Vegan* (Oksanen et al., 2013) and *Ade-4* packages (Dray and Dufour, 2007).

RESULTS

We recorded 116 palm species in the 458 transects that together encompassed a total of 114.75 ha. The most diverse genus was *Bactris*, with 27 species, followed by *Geonoma* (20), *Astrocaryum* (12), and *Attalea* (8). The most abundant species was *Oenocarpus bataua*, with 45,568 individuals, followed by *Lepidocaryum tenue* and *Geonoma macrostachys*, with 34,385 and 29,016 individuals, respectively.

Most palm individuals in western Amazonia (86%) had erect growth forms. They were dominant in all of habitats (**Figure 2A**). Most individuals (43%) were solitary and the cespitose life form were represented by 38% of the individuals; solitary palms were more abundant in premontane hills (PrH), and the cespitose palms were evenly distributed between forests that were inundated (Inun), Ninu, on PrH, and growing on white sands (WhS). Palms with both life forms (solitary/cespitose) were more abundant in WhS (**Figure 2B**). The highest proportion of individuals had short stems (54%); but in forests growing on WhS tall palms were more abundant. Short palms (0–8 m) were evenly distributed between not-inundated (Ninu) and inundated (Inun) forests. Tall (>18 m) and medium tall palms (9–17 m) were more abundant in PrH and forests on white sand (WhS; **Figure 2C**). Similarly, most individuals (53%) had small stem diameters (0–10 cm).

Most individuals (90%) had few leaves (7–21). The individuals with medium numbers of leaves (22–35) were more abundant in

TABLE 1 | Functional traits of 116 palm species registered in western Amazonia.

Traits	Categories	Trait type
Lifeform (LF)	Cespitose = ces, solitary = sol	Categorical, structural trait
Growth form (GF)	acaulescent = aca, erect = ere, climbing = cli	Categorical, structural trait
Stem armed (StAr)	Unarmed = unar, armed = arm	Categorical, defense
Leaves armed (Lar)	Unarmed = unar, armed = arm	Categorical, defense
Maximum stem height (StH)	Short = 0–8 m, medium = 9—17 m, tall = > 18 m;	Continuous, structural trait
Maximum stem diameter (StD)	Small = 0–10 cm, medium = 10.1–20, large > 20	Continuous, structural trait
Maximum leaf number (LN)	Low = 7–21, medium = 22–35, high = 36–50	Continuous, leaf trait
Maximum petiole length (PeL)	Short = 45–120 cm, medium = 121–225 cm, long = 226–330 cm	Continuous, leaf trait
Maximum leaf rachis length (RL)	Short = 0–3 m, medium = 3.1–7, Long > 7	Continuous, leaf trait
Maximum blade length (BL)	Short = 0–5 m, medium = 5.1–10, long > 10	Continuous, leaf trait
Average fruit width (FrW)	Thin < = 2.4 cm, medium = 2.5–4.2, wide = > 4.3	Continuous, reproductive trait
Average fruit length (FrL)	Short = 0–3 cm, medium = 3.1–6, Long > 6	Continuous, reproductive trait
Fruit conspicuicence (FrCo)	Conspicuous = cons, cryptic = cryp	Categorical, reproductive trait

the inundated forest (Inun, **Figure 2D**). Of all individuals, 50% had short petioles (45—120 cm, **Figure 2E**), which were more abundant in forests on PrH. Moreover, most individuals (57 and 63%, respectively) had short leaf rachises (0–3 m) and blades (0–5 m), and were better represented in forest growing on white sand (WhS; **Figure 2F**).

Most individuals had unarmed stems and leaves (85 and 79%, respectively), with a high proportion of palms with armed leaves in inundated forests (Inun; **Figures 2G,H**). Fruit size were evenly distributed between the forest types and most individuals had small fruits (<2.4 cm; **Figure 2I**). Most individuals (65%) had cryptic fruits.

Soil Gradients and Flooding Regime

The PCA summarizes the 12 environmental variables (11 soil variables) with two axes generated (**Figure 3**) explained 43 and 20%, respectively. PC1 described a gradient negatively related to pH, K^+, BS, Ca^{2+}, ECEC, and Mg^{2+}. The second axis (PC2) mainly described Al^{3+}, acidity, and Na^+ (**Table 2**). Essentially, PC1 is a fertility gradient and PC2 is an acidity gradient.

Palm Functional Trait-Environmental Variables Relationship

The palms that present both growth forms (acaulescent and erect) were positively correlated with pH, K^+, BS, Ca^{2+}, Mg^{2+} and negatively correlated with Al^{3+} and acidity. That is, on fertile soils there is a greater number of palms that have both acaulescent and erect growth forms, and in the same way the number of these palms decreases in soils with high Al^{3+}content. The cespitose life form (LF.ces) was also correlated with Na^+, which indicates that the cespitose palms increase their abundance in soils with high concentrations of this cation.

In relation to vegetative traits, we found that leaf blade length (BL) was positively correlated with ECEC. The positive correlation between armed leaves (LAr) and Na^+ indicates that the number of palms with armed leaves increases in soils with high sodium concentration. Presence of unarmed leaves (LAr.unar) were positively correlated with non-flooded forests (FT.nin).

Fruit size (FrL, FrW) was correlated with soil variables (**Figure 4**). Palms with large fruits are abundant in soils with high contents of K^+, BS, Ca^{2+}, ECEC, Mg^{2+} and in basic soils with high pH values. We found a negative correlation between the Al^{3+} in soil and fruit size (FrL, FrW) indicating that small-fruited palms are dominant in soils with low Al^{3+}concentration. In soils with a high content of P, most individuals had cryptic fruits (FrCo.cryp), with colors such as brown, black, green, blue, cream, gray, ivory, straw-colored, white, or purple.

DISCUSSION

The patterns found in our analysis shows a first approximation to the understanding of the environmental mechanisms that explain the distribution of palm species in the Amazon. The causal interpretation of the results that may not necessarily reflect underlying mechanisms that govern the distribution of species in the different soil types, and that it may be necessary to analyze other variables involved such as phylogeny and intraspecific variation of the species. However, we found a primary soil fertility gradient and a secondary Al^{3+} and acidity gradient (**Figure 3**) correlated to the functional traits. This pattern has been found in other studies (Fyllas et al., 2012; Liu et al., 2012). The gradient goes from the *terra firme* soils Ninu and white sand forests that are more sterile to the flooded forests with a high content of nutrients. Previous research has shown that plant traits vary predictably along soil gradients on a regional and global scale (Ordoñez et al., 2009). In general, the results show that palms with large leaves and fruits and acaulescent and erect growth forms are associated with fertile soils. In contrast, leaves and stems armed traits are associated with non-inundated environments (**Figure 5**). These results suggest that the functional traits of palms vary consistently along with the soil gradients on a regional scale and that this variation could be explained by the soil fertility and acidity plus Al^{3+}gradients, suggesting an environmental filter related to resource availability and stressful environments such as acid and high aluminum content soils. These results on a regional scale are reported here for the first time for palms and represent the basis for additional specific studies of the significant correlations found between morphological functional traits and soil variables, which permits the elucidation of underlying mechanisms of the structuring of palm communities in Amazonia, incorporating functional dimension of the biodiversity.

Previous studies have shown an increase in the values of foliar traits (leaf area and specific leaf area) on fertile

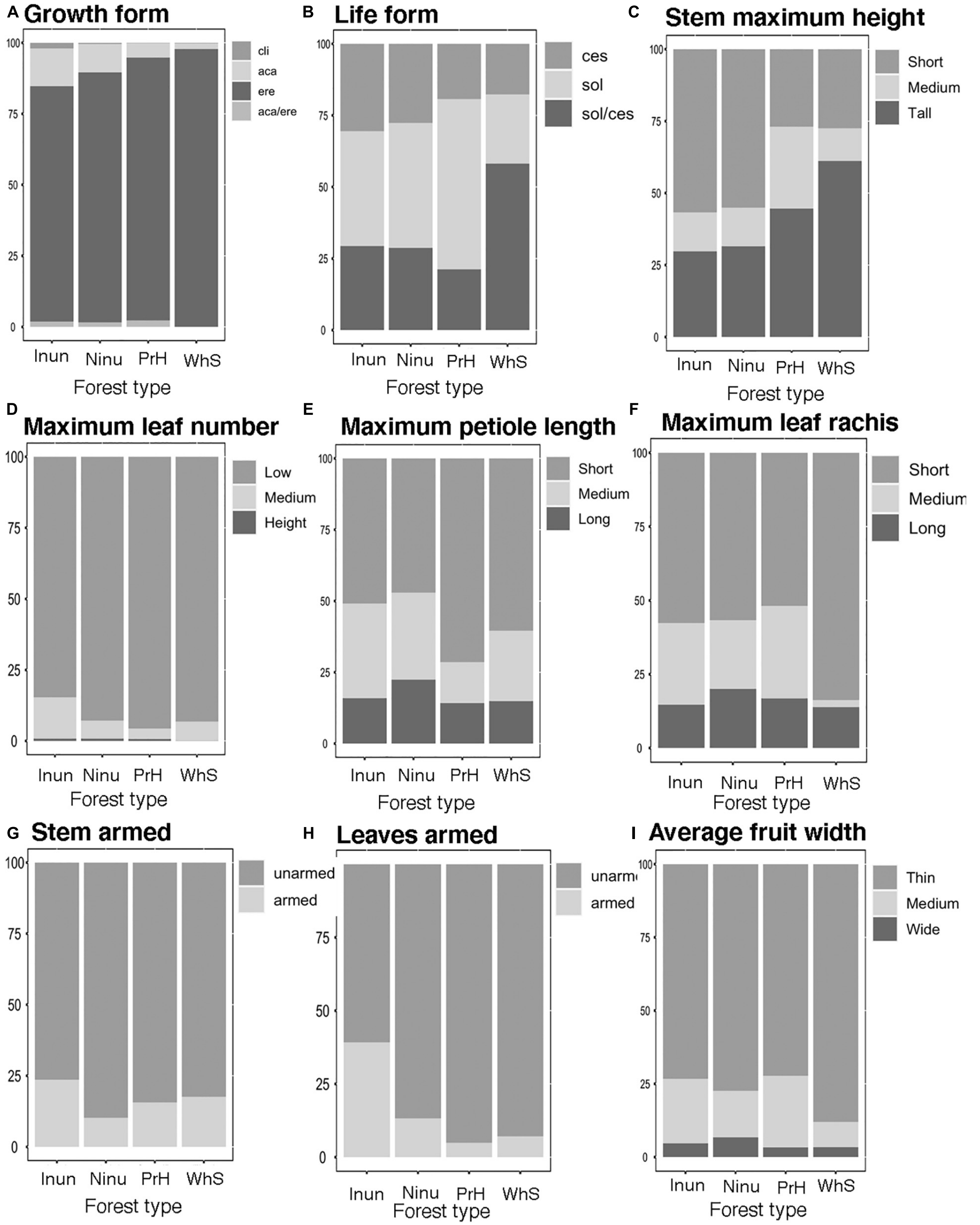


FIGURE 2 | Relative frequency distribution of functional traits in a palm community in inundated (Inun), non-inundated (Ninu), Premontane hills (PrH), and white sand (WhS) forest types along the west Amazonian. Growth forms: aca, acaulescent; ere, erect; aca/ere, both; cli, climbing. Life forms: sol, solitary; ces, cespitose; sol/ces, both. **(A)** Growth form, **(B)** Life form, **(C)** Stem maximum height, **(D)** Maximum leaf number, **(E)** Maximum petiole length, **(F)** Maximum leaf rachis, **(G)** Steam armed, **(H)** Leaves armed, and **(I)** Average fruit width.

TABLE 2 | Correlations between soil variables and the two axes generated from principal component analysis.

Variable	PC1	PC2
pH	**−0.358**	0.173
loi	−0.106	**−0.345**
Al^{3+}	0.205	**−0.453**
K^{+}	**−0.365**	−0.062
acidity	0.028	**−0.499**
BS	**−0.371**	0.228
Ca^{2+}	**−0.416**	0.022
Na^{+}	−0.184	**−0.321**
P	−0.172	−0.110
ECEC	**−0.334**	−0.309
Mg^{2+}	**−0.401**	−0.116

PC1, Axis 1; PC2, Axis 2.
Bold values are the highest correlations.

soils. The average leaf area of trees in tropical forests in Panama is related to the fertility and acidity of the soil (Liu et al., 2012). For palms, the specific leaf area (SLA) increased through a gradient of nutrient availability in the soil (Andersen et al., 2012). We found that leaf size (BL, RL) increases with Ca^{2+}, Mg^{2+}, and ECEC. Species with high leaf area and SLA values have relatively high photosynthetic and respiration rates, associated with an acquisitive strategy (Wright and Westoby, 2002; Cornelissen et al., 2003; Sterck et al., 2006).

The biotic factors that determine fruit size have been extensively studied, mainly under hypotheses of dispersal syndromes (Gautier-Hion et al., 1985) in which the presence and type of dispersers exert selective pressure on the fruit size. For palms, small-conspicuous fruits are dispersed by birds, and large-cryptic fruits are dispersed by large mammals (do Nascimento et al., 2020). We found, on a regional scale, a correlation of soil fertility with fruit size. Some studies of other angiosperms have shown a weak relationship between the fruit size and disperser availability. On the other hand, they demonstrated that abiotic factors such as light availability in the canopy are more strongly correlated with fruit size (Eriksson et al., 2000). It has been suggested that large seeds have less dispersal capacity and require suitable environments to germinate due to their low possibility of moving (do Nascimento et al., 2020). Producing large fruits and seeds is costly for the plant (Goheen et al., 2007), but large seeds often have a greater chance of germination (Galetti et al., 2013). In this sense, the functional dominance of large fruits in fertile soils, found in this study, can be explained in part by the requirement of the palms to find soils with abundant resources that allow them to compensate the dispersal limitations and the cost of producing large fruits.

Additionally, the PCA analysis shows a fertility gradient in which flooded forests have more fertile soils than non-flooded forests (**Figure 5**), showing an indirect association of both environmental variables. Some studies in *varzea* and *igapo* forests in central Amazonia have demonstrated that species with large seeds are adapted to areas with high levels of flooding by promoting rapid seedling establishment (Parolin et al., 2003). Other studies have found contrasting results where species with large seeds are abundant in less fertile soils (Liu et al., 2012). These results are adapted to the hypothesis that suggests that species with low values of seed mass are expected to be located in soils with low nutrient levels (Liu et al., 2012). In low resource environments, large seeds could provide more reserves for individuals early in their life cycle. Small seeds have the potential advantage of greater dispersal ability and rapid growth in high-resource environments (Westoby et al., 1996). Additional studies of palms are necessary to evaluate alternative mechanisms in this regard.

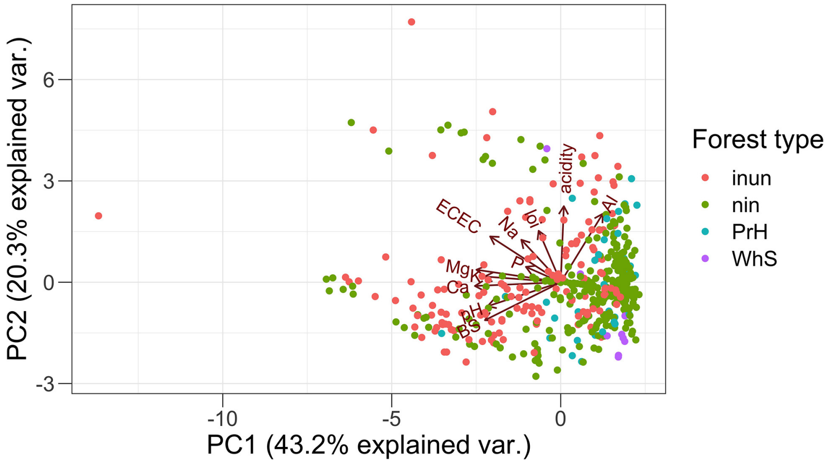
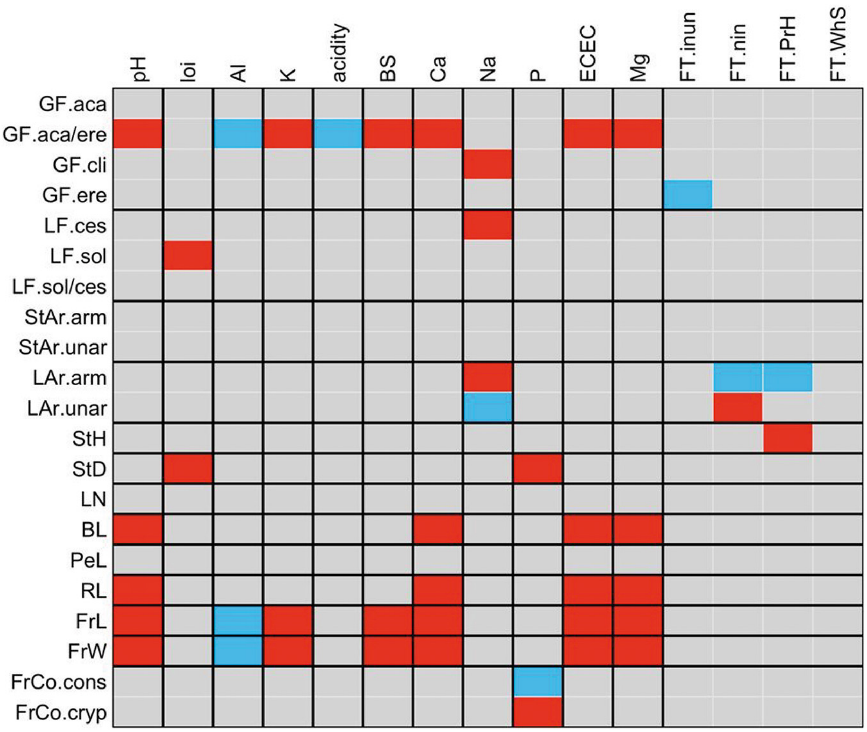


FIGURE 3 | PCA of environmental variables in the 458 transects in western Amazonia. *local environmental variables*: inun, inundated forest; nin, non-inundated forest; PrH, premontane hills; and WhS, white sand forest. *Soil variables*: pH, loi, loss-on-ignition; Al, aluminum concentration; K, Potassium concentration; acidity, exchangeable acidity; BS, base saturation; Ca, Calcium concentration; Na, Sodium concentration; P, Phosphorus concentration; ECEC, effective cation exchange capacity; and Mg, Magnesium concentration.



	pH	loi	Al	K	acidity	BS	Ca	Na	P	ECEC	Mg	FT.inun	FT.nin	FT.PrH	FT.WhS
GF.aca															
GF.aca/ere	🟥		🟦	🟥	🟦	🟥	🟥			🟥	🟥				
GF.cli								🟥							
GF.ere												🟦			
LF.ces								🟥							
LF.sol		🟥													
LF.sol/ces															
StAr.arm															
StAr.unar															
LAr.arm								🟥					🟦	🟦	
LAr.unar								🟦					🟥		
StH														🟥	
StD		🟥							🟥						
LN															
BL	🟥						🟥			🟥	🟥				
PeL															
RL	🟥						🟥			🟥	🟥				
FrL	🟥		🟦	🟥		🟥	🟥			🟥	🟥				
FrW	🟥		🟦	🟥		🟥	🟥			🟥	🟥				
FrCo.cons									🟦						
FrCo.cryp									🟥						

FIGURE 4 | Fourth-corner analysis carried out for functional traits of palm and environmental variables. Colored squares show significant correlations ($P < 0.05$) measured by a Pearson correlation coefficient for two quantitative variables, by a Pearson χ^2 and G statistic for two qualitative variables and by a Pseudo-*F* and Pearson r for one quantitative variable and one qualitative variable. Red, positive correlation and blue, negative correlation. *local environmental variables*; FT.inun, inundated forest; FT.nin, non-inundated forest; FT.PrH, premontane hills and FT. WhS, white sand forest. *Soil variables*: pH, loi, loss-on-ignition; Al, aluminum concentration; K, Potassium concentration; acidity, exchangeable acidity; BS, base saturation; Ca, Calcium concentration; Na, Sodium concentration; P, Phosphorus concentration; ECEC, effective cation exchange capacity, and Mg, Magnesium concentration.

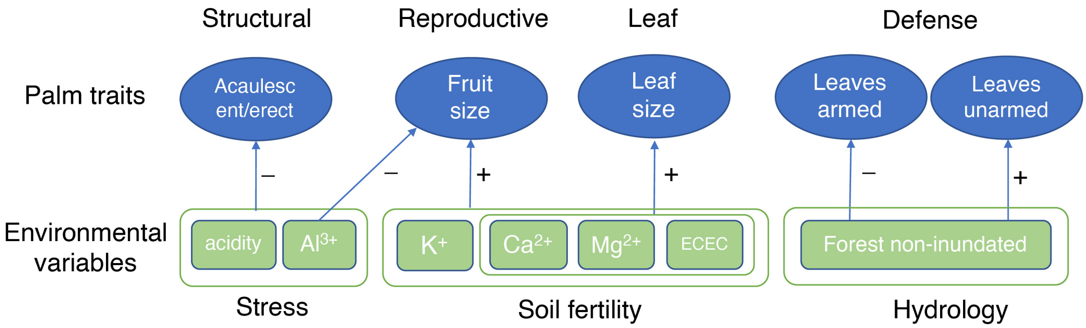


FIGURE 5 | Summary of the palm traits-environment correlations for the 116 palm species present in western Amazonia.

Hydrology has been reported to be a driver of community composition and distribution of palm species only on a local scale and not on a regional scale (Eiserhardt et al., 2011). In this work, we found that the functional composition, at least in growth form, is also scale-dependent since we did not find a correlation between the acaulescent growth form and flooding forest when using all our data from western Amazonia. However, when analyzing subregions separately, we found that the acaulescent growth form was significantly correlated with *terra firme* forests in Brazil and Guaviare. That is, the acaulescent palms are abundant on *terra firme* and absent in flooded forests. Tall palm is a functional response to prevent leaves and leaf buds from becoming submerged, making survival and growth in flooded zones possible. Therefore, it is an evasion strategy to avoid anoxic effects caused by water (Garssen et al., 2015). Spatial scale is central to geographical ecology (Levin, 1992) because patterns and processes in ecological systems are scale-dependent (Pearson and Dawson, 2003) this may influence patterns and underlying drivers of species diversity. Previous studies have found that the inundation regime is an essential determinant of palm species richness on a landscape scale, at least in the presence of sizeable hydrological variation, as is the case in Amazonia. However, it is obvious that in PrH, the inundation regimens were different because the topography is more pronounced.

Regarding defense traits, the presence of spines is a conspicuous feature of many palm species in western Amazonia. The presence, type, size, and density of spines play a role in anti-herbivore defense, which may act against different potential herbivores, mostly vertebrates (Cornelissen et al., 2003). It is possible that armed palms are not an ecological response to flooding, as there is no evidence that herbivory increases in flooded areas. One possible explanation is that large fruits and defensive structures evolved simultaneously because large frugivores such as the extinct megafauna, in addition to consuming fruits and dispersing seeds, could also have consumed leaves and damaged plants (do Nascimento et al., 2020). Producing spines constitutes resource allocation costs to plants (Goheen et al., 2007), whereby resources that otherwise would be devoted to growth or reproduction are used to produce defensive structures. In this sense, it appears reasonable to suggest that because floodplain forests are more fertile than *terra firme*, palms prefer environments with high amounts of nutrients in the soil that allow them to compensate for the expense invested in defense structures. Additional research to elucidate this correlation and reveal alternative mechanisms of these functional groups would be pertinent to show the structuring of communities on a regional scale.

CONCLUSION

Life form, fruit size, and leaf size were positively correlated with soil fertility. Defense traits (armed leaves and stems) were correlated with hydrology (non-inundated forests). This suggests that the functional traits of palms vary consistently along soil gradients on a regional scale and that this variation could be explained by the soil fertility and acidity + aluminum gradients, suggesting environmental filters related to resource availability and stressful environments.

In this study, it is reported for first time for palms that, as well as the composition and distribution of species, the functional composition is scale-dependent and that possibly some traits such as growth form respond differently on a local scale than on a regional scale. Likewise, large leaves of palms on fertile soils mean a competitive strategy that confers a competitive advantage to maximize growth. Large fruits in fertile soils do not suggest a conservative strategy and instead, the results may be due to large fruits having less dispersal capacity and requiring suitable environments to germinate. Because the production of spines constitutes resource allocation costs to plants, palms prefer environments with high amounts of nutrients in the soil that allow them to compensate for the expense invested in defense structures. The results found here, enhance the need to deepen the study of morphological and physiological aspects of palms, in such a way that a greater understanding of their response to the complexity and environmental variability in the Amazon will be achieved.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://doi.org/10.1002/ecy.2841.

AUTHOR CONTRIBUTIONS

HB collected the data. WT, CR-R, and HB contributed to conception and design of the study and wrote sections of the manuscript. WT organized the database and wrote the first draft of the manuscript. WT and CR-R performed the statistical analysis. All authors contributed to manuscript revision, read, and approved the submitted version.

FUNDING

Funding was received Danish Council for Independent Research – Natural Sciences (grants #4181–00158 and #9040-00136B to HB).

REFERENCES

Andersen, K. M., Endara, M. J., Turner, B. L., and Dalling, J. W. (2012). Trait-based community assembly of understory palms along a soil nutrient gradient in a lower montane tropical forest. *Oecologia* 168, 519–531. doi: 10.1007/s00442-011-2112-z

Andersen, K. M., Turner, B. L., and Dalling, J. W. (2010). Soil-based habitat partitioning in understorey palms in lower montane tropical forests. *J. Biogeogr.* 37, 278–292. doi: 10.1111/j.1365-2699.2009.02192.x

Balslev, H., Kristiansen, S. M., and Muscarella, R. (2019). Palm community transects and soil properties in western Amazonia. *Ecology* 100:e02841. doi: 10.1002/ecy.2841

Baribault, T. W., Kobe, R. K., and Finley, A. O. (2012). Tropical tree growth is correlated with soil phosphorus, potassium, and calcium, though not for legumes. *Ecol. Monogr.* 82, 189–203. doi: 10.1890/11-1013.1

Borchsenius, F., and Bernal, R. (1996). *Aiphanes (Palmae)*. New York: The New York Botanical Garden.

Cámara, R., Tuomisto, H., Ruokolainen, K., Balslev, H., and Munch Kristiansen, S. (2017). Modelling responses of western Amazonian palms to soil nutrients. *J. Ecol* .105, 367–381. doi: 10.1111/1365-2745.12708

Clark, D. A., Clark, D. B., Sandoval, R., and Castro, M. (1995). Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. *Ecology* 76, 2581–2594. doi: 10.2307/2265829

Condit, R., Engelbrecht, B. M., Pino, D., Pérez, R., and Turner, B. L. (2013). Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *PNAS* 110, 5064–5068. doi: 10.1073/pnas.1218042110

R Core Team. (2016). *R: a Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Cornelissen, J. H., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D. E., et al. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51, 335–380. doi: 10.1071/BT02124

De Deyn, G. B., Cornelissen, J. H. C., and Bardgett, R. D. (2008). Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecol. Lett.* 11, 516–531. doi: 10.1111/j.1461-0248.2008.01164.x

Díaz, S., Kattge, J., Cornelissen, J. H., Wright, I. J., Lavorel, S., Dray, S., et al. (2016). The global spectrum of plant form and function. *Nature* 529, 167–171. doi: 10.1038/nature16489

do Nascimento, L. F., Guimarães, P. R., Onstein, R. E., Kissling, W. D., and Pires, M. M. (2020). Associated evolution of fruit size, fruit colour and spines in Neotropical palms. *J. Evol. Biol.* 33, 858–868. doi: 10.1111/jeb.13619

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S., et al. (2014). Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95, 14–21. doi: 10.1890/13-0196.1

Dray, S., and Dufour, A. B. (2007). The ade4 package: implementing the duality diagram for ecologists. *J. Stat. Softw.* 22, 1–20.

Eiserhardt, W. L., Svenning, J. C., Borchsenius, F., Kristiansen, T., and Balslev, H. (2013). Separating environmental and geographical determinants of phylogenetic community structure in Amazonian palms (Arecaceae). *Bot. J. Linn. Soc.* 17, 244–259. doi: 10.1111/j.1095-8339.2012.01276.x

Eiserhardt, W. L., Svenning, J. C., Kissling, W. D., and Balslev, H. (2011). Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Ann. Bot.* 108, 1391–1416. doi: 10.1093/aob/mcr146

Eriksson, O., Friis, E. M., and Löfgren, P. (2000). Seed size, fruit size, and dispersal systems in angiosperms from the Early Cretaceous to the Late Tertiary. *Amer. Natural.* 156, 47–58. doi: 10.1086/303367

Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K., et al. (2009). Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. *Ecology* 90, 598–611. doi: 10.1890/08-0418.1

Fyllas, N. M., Quesada, C. A., and Lloyd, J. (2012). Deriving plant functional types for Amazonian forests for use in vegetation dynamics models. *Perspect. Plant Ecol. Evol. Syst.* 14, 97–110. doi: 10.1016/j.ppees.2011.11.001

Galeano, G., and Bernal, R. (2010). *Palmas de Colombia: guía de Campo*. Bogotá: Universidad Nacional de Colombia.

Galetti, M., Guevara, R., Cortes, M. C., Fadini, R., Von Matter, S., Leite, A. B., et al. (2013). Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* 340, 1086–1090. doi: 10.1126/science.1233774

Garssen, A. G., Baattrup-Pedersen, A., Voesenek, L. A., Verhoeven, J. T., and Soons, M. B. (2015). Riparian plant community responses to increased flooding: a meta-analysis. *Glob. Change Biol.* 21, 2881–2890. doi: 10.1111/gcb.12921

Gautier-Hion, A., Duplantier, J. M., Quris, R., Feer, F., Sourd, C., Decoux, J. P., et al. (1985). Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65, 324–337.

Goheen, J. R., Young, T. P., Keesing, F., and Palmer, T. M. (2007). Consequences of herbivory by native ungulates for the reproduction of a savanna tree. *J. Ecol.* 95, 129–138. doi: 10.1111/j.1365-2745.2006.01196.x

Grigulis, K., Lavorel, S., Krainer, U., Legay, N., Baxendale, C., Dumont, M., et al. (2013). Relative contributions of plant traits and soil microbial properties to mountain grassland ecosystem services. *J. Ecol.* 101, 47–57. doi: 10.1111/1365-2745.12014

Henderson, A. (2000). *Bactris (Palmae)*. New York: The New York Botanical Garden.

Jordano, P. (2000). "Fruits and frugivory" in *Seeds: the Ecology of Regeneration in Plant Communities*, . ed. M. Fenner UK: Commonwealth Agricultural Bureau International. 125–166.

Kahn, F., and Ferreira, E. J. L. (1995). A new species of Astrocaryum (Palmae) from Acre, Brazil. *Candollea* 50, 321–328.

Kahn, F., and Millán, B. (2013). *Las Palmeras Huicungo*. Perú: Universidad Mayor de San Marcos.

Keddy, P. A. (1992). Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* 3, 157–164. doi: 10.2307/3235676

Kissling, W. D., Balslev, H., Baker, W. J., Dransfield, J., Göldel, B., Lim, J. Y., et al. (2019). PalmTraits 1.0, a species-level functional trait database of palms worldwide. *Sci. Data* 6, 1–13. doi: 10.1038/s41597-019-0189-0

Kristiansen, T., Svenning, J. C., Pedersen, D., Eiserhardt, W. L., Grández, C., and Balslev, H. (2011). Local and regional palm (Arecaceae) species richness patterns and their cross-scale determinants in the western Amazon. *J. Ecol.* 99, 1001–1015. doi: 10.1111/j.1365-2745.2011.01834.x

Laughlin, D. C., Richardson, S. J., Wright, E. F., and Bellingham, P. J. (2015). Environmental filtering and positive plant litter feedback simultaneously explain correlations between leaf traits and soil fertility. *Ecosystems* 18, 1269–1280. doi: 10.1007/s10021-015-9899-0

Lavorel, S., and Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16, 545–556. doi: 10.1046/j.1365-2435.2002.00664.x

Legay, N., Baxendale, C., Grigulis, K., Krainer, U., Kastl, E., Schloter, M., et al. (2014). Contribution of above- and below-ground plant traits to the structure and function of grassland soil microbial communities. *Ann. Bot.* 114, 1011–1021. doi: 10.1093/aob/mcu169

Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology**,. 73, 1943–1967.

Liu, X., Swenson, N. G., Wright, S. J., Zhang, L., Song, K., Du, Y., et al. (2012). Covariation in plant functional traits and soil fertility within two species-rich forests. *PLoS One* 7:e34767. doi: 10.1371/journal.pone.0034767

Maire, V., Wright, I. J., Prentice, I. C., Batjes, N. H., Bhaskar, R., Bodegom, P. M., et al. (2015). Global effects of soil and climate on leaf photosynthetic traits and rates. *Glob. Ecol Biogeogr.* 24, 706–717. doi: 10.1111/geb.12296

Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., et al. (2009). Global patterns in plant height. *J. Ecol.* 97, 923–932. doi: 10.1111/j.1365-2745.2009.01526.x

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., et al. (2013). Package 'vegan'. *Community Ecol.* 2, 1–295.

Ordoñez, J. C., Van Bodegom, P. M., Witte, J. P., Wright, I. J., Reich, P. B., and Aerts, R. (2009). A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Glob. Ecol. Biogeogr.* 18, 137–149. doi: 10.1111/j.1466-8238.2008.00441.x

Parolin, P., Ferreira, L., and Junk, W. (2003). Germination characteristics and establishment of trees from Central Amazonian flood plains. *Trop. Ecol.* 44, 155–168.

Pearson, R. G., and Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* 12, 361–371. doi: 10.1046/j.1466-822X.2003.00042.x

Phillips, O. L., Vargas, P. N., Monteagudo, A. L., Cruz, A. P., Zans, M. E., Sánchez, W. G., et al. (2003). Habitat association among Amazonian tree species: a landscape-scale approach. *J. Ecol.* 91, 757–775. doi: 10.1046/j.1365-2745.2003.00815.x

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *J. Ecol.* 102, 275–301. doi: 10.1111/1365-2745.12211

Silman, M. R. (2007). "Plant species diversity in Amazonian forests" in *Tropical Rainforest Responses to Climatic Change**,. eds M. B. Bush and J. R. Flenley Germany: Springer. 269–294.

Sombroek, W. (2000). Amazon landforms and soils in relation to biological diversity. *Acta Amaz.* 30, 81–100. doi: 10.1590/1809-43922000301100

Sterck, F. J., Poorter, L., and Schieving, F. (2006). Leaf traits determine the growthsurvival trade-off across rain forest tree species. *Am. Nat.* 167, 758–765. doi: 10.1086/503056

Tuomisto, H., Ruokolainen, K., Aguilar, M., and Sarmiento, A. (2003a). Floristic patterns along a 43-km long transect in an Amazonian rain forest. *J. Ecol.* 91, 743–756. doi: 10.1046/j.1365-2745.2003.00802.x

Tuomisto, H., Ruokolainen, K., and Yli-Halla, M. (2003b). Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299, 241–244. doi: 10.1126/science.1078037

Van der Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., et al. (2013). Plant–soil feedbacks: the past, the present and future challenges. *J. Ecol.* 101, 265–276. doi: 10.1111/1365-2745.12054

Vitousek, P. M. (1984). Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65, 285–298. doi: 10.2307/1939481

Vormisto, J., Tuomisto, H., and Oksanen, J. (2004). Palm distribution patterns in Amazonian rainforests: what is the role of topographic variation? *J. Veg. Sci.* 15, 485–494. doi: 10.1111/j.1654-1103.2004.tb02287.x

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199, 213–227.

Westoby, M., Leishman, M., and Lord, J. (1996). Comparative ecology of seed size and dispersal. *Phil. Trans. R. Soc. Lond. B* 351, 1309–1317. doi: 10.1098/rstb.1996.0114

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

Wright, I. J., and Westoby, M. (2002). Leaves at low versus high rainfall: coordination of structure, lifespan and physiology. *N. Phytol.* 155, 403–416. doi: 10.1046/j.1469-8137.2002.00479.x

Xi, N., Adler, P. B., Chen, D., Wu, H., Catford, J. A., van Bodegom, P. M., et al. (2021). Relationships between plant-soil feedbacks and functional traits. *J. Ecol.* 104, 1608–1617. doi: 10.1111/1365-2745.13731

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

frontiers
in Forests and Global Change

ORIGINAL RESEARCH
published: 28 September 2021
doi: 10.3389/ffgc.2021.711414

Global *ex situ* Conservation of Palms: Living Treasures for Research and Education

***M. Patrick Griffith*[1]*, *Abby Meyer*[2] *and Ayress Grinage*[3]**

[1] *Montgomery Botanical Center, Coral Gables, FL, United States,* [2] *Botanic Gardens Conservation International US, San Marino, CA, United States,* [3] *LH Bailey Hortorium, Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, NY, United States*

Under the old taxon Principes, palms were once the Princes of the Kingdom Plantae. First on Engler's list, they occupy a cherished place to botanists, and remain treasured centerpieces of many gardens. In turn, botanic gardens have put forward a decades-long effort to conserve these widely admired plants, keeping a number of palm species from extinction. Living palm collections also have critical value for comparative ecological studies. In this paper we highlight successful *ex situ* conservation programs for palms, review how the promising new field of collections genetics can guide *ex situ* conservation of palms, conduct a family-wide gap analysis for living collections in the Arecaceae, and provide an in-depth case study of *ex situ* conservation of the genus *Sabal*. These analyses highlight ways in which gardens can advance palm conservation following four recommendations: *collect, cultivate, communicate,* and *collaborate.*

Keywords: Arecaceae, curation, gap analysis, living collection, metacollection

OPEN ACCESS

Edited by:
Silvia Alvarez-Clare,
Morton Arboretum, United States

Reviewed by:
Gerardo Avalos,
University of Costa Rica, Costa Rica
Rafael Acuña Castillo,
University of Costa Rica, Costa Rica

Correspondence:
M. Patrick Griffith
patrick@montgomerybotanical.org

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

Received: *18 May 2021*
Accepted: *13 August 2021*
Published: *28 September 2021*

Citation:
Griffith MP, Meyer A and Grinage A (2021) Global ex situ Conservation of Palms: Living Treasures for Research and Education. Front. For. Glob. Change 4:711414. doi: 10.3389/ffgc.2021.711414

INTRODUCTION

In one of the earliest global florae, Engler (1889) designated the palms as the only family in the Order Principes, meaning "the first." Through his coronation of Palmae (Arecaceae) as the princes of Kingdom Plantae, Engler reveals his own love for these cherished plants. Engler also brought together a fantastic palm collection at Botanic Garden and Botanical Museum Berlin-Dahlem, where he directed construction of their great Palm House. But Engler was certainly not alone in this regard—the Palm House was a potent status symbol in Victorian Britain, requiring not only expensive craftsmanship but also constant heat to protect these tropical gems throughout the year. Dedicated cultivation of these plants goes back much further, though (**Figure 1**). Representations of date palms (*Phoenix dactylifera* L.) and doum palms (*Hyphaene thebaica* Mart.)—ornamentally grown, not depicted as crops—date to 1450 BC in Thebes (Janick, 2002). The appreciation continues to our own era, with palms widely grown at civic landscapes and private gardens. At botanic gardens, palms remain a celebrated landscape feature that define spaces, frame vistas and evoke a tropical feel (Carricarte, 2021; **Figure 2**).

Beyond the unrivaled aesthetic value of palms in these gardens, the utility of these living collections for scientific study is also vital. Many studies of comparative ecology have been facilitated by botanic garden palm collections (Tomlinson, 1979), as these collections bring a diversity of species into parallel cultivation. The robust and diverse holdings of botanic gardens make them well suited for studies of functional ecology (Perez et al., 2019). For example, abiotic

FIGURE 1 | Ornamental palms recorded in ca. 1450 BC. Detail from *Deceased Being Towed in a Boat, Tomb of Rekhmire;* facsimile by Nina de Garis Davies. This scene shows *Phoenix dactylifera* and *Hyphaene thebaica* planted in an ornamental garden, perhaps the earliest known depiction of horticultural cultivation of palms.

FIGURE 2 | A modern palm collection: Lowland Palmetum at the Montgomery Botanical Center, Florida, United States. While arranged and appreciated for aesthetics, these documented living collections also represent a rich resource for scientific study: between 2016 and 2020, 171 known publications made use of the plant resources at Montgomery.

natural selection for cyclone tolerance has been studied via differential morphology and mortality among palm collections (Griffith et al., 2008, 2013), relying on detailed records of provenance and taxonomy. Indeed, one of the best aspects of living palm collections is reliable taxonomy, as such collections are often used for systematics research and in some cases can even be associated with type specimens (Crane et al., 2009). A potential concern with using *ex situ* palm collections may be limited sampling (Pérez-Harguindeguy et al., 2013). This is increasingly a less relevant concern as gardens move from synoptic collections toward collections designed for genetic breadth (Oldfield, 2009). In many cases botanic gardens can provide more geolocated and taxonomically verified species than are available in field plots (Perez et al., 2019), making such collections especially useful for functional ecology studies. Realizing and activating the research value of the more passive palm collections in gardens would provide further resources for such studies.

Ex situ Conservation of Palms

Ex situ collections are well-established as an essential aspect of integrated plant conservation planning to help conserve plant species (Convention on Biological Diversity, 2020). Palms provide an apt model to illustrate the vital importance of living collections. For example, fewer than 25 *Attalea crassispatha* Burret survive in southern Haiti, but *ex situ* collections augment these numbers (Johnson, 1998). Seeds of these palms are eaten, limiting seedling recruitment. *Copernicia fallaensis* León is limited to 84 extant mature palms near Falla, Cuba, where it is overexploited for thatching (Verdecia, 2015). Establishment of a nearby *ex situ* collection of 50 plants helps to ensure its survival (Verdecia, 2015; Hodel et al., 2016). An extreme example is *Pritchardia aylmer-robinsonii* H. St. John, limited to 2 *in situ* plants on Niihau, which have not been observed to set seed for many years (Chapin et al., 2004). Thankfully, specimens growing in over 30 gardens have set seed (Chapin, 2005).

In addition, a number of palm species are fully extirpated from the wild, and survive only in cultivation. *Corypha taliera* Roxb., once native to Bangladesh and India, saw its last wild individual felled by mistake in 1979 (Johnson, 1998), but is known from at least 6 botanic gardens (Botanic Gardens Conservation International (BGCI), 2020). *Hyophorbe amaricaulis* Mart. survives as a single individual palm at Curepipe Botanical Gardens, Mauritius (Ludwig et al., 2010). *Sabal miamiensis* Zona was once known from Southeastern Florida, and now only survives in 5 *ex situ* collections (see below).

The examples above are also augmented by successes in restoration plantings derived from *ex situ* collections. *Pseudophoenix sargentii* H. Wendl. collections produced seedlings that have successfully augmented wild populations (Fotinos et al., 2015). *Nypa fruticans* Wurmb., a species widely used for thatching, has been used as restoration plantings in reclaimed agricultural areas (Bamroongrugsa et al., 2008). Research on seed collections of *Pritchardia remota* Becc. has provided guidance on breaking dormancy to better establish outplants for restoration on Nihoa (Pérez et al., 2008). All of these examples illustrate the great potential of *ex situ* collections to help secure survival of wild palm species.

While some palms can be propagated via *in vitro* tissue culture (Wang et al., 2003) or conventional vegetative propagation (Devanand and Chao, 2003), many threatened palms are in fact “exceptional species” sensu Pence (2013), and thereby require seed-grown living garden collections as *ex situ* safeguards, as the seeds do not survive conventional seedbanking storage (e.g., Porto et al., 2018). Advancements to *in vitro* propagation of threatened palms would help immensely, especially in the case of *Hyophorbe amaricaulis* mentioned above. Beyond such extreme cases, general research into the reproduction of palms in collections (e.g., Valdes et al., 2021; Tucker Lima et al., 2021) can inform how to functionally increase low census numbers within threatened *in situ* populations also.

Collections Genetics of Palms

Genetic analysis of *in situ* palm populations is a well-established tool for informing conservation actions. Many population genetic questions have been explored in Arecaceae, providing a robust background for conservation strategies. For example, Shapcott (1998) showed low genetic variation in the rare *Ptychosperma bleeseri* Burret, highlighting the threat of genetic swamping via ornamental palm production. In another example Bacon and Bailey (2006) demonstrated how accurate taxonomic circumscription advances palm conservation, using population genetics of *Chamaedorea alternans* H. Wendl.

Recent attention to the genetics of *ex situ* collections of palms has offered unique insight into how best to manage these resources for conservation benefit. An early pan-African survey of *ex situ* collections of *Elaeis guineensis* Jacq. (African Oil Palm; Hayati et al., 2004) examined polymorphism in this important genetic resource. Examination of the genetic variation held in a collection of *Leucothrinax morrisii* (H. Wendl.) C. Lewis and Zona (Namoff et al., 2010) demonstrated the value of maintaining multiple individuals from each palm population in cultivation. This work was followed by studies of how well garden palm collections represent variation in the wild, or how well these collections can help with restoration efforts. Asmussen-Lange et al. (2011) showed that collections of *Hyophorbe lagenicaulis* (L. H. Bailey) H. E. Moore can help to augment the eroded genetic diversity of the small, relict *in situ* population; as this very popular ornamental species is kept in at least 84 collections worldwide (Botanic Gardens Conservation International (BGCI), 2020), the potential for securing its survival is great. *Ceroxylon quindiuense* (H. Karst.) H. Wendl. is another spectacular, highly charismatic plant holding the record as the world’s tallest palm species. Comparing *C. quindiuense* populations with neighboring *ex situ* collections showed that diversity in collections was not as great as in the wild, and that careful selection among *ex situ* collections is critical for restoration efforts (Chacón-Vargas et al., 2020).

Another cherished charismatic megafloral palm, *Pseudophoenix ekmanii* Burret, provided a model to examine how combined holdings from multiple sites (i.e., “metacollections” sensu Griffith et al., 2019a) represented *in situ* diversity. It was found that pooled collections from more than one garden captured more genetic diversity than a single-garden collection, and captured it more efficiently (Griffith et al., 2020). Study of its sister species (*P. sargentii*) showed that tailored collection protocols for small and large populations should be considered, and that emphasis on maximizing maternal lines in a collection captures genetic diversity most efficiently (Griffith et al., 2021). Furthermore, comparing *P. sargentii* and *P. ekmanii* among non-palm species showed that taxonomic closeness does not predict genetic capture in *ex situ* collections (Hoban et al., 2020). This area of work shows great promise and potential for palm conservation collections. Further studies are underway at several labs and will help illustrate best practices for developing the most representative collections.

Ex situ Gap Analysis of Palms

With all of the above reasons to cultivate and protect palms in networked botanic garden metacollections, it is important to grasp the broader, overall scope of what currently exists in *ex situ* living collections. Botanic gardens are museums of living collections, and initial intellectual control (i.e., cataloging) is an essential part of museum and garden management. Knowledge of holdings facilitates access and use of these living treasures (Perez et al., 2019) for research, conservation, education and aesthetic purposes. Thus, we seek to define and measure how thoroughly botanic garden collections represent the world's extant palm diversity.

MATERIALS AND METHODS

Records on *ex situ* palm holdings were obtained from BGCI PlantSearch (Botanic Gardens Conservation International (BGCI), 2020) on 25 September 2020. This dataset encompassed all palms recorded as present in living collections globally, and included taxonomy, site, and institution type (e.g., botanic garden, zoo, seed bank, gene bank, etc.) The raw data included 16,313 records of palm taxa held at a total of 523 sites, all self-reported to BGCI from participating botanic gardens and similar organizations.

First, these data were limited in scope to *ex situ* living sporophyte collections, i.e., excluding seed banks, tissue banks, networks which potentially duplicate records from other gardens, and observance data from the ornamental horticulture trade (e.g., Imada et al., 1989). This parsing left a total of 15,723 records. Then, garden hybrids (5 records) were removed, however, naturally occurring hybrids (e.g., *Syagrus* × *costae* Glassman) were retained.

Finally, these 15,718 records were reconciled against the World Checklist of Arecaceae (Govaerts et al., 2020). This continuously updated online resource supercedes the World Checklist of Palms (Govaerts and Dransfield, 2005), both of which have long provided vital, stable consensus taxonomy for this family with so many active researchers worldwide. This reconciliation removed unplaced names from older literature (e.g., *Sabal ghiesbrechtii* R. Pfister), corrected orthographic variants (e.g., "*Sabal japa*" = *Sabal yapa* C. Wright ex Becc.) and synonymized all records in accordance with Govaerts et al. (2020). Taxonomic reconciliation with the world checklist and removal of any subsequent duplicate records at each garden left a total of 14,779 records.

We also selected the genus *Sabal* for a more focused case study which also considered *in situ* threat level. We chose *Sabal* based on the experience and expertise of the authors. Methods for this case study were similar to the above, with exceptions noted below. BGCI PlantSearch contained 730 records of *Sabal* as of 25 September 2020. After excluding seed banks, checklists, and networks (as above), 699 records remained. We reconciled these records with Govaerts et al. (2020) as above, but with two exceptions: we chose to recognize *Sabal guatemalensis* Becc. and *S. miamiensis* as accepted species. *Sabal guatemalensis* is known from Guatemala, Southern Mexico, and Belize, and has sometimes been synonymized with *S. mexicana* Mart., a much more widespread species that (sensu lato) occurs from Texas to Central America. It is important to note that even though *S. guatemalensis* and *S. mexicana* look similar, they are not resolved as sister species in recent phylogenetic analysis (Heyduk et al., 2016). *Sabal miamiensis* was previously known from Broward County and Miami-Dade County, Florida, United States, but is sometimes synonymized with *S. etonia* Swingle, a species more widely distributed in Florida. Based on the phylogenetic analyses of Heyduk et al. (2016) and Cano et al. (2018), and the gene conflict analysis of Grinage et al. (2021), there is extensive gene conflict at the node leading to *S. miamiensis* and *S. etonia*, and we believe that further work with the advent of genomic data is necessary to more conclusively resolve the status of *S. miamiensis*. For these reasons and our familiarity with these species in the field and in collections, we are of the opinion that *S. guatemalensis* and *S. miamiensis* are each distinct taxa, and they are treated as such in multiple collections.

Four records in the dataset were unplaced names (published in 1853 and 1892), and 12 records were not validly published and appeared to be horticultural appellations (e.g., *S. macrophylla*). All of these 16 records were at older, European gardens, suggesting perhaps collection and "naming" prior to the wide establishment of modern taxonomic convention. Ninety of the remaining records were either synonyms or orthographic variants. For example one site self-reported 4 species all assigned to *Sabal bermudana* L. H. Bailey. After resolving synonymy and spelling, 634 records of *Sabal* remained.

IUCN Red List category was obtained from official sources (IUCN, 2020) for those palms with formal assessments published. For a number of *Sabal* spp. that are not formally listed we either reviewed literature for provisional assessments (e.g., Zona et al., 2007), reviewed literature for conservation information to provide our own provisional assessment (e.g., Paiz and Stuardo, 1999 for *S. guatemalensis*), and provided our own primary information from current ongoing fieldwork (e.g., Grinage pers. obs., Noblick pers. obs. for *S. miamiensis*).

RESULTS

The Global Palm Metacollection

Botanic gardens hold 1,380 of the world's recognized wild palm taxa (out of 2,566 per Govaerts et al., 2020), in 178 of the 184 recognized genera (**Figure 3**), kept at 477 unique sites around the world (**Table 1** and **Figure 4**; Botanic Gardens Conservation International (BGCI), 2020). Many sites (83) hold a single palm species in cultivation, and the largest number of species held at a single site is 863 (Nong Nooch Tropical Botanic Garden, Thailand; NNTBG). The median number of palm species at gardens with palms is 8, while the mean is 31, showing a large skew in distribution toward a few large gardens in the

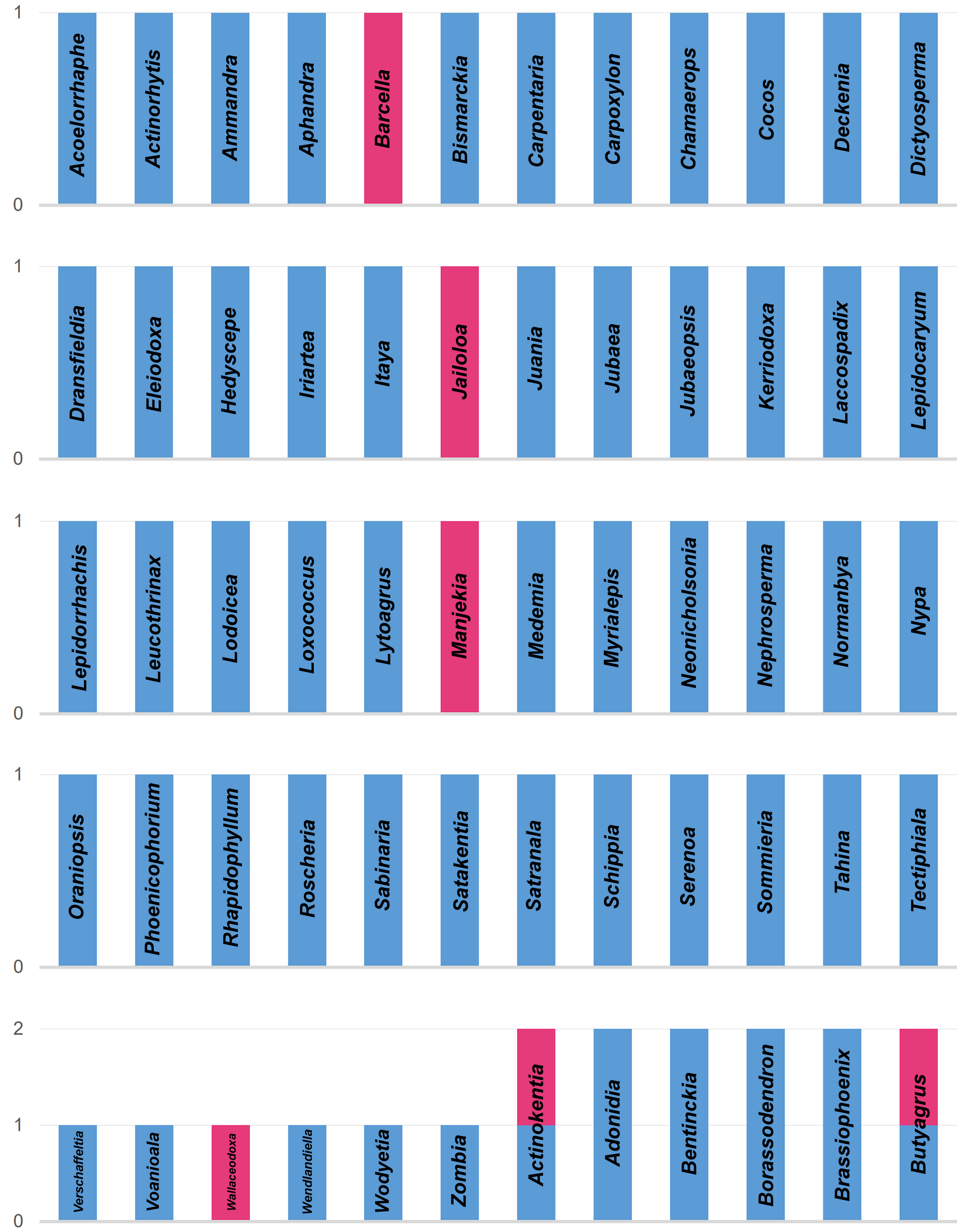


FIGURE 3 | (Continued)

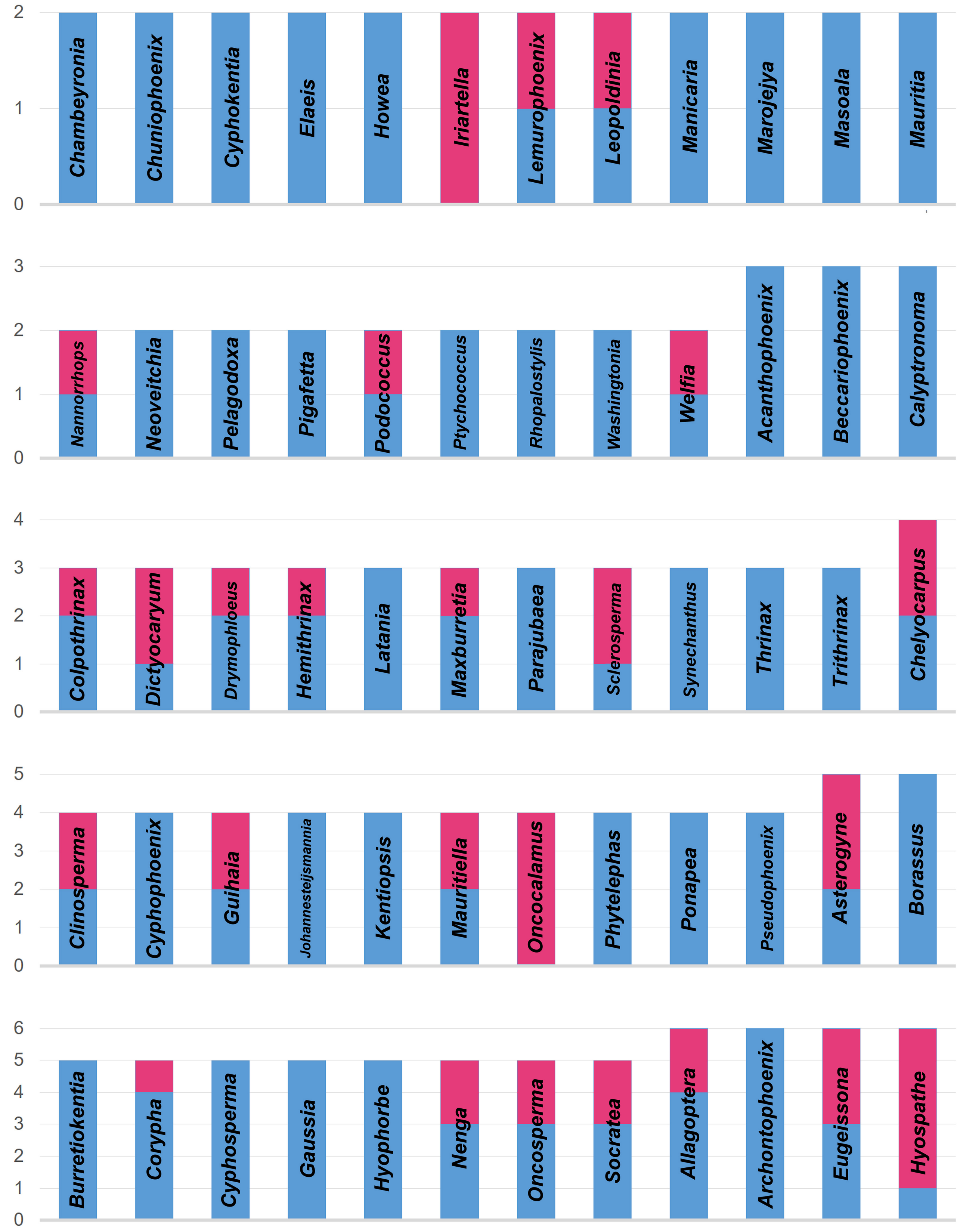


FIGURE 3 | (Continued)

FIGURE 3 | (Continued)

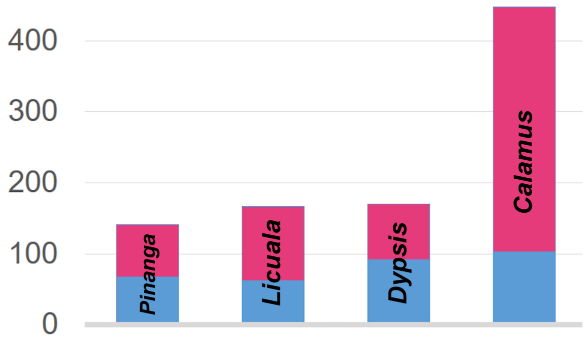


FIGURE 3 | Conservation gap analysis of the palms by genus: Comparative number of species in Arecaceae genera, and presence of palm species in the global metacollection. The 184 accepted genera (Govaerts et al., 2020), are arranged by number of species (total spp. = 2,566). Proportion of species in *ex situ* collections shown in blue, and proportion of species not maintained in collections shown in magenta. Note changes in scale of Y-axis. Slightly over half of the world's palm species (*n* = 1,380; 54%) are in protective cultivation.

TABLE 1 | Metrics for the global palm metacollection.

Palm species known	2,566 (Govaerts et al., 2020)
Palm species *ex situ*	1,380
Palm species *ex situ* and extinct in the wild	3
Ex situ sites with palms	477
Palm spp. kept at only a single *ex situ* site	347
Palm spp. kept at only two sites	422

tropics, e.g., NNTBG, Cairns Botanical Garden (CBG), Singapore Botanic Garden (SBG), and Bogor Botanic Gardens (BBG). The 10 botanic gardens with the highest number of palm species collectively hold 1,207 taxa.

Within this global metacollection, 347 palm species (including 58 *Calamus* spp.) are reported by only one garden. At the other end of the scale, *Phoenix canariensis* H. Wildpret is grown at 155 gardens, *Trachycarpus fortunei* (Hook.) H. Wendl. is grown at 183 gardens, and *Chamaerops humilis* L. is kept at 186 sites worldwide.

The Sabal Metacollection

All 19 species of *Sabal* we recognize are currently kept in living botanic garden collections (**Table 2** and **Figure 5**). The breadth of representation of these species varies in ways that suggest a correlation with threat level (**Figure 5**; $R^2 = 0.47$ when ordered by threat level); for example, *S. miamiensis*, considered to be extinct in the wild (see below), is known in only 5 collections, while *S. minor* (Jacq.) Pers. is stable and listed as Least Concern (IUCN, 2020) and is recorded in 146 collections.

DISCUSSION

Slightly over half (54%) of the world's palm species are in protective cultivation at botanic gardens and similar sites. Thus, this analysis highlights the great potential for developing further *ex situ* diversity in palm collections, as nearly 1,200 recognized palm species are not yet recorded in cultivation. Primary desiderata among these uncultivated taxa include the 6 genera not currently recorded at gardens (**Figure 3**): *Barcella* (1 sp.), *Jailoloa* (1 sp.), *Manjekia* (1 sp.), *Wallaceodoxa* (1 sp.), *Iriartella* (2 spp.), and *Oncocalamus* (4 spp.), given that these genera represent phylogenetically diverse lineages (Larkin et al., 2016).

Three of these genera are monotypic and only recently described from modern explorations on islands near northwestern New Guinea (*Jailoloa*, *Manjekia*, and *Wallaceodoxa*; Heatubun et al., 2014a). Notably, *Manjekia* was known to be in cultivation in one garden from at least 2012 (Heatubun et al., 2014b), but records from that garden in 2020 (current dataset) no longer report this palm species. This highlights the great importance of distributing collections among gardens—plant collections are not static and can change greatly over short time scales (Griffith et al., 2017a). This highlights the importance of regular reporting of collection data to such networked databases—BGCI PlantSearch encourages gardens to update their data annually.

Beyond these uncultivated genera, many other palm species are less obvious goals but still very important for collection and cultivation. One example is *Coccothrinax jimenezii* M. M. Mejía and R. G. García. This critically endangered species is limited to 61 individuals in the Dominican Republic and Haiti and is overexploited for broom making (Jestrow et al., 2016). *Ex situ* collections are recommended to safeguard this very imperiled species (Peguero et al., 2015; Harvey-Brown, 2018). As of September 2020, there is no record of this species in living collections. This is one example of many threatened palms that would benefit from protective cultivation. An Arecaceae-wide comparison of threat status with collections holdings would identify all such critical priorities and allow for informed conservation planning.

As noted above, the 10 largest palm collections together keep 1,207 species. This shows the important value of all gardens in stewarding palm diversity, as even the largest collections cannot keep all species, let alone all infraspecific (population) diversity. For example, *Pinanga manii* Becc. is currently only recorded at the Experimental Garden of the Botanical Survey of India (Kolkata), a site holding 2 palm species. This highlights the value that all *ex situ* sites of any size or type bring to a metacollection (Griffith et al., 2019a), and the importance of networking such collections in service of conservation goals. As noted above for *Manjekia*, facilitating distribution of such monosite collections should be an important safeguarding procedure for the palm metacollection. Natural disasters are but one example of why single-site *ex situ* collections should be avoided.

Also suggested here is a reversal of the "positive latitudinal bias" (Pautasso and Parmentier, 2007) shown in the overall species richness of botanic garden collections (Mounce et al., 2017) when palms alone are considered. While the global north has a large number of established botanic garden collections (as shown on **Figure 4**), many of the most diverse palm collections are found in the tropical latitudes and southern hemisphere (e.g., NNTBG, SBG, CBG, and BBG). Furthermore, the three most widely grown palms (*Phoenix canariensis*, *Trachycarpus fortunei*, and *Chamaerops humilis*) are considered the three

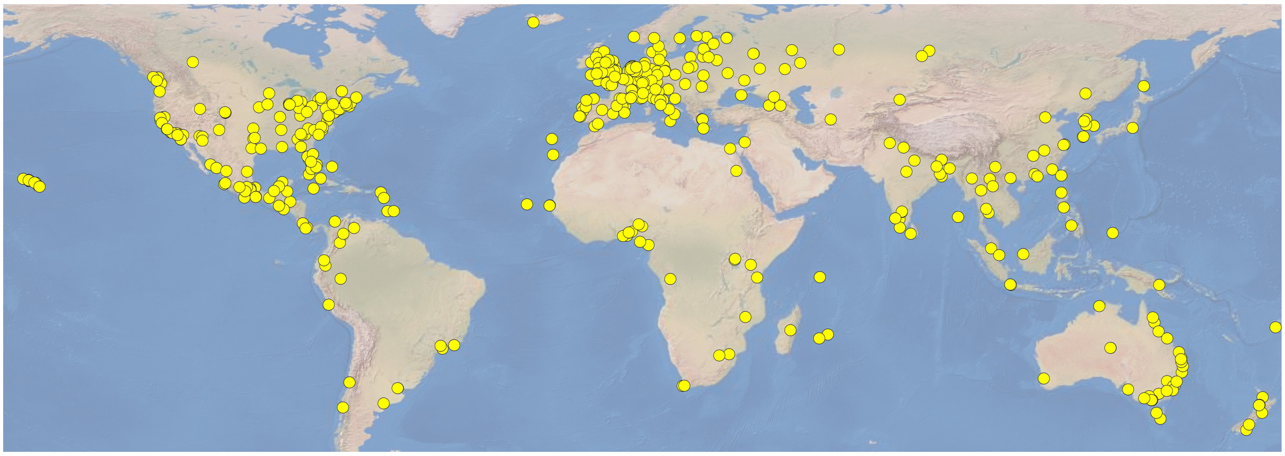


FIGURE 4 | Location of the global palm metacollection. These 477 sites cultivate 1,380 spp. of palms collectively (Botanic Gardens Conservation International (BGCI), 2020). While palm species diversity is highest in the tropics and subtropics, the majority of palm-hosting sites are located in temperate regions. While this distribution of sites suggests a latitudinal bias toward the north (Pautasso and Parmentier, 2007; Mounce et al., 2017), the largest collections by number of palm species are in the tropics (see text).

most temperate species in the family. Thus, the species richness patterns of palm collections follow the species richness patterns of *in situ* palm diversity, with more diverse collections in tropical latitudes.

A caveat about this analysis is based in the breadth of coverage of this dataset. While BGCI PlantSearch is the widest-reaching and most complete global botanic garden collections database, coverage is estimated at only 34% of botanic gardens worldwide (Mounce et al., 2017). Community encouragement of all *ex situ* sites to freely upload collections data to PlantSearch would increase discoverability of other vital palm collections which likely exist (Vovides et al., 2018). For example, *Attalea crassispatha* is recorded at 3 gardens in PlantSearch, but at least 3 other *ex situ* sites also maintain living collections (Griffith, in prep.)—all of which are vital to conservation of this critically endangered species.

Another caveat of this analysis is based on the applicability of a single consensus taxonomy for palms. Certainly, for such a large and diverse family with voluminous active taxonomic research, consensus taxonomy is a major challenge, and we applaud the efforts of Govaerts et al. (2020) in assembling this important resource, as a common language for palm diversity allows clear communication and facilitates prioritization of coordinated conservation actions. However, reconciling the self-reported occurrence data with the up-to-date synonymy highlighted great variation in how individual gardens handle palm taxonomy: like systematists generally, some gardens appear to be "lumpers" and others are "splitters." In the most extreme case, resolving synonyms reduced the number of species at a single garden by 72. The number of synonyms resolved in each collection was strongly correlated with overall collection diversity (n = spp. in collection vs. n = synonyms resolved: R^2 = 0.77); more diverse collections seem to use more controversial labeling! At one of the authors' gardens (Montgomery Botanical Center, Florida, United States) 6.5% of records were synonyms, reducing an initial 370 self-reported palm spp. to 346. But we are in good company: even Royal Botanic Gardens Kew—where this consensus taxonomy is produced—lost 7.5% of its self-reported palm diversity when the consensus was applied.

With our study of *Sabal*, we find that threat level correlates with the breadth of presence in collections (**Figure 5** and **Table 2**), as is also seen in many other groups, including Australian plants (Botanic Gardens Conservation International (BGCI), 2013), conifers (Shaw and Hird, 2014), maples (*Acer* L.; Crowley et al., 2020), oaks (*Quercus* L.; Beckman et al., 2019; Carrero et al., 2020), and US plants (Botanic Gardens Conservation International (BGCI), 2014).

TABLE 2 | *Sabal* metacollection.

Taxon	n *ex situ* sites	IUCN red list status
S. antillensis	1	VU (Griffith et al., 2017b; De Freitas et al., 2019)
S. bermudana	76	EN (Copeland and Roberts, 2016)
S. × *brazoriensis*	5	VU (Goldman et al., 2011)
S. causiarum	36	VU (Bárrios and Hamilton, 2018)
S. domingensis	21	LC (Zona et al., 2007)
S. etonia	26	VU (Zona, 1990)
S. gretherae	1	VU (Quero, 1998a)
S. guatemalensis	6	VU (Paiz and Stuardo, 1999)
S. lougheediana	1	CR (Griffith et al., 2019b)
S. maritima	12	LC (Zona et al., 2007)
S. mauritiiformis	41	LC (Zona, 1990)
S. mexicana	62	LC (Zona, 1990)
S. miamiensis	5	EW (Zona, 1990; Walter and Gillett, 1998, this paper)
S. minor	146	LC (IUCN SSC GTSG, 2020)
S. palmetto	109	LC (Zona, 1990)
S. pumos	6	VU (Quero, 1998b)
S. rosei	22	LC (Zona et al., 2007)
S. uresana	33	VU (Quero, 1998c)
S. yapa	25	LC (Zona et al., 2007)

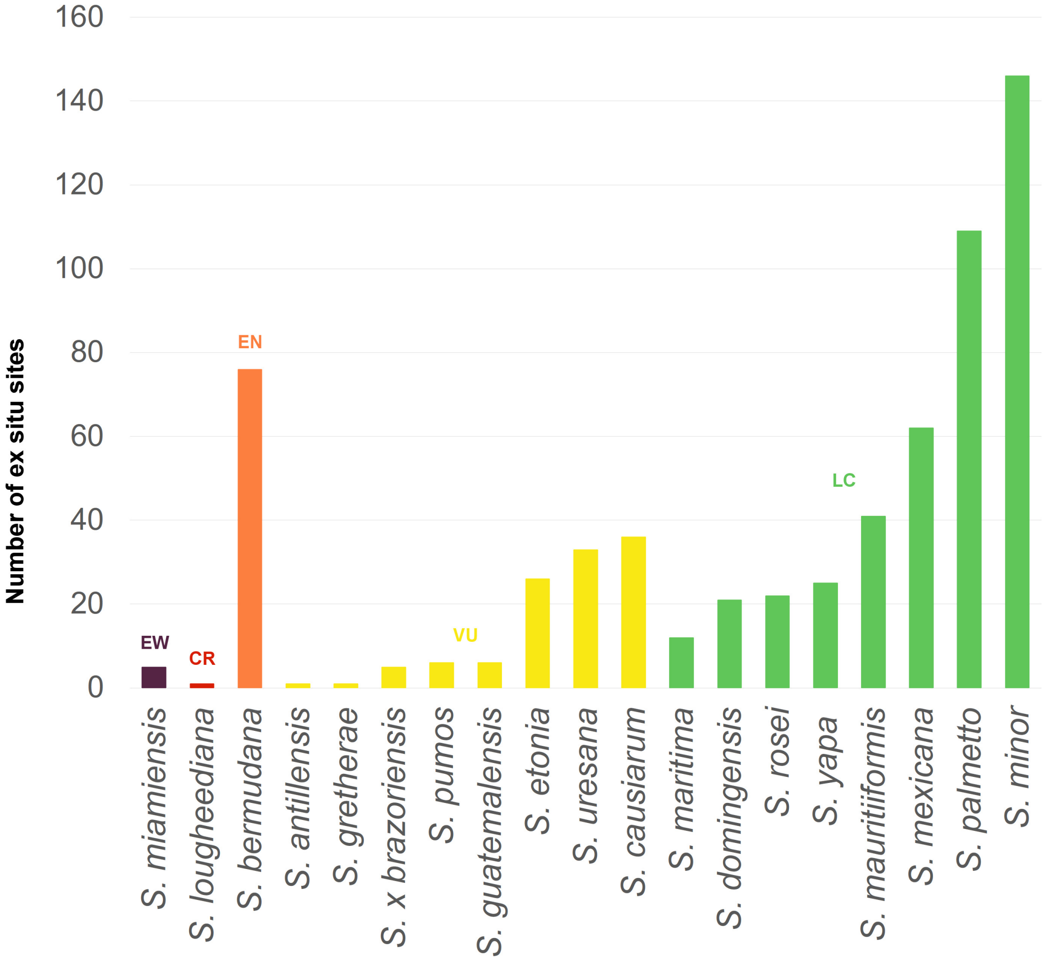


FIGURE 5 | The global *Sabal* metacollection: Number of *ex situ* sites holding living palms of each species, arranged by IUCN Red List Category, and then arranged by number of sites (Botanic Gardens Conservation International (BGCI), 2020). This visualization highlights relative security for each taxon. For example, (1) *Sabal miamiensis* requires urgent propagation, distribution, and restoration efforts to ensure against extinction, as the plant is no longer found in the wild and only occurs in 5 gardens so far as known. (2) *S. lougheediana* must also be propagated and distributed in order to provide a more secure complement to *in situ* conservation efforts. (3) While efforts must be made to protect the remaining wild stands of *S. bermudana*, a robust group of gardens can provide germplasm for restoration efforts. (4) *S. antillensis* and *S. gretherae* are also high priorities for propagation and distribution. (5) At the other end of the security scale, *S. palmetto* and *S. minor* are of least concern for threats in its widespread natural range, and both are also widely grown at over 100 botanic gardens each. This breadth of plants in protective cultivation could prove vital if Lethal Bronzing greatly reduces the wild stands of these palms (Oates et al., 2020).

This again illustrates the need for garden curators to actively propagate and distribute palm collections as a potential hedge against natural disasters (Griffith et al., 2008). Of particular concern in this way are the species *Sabal lougheediana* M. P. Griff. and Coolen and (to a lesser extent) *S. antillensis* M. P. Griff. *Sabal lougheediana* is Critically Endangered and currently limited to only 25 mature specimens in an area of less than 1 km^2 due to overgrazing by feral ungulates (De Freitas et al., 2019; Griffith et al., 2019b). While *S. antillensis* is more secure in the wild, it remains vulnerable due to limited range and potential threats from invasive pests (Griffith et al., 2017b). Alarmingly, both taxa were currently known from only a single garden as of September 2020. Since that time, efforts to distribute both species to other gardens have been made. This work is especially important for the palm research community because the phylogenetic relationship with both *S. lougheediana* and *S. antillensis* are unknown in relation to the rest of the species of *Sabal*. Because both *S. lougheediana* and *S. antillensis* are distributed in the Leeward Antilles, these species represent a potentially important link to the biogeographic history of *Sabal* as only one other species [*S. mauritiiformis* (H. Karst.) Griseb. and H. Wendl.] is known from South America (Grinage et al., 2021).

Our study of *Sabal* also illustrates some of the challenges with stewarding a broad consensus taxonomy. In describing the already very-restricted species *S. miamiensis*, Zona (1985) highlighted that its habitat “is fast disappearing because of extensive urban development in the Miami area,” and “is in danger of extinction unless it can be brought into cultivation or its habitat can be preserved.” Collections at the Montgomery Botanical Center include plants of *Sabal miamiensis* which were obtained in habitat as seed or transplants (rescued from the path of development) shortly after the species was described. Revisits to these same sites in recent years, as well as sites of specimens cited in the protolog (Zona, 1985) yielded no further observations of these palms in the wild. The morphological distinctiveness of these collections compared to its supposed prior synonym (*S. etonia*) prompted our decision to retain the name *S. miamiensis* for these plants. If the consensus taxonomy was followed, these collections of extirpated palm diversity would be subsumed under *S. etonia;* while that synonymy is not problematic on its own, it does render this unique morphological, ecological and conservation phenomenon less discoverable and communicable. Planned upgrades to BGCI PlantSearch to store and retrieve accession-level data may help address such "lost information" wrought by such synonymy.

Synonymy is important to consider in a group such as *Sabal* for which there is a long botanical history (over 250 years). Similar to the taxonomy of *S. miamiensis* and *S. etonia*, *S. minor* s.l. was once divided into *S. minor* s.s. and *S. louisiana* (Darby) Bomhard (Small, 1926; Bailey, 1934; Bomhard, 1935; Bomhard, 1943). *Sabal louisiana* unlike *S. minor* is restricted in range to annual floodplain forests along the Mississippi Delta, United States. Furthermore, *S. louisiana* develops an above-ground trunk while *S. minor* does not. Aside from the presence of a trunk, the morphology of *S. minor* s.s. and *S. louisiana* is not easily distinguishable. This lack of distinguishing characteristics is one of the reasons it was synonymized by L. H. Bailey nearly 80 years ago (Bailey, 1944). Since then, new scientific tools (e.g., genetics and genomics) provide the ability to revisit these synonymies with modern methodologies. Luckily for *S. louisiana*, there are still enough wild populations available for study and *ex situ* collections development. This is a case where the synonymy obscures morphological diversity within a species considered "Least Concern" for extinction (IUCN SSC GTSG, 2020). We argue here that even though the current taxonomy combines these morphologies into one species, botanical gardens should strive to include all forms of diversity—not just taxonomic, but also morphologic, genetic and geographic. As technology continues to advance and destruction of wild habitats expands, it is important to maintain representatives of these original growth forms so that we can eventually solve these taxonomic and ecological puzzles.

Moving Forward: Recommendations

This review and analysis illuminate a clear path forward for palm collections. In order to better serve the ecological field, the scientific community generally, the conservation field, students worldwide, and the broader global public, palm collections should *collect, cultivate, communicate,* and *collaborate.*

Collect

Gap analysis of the global palm metacollection highlights significant taxonomic gaps in worldwide collections holdings. Botanic gardens should prioritize bringing these taxa into collections that serve their communities through education, display, and research. Bring these palms into the gardens!

Cultivate

Active horticultural management of these living treasures is essential. Examples of palms brought into cultivation and then lost highlights the need for broader propagation and sharing of such rare material among gardens and others. Grow more palms!

Communicate

Even the world's broadest and most extensive networked database of palm collections still sees significant gaps in coverage. This is especially noted in cases of very rare and imperiled species. We encourage all gardens to upload their data to BGCI PlantSearch, and we especially implore the larger and more established botanic gardens to share resources and expertise to facilitate this process. Share your data!

Collaborate

As shown here, the global palm collection is greater than the sum of its parts. More deliberate networking of palm collections also demonstrably improves conservation outcomes. We encourage gardens to directly partner to advance conservation goals. Work together!

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

MPG designed the article. MPG, AM, and AG performed analysis and wrote the article. All authors contributed to the article and approved the submitted version.

FUNDING

This work was funded by the Institute of Museum and Library Services (Grants MG-60-19-0064-19 and MG-245575-OMS-20) and funds from the authors' organizations.

ACKNOWLEDGMENTS

We thank Claudia Calonje, Michael Calonje, Eliza Gonzalez, Vickie Murphy, Larry Noblick, Joanna Tucker Lima, Paul Smith, and Andrew Street for discussion, input, and collections management. We also thank the Metropolitan Museum of Art for making the image for **Figure 1** available, and all of the botanic gardens worldwide for uploading their plant records data to BGCI PlantSearch.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2021.711414/full#supplementary-material

REFERENCES

Asmussen-Lange, C. B., Maunder, M., and Fay, M. F. (2011). Conservation genetics of the critically endangered Round Island bottle palm, *Hyophorbe lagenicaulis* (Arecaceae): can cultivated stocks supplement a residual wild population? *Bot. J. Linn. Soc.* 167, 301–310. doi: 10.1111/j.1095-8339.2011.01175.x

Bacon, C. D., and Bailey, C. D. (2006). Taxonomy and Conservation: a Case Study from *Chamaedorea alternans. Ann. Bot.* 98, 755–763. doi: 10.1093/aob/mcl158

Bailey, L. H. (1934). American Palmettoes. *Gentes Herbarum* 3, 275–339.

Bailey, L. H. (1944). Revision of the American Palmettoes. *Gentes Herbarum* 6, 365–459.

Bamroongrugsa, N., Buachum, S., and Purintavaragu, C. (2008). Nipa Palm (*Nypa fruticans* Wurmb.) cultivation in salt affected paddy fields. *J. Trop. Plants Res.* 1, 93–102.

Bárrios, S., and Hamilton, M. A. (2018). *Sabal causiarum. The IUCN Red List of Threatened Species 2018: e.T57356844A125646226.* Gland: IUCN.

Beckman, E., Meyer, A., Denvir, A., Gill, D., Man, G., Pivorunas, D., et al. (2019). *Conservation Gap Analysis of Native U.S. Oaks*. Lisle: The Morton Arboretum.

Botanic Gardens Conservation International (BGCI) (2013). *Botanic Gardens of Australia and New Zealand (BGANZ) ex situ collections survey*. Chicago: BGCI-US.

Botanic Gardens Conservation International (BGCI) (2014). *Progress report on Target 8 of the Global Strategy for Plant Conservation in the United States.* Chicago: BGCI-US.

Botanic Gardens Conservation International (BGCI) (2020). *PlantSearch online database. Botanic Gardens Conservation International. Richmond, U.K.* Available online at: https://tools.bgci.org/plant_search.php (Accessed September 25, 2020).

Bomhard, M. L. (1935). *Sabal louisiana*, the correct name for the polymorphic palmetto of Louisiana. *J. Wash. Acad. Sci.* 25, 35–44.

Bomhard, M. L. (1943). Distribution and character of *Sabal louisiana*. *J. Wash. Acad. Sci.* 33, 170–182.

Cano, Á, Bacon, C. D., Stauffer, F. W., Antonelli, A., Serrano-Serrano, M. L., and Perret, M. (2018). The roles of dispersal and mass extinction in shaping palm diversity across the Caribbean. *J. Biogeogr.* 45, 1432–1443. doi: 10.1111/jbi.13225

Carrero, C., Jerome, D., Beckman, E., Byrne, A., Coombes, A. J., Deng, M., et al. (2020). *The Red List of Oaks 2020*. Lisle: The Morton Arboretum.

Carricarte, G. (2021). *Tropical Obsession*. Coral Gables: Coral Gables Magazine, 74–80.

Chacón-Vargas, K., García-Merchán, V. H., and Sanín, M. J. (2020). From keystone species to conservation: conservation genetics of wax palm *Ceroxylon quindiuense* in the largest wild populations of Colombia and selected neighboring ex situ plant collections. *Biodivers. Conserv.* 29, 283–302. doi: 10.1007/s10531-019-01882-w

Chapin, M. (2005). *Pritchardia aylmer-robinsonii St. John*. Available online at: https://www.iucn.org/sites/dev/files/import/downloads/psg_pritchardia_aylmer_robinsonii.pdf (Accessed August 17, 2020).

Chapin, M. H., Wood, K. R., Perlman, S. P., and Maunder, M. (2004). A review of the conservation status of the endemic *Pritchardia* palms of Hawaii. *Oryx* 38, 273–281. doi: 10.1017/S003060530400050X

Convention on Biological Diversity (2020). *Targets*. Available online at: https://www.cbd.int/gspc/targets.shtml (Accessed August 19, 2020).

Copeland, A., and Roberts, A. (2016). *Sabal bermudana. The IUCN Red List of Threatened Species 2016: e.T38691A101378743.* Switzerland: IUCN.

Crane, P. R., Hopper, S. D., Raven, P. H., and Stevenson, D. W. (2009). Plant science research in botanic gardens. *Trends Plant Sci.* 14, 575–577. doi: 10.1016/j.tplants.2009.09.007

Crowley, D., Barstow, M., Rivers, M., and Harvey-Brown, Y. (2020). *The Red List of Acer Revised and Extended.* Richmond: Botanic Gardens Conservation International.

De Freitas, J., Camilleri, J., van Eijk, S., Posno, V., Valdes, I., Coolen, Q., et al. (2019). Sabalpalm (*Sabal antillensis*) recovery over 40 years: lessons for successful palm conservation. *Palms* 63, 57–68.

Devanand, P. S., and Chao, C. T. (2003). Genetic variation within 'Medjool'and 'Deglet Noor'date (*Phoenix dactylifera* L.) cultivars in California detected by fluorescent-AFLP markers. *J. Hortic. Sci. Biotechnol.* 78, 405–409. doi: 10.1080/14620316.2003.11511639

Engler, A. (1889). *Die Natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten, insbesondere den Nutzpflanzen, unter Mitwirkung zahlreicher hervorragender Fachgelehrten begründet. Teil II, Abt. 3.* Leipzig: W. Engelmann.

Fotinos, T. D., Namoff, S., Lewis, C., Griffith, M. P., Maschinski, J., and von Wettberg, E. J. B. (2015). Genetic evaluation of a reintroduction of Sargent's Cherry Palm, *Pseudophoenix sargentii. J. Torrey Bot. Soc.* 142, 51–62. doi: 10.3159/torrey-d-14-00004.1

Goldman, D. H., Klooster, M. R., Griffith, M. P., Fay, M. F., and Chase, M. W. (2011). A preliminary evaluation of the ancestry of a putative *Sabal* hybrid (Arecaceae: Coryphoideae), and the description of a new nothospecies, *Sabal × brazoriensis*. *Phytotaxa* 27, 8–25. doi: 10.11646/phytotaxa.27.1.2

Govaerts, R., and Dransfield, J. (2005). *World checklist of palms*. Richmond: Royal Botanic Gardens.

Govaerts, R., Dransfield, J., Zona, S., Hodel, D. R., and Henderson, A. (2020). *World Checklist of Arecaceae*. Richmond: Royal Botanic Gardens, Kew.

Griffith, M. P., Barber, G., Tucker Lima, J., Barros, M., Calonje, C., Noblick, L. R., et al. (2017a). Plant Collection "Half-life:" Can Botanic Gardens Weather the Climate? *Curator* 60, 395–410. doi: 10.1111/cura.12229

Griffith, M. P., De Freitas, J., Barros, M., and Noblick, L. R. (2017b). *Sabal antillensis* (Arecaceae): a new palmetto species from the Leeward Antilles. *Phytotaxa* 303, 56–64. doi: 10.11646/phytotaxa.303.1.4

Griffith, M. P., Beckman, E., Callicrate, T., Clark, J., Clase, T., Deans, S., et al. (2019a). *TOWARD THE METACOLLECTION: Safeguarding plant diversity and coordinating conservation collections*. San Marino: Botanic Gardens Conservation International US.

Griffith, M. P., Coolen, Q., Barros, M., and Noblick, L. R. (2019b). *Sabal lougheediana* (*Arecaceae*), a critically endangered, endemic palm species from Bonaire. *Phytotaxa* 420, 95–101. doi: 10.11646/phytotaxa.420.2.1

Griffith, M. P., Cartwright, F., Dosmann, M., Fant, J., Freid, E., Havens, K., et al. (2021). Ex Situ Conservation of Large and Small Plant Populations Illustrates Limitations of Common Conservation Metrics. *Int. J. Plant Sci.* 182, 263–276.

Griffith, M. P., Clase, T., Toribio, P., Piñeyro, Y. E., Jiménez, F., Gratacos, X., et al. (2020). Can a botanic garden metacollection better conserve wild plant diversity? A case study comparing pooled collections with an ideal sampling model. *Int. J. Plant Sci.* 181, 485–496. doi: 10.1086/707729

Griffith, M. P., Noblick, L. R., Dowe, J. L., Husby, C. E., and Calonje, M. A. (2008). Cyclone tolerance in New World Arecaceae: biogeographic variation and abiotic natural selection. *Ann. Bot.* 102, 591–598. doi: 10.1093/aob/mcn132

Griffith, M. P., Witcher, E., Noblick, L., and Husby, C. (2013). Palm stem shape correlates with hurricane tolerance, in a manner consistent with natural selection. *Palms* 57, 115–122.

Grinage, A., Landis, J., Majure, L. C., Valderrama, E., Gandolfo, M., and Specht, C. (2021). Deciphering the tales of sabal from the crypt: insights from past collections. *Botany*.

Harvey-Brown, Y. (2018). *Coccothrinax jimenezii. The IUCN Red List of Threatened Species 2018: e.T129768110A129768126.* Switzerland: IUCN.

Hayati, A., Wickneswari, R., Maizura, I., and Rajanaidu, N. (2004). Genetic diversity of oil palm (*Elaeis guineensis* Jacq.) germplasm collections from Africa: implications for improvement and conservation of genetic resources. *Theor. Appl. Genet.* 108, 1274–1284. doi: 10.1007/s00122-003-1545-0

Heatubun, C. D., Zona, S., and Baker, W. J. (2014a). Three new genera of arecoid palm (Arecaceae) from eastern Malesia. *Kew Bull.* 69:9525.

Heatubun, C. D., Zona, S., and Baker, W. J. (2014b). Three new palm genera from Indonesia. *Palms* 58, 197–202.

Heyduk, K., Trapnell, D. W., Barrett, C. F., and Leebens-Mack, J. (2016). Phylogenomic analyses of species relationships in the genus *Sabal* (Arecaceae) using targeted sequence capture. *Biol. J. Linn. Soc.* 117, 106–120. doi: 10.1111/bij.12551

Hoban, S., Callicrate, T., Clark, J., Deans, S., Dosmann, M., Fant, J., et al. (2020). Taxonomic similarity does not predict necessary sample size for ex situ conservation: a comparison among five genera. *Proc. R. Soc. B* 287:20200102. doi: 10.1098/rspb.2020.0102

Hodel, D. R., Verdecia Pérez, R., Suárez Oropesa, D., Rodríguez Lima, M., and Mera, L. A. (2016). *Copernicia fallaensis* The Greatest Fan Palm of Them All. *PalmArbor* 2016-4, 1–11.

Imada, C. T., Wagner, W. L., and Herbst, D. R. (1989). Checklist of native and naturalized flowering plants of Hawaii. *Bishop Mus. Occas. Pap* 29, 31–87.

IUCN (2020). *The IUCN Red List of Threatened Species. Version 2020-1*. Available online at: https://www.iucnredlist.org

IUCN SSC GTSG. (2020). *Sabal minor. The IUCN Red List of Threatened Species 2020: e.T79521201A79521207*. Gland: IUCN.

Janick, J. (2002). Ancient Egyptian agriculture and orgins of horticulture. *Acta Hortic.* 582, 23–39. doi: 10.17660/actahortic.2002.582.1

Jestrow, B., Peguero, B., Jiménez, F., Cinea, W., Hass, M., Reeve, A., et al. (2016). Genetic diversity and differentiation of the Critically Endangered Hispaniolan palm *Coccothrinax jimenezii* M.M. Mejía & García based on novel SSR markers. *Biochem. Syst. Ecol.* 66, 216–223. doi: 10.1016/j.bse.2016.04.013

Johnson, D. (1998). *Corypha taliera. In: IUCN (2014). IUCN Red List of Threatened Species. Version 2014.1*. Gland: IUCN.

Larkin, D. J., Jacobi, S. K., Hipp, A. L., and Kramer, A. T. (2016). Keeping all the PIECES: phylogenetically informed ex situ conservation of endangered species. *PLoS One* 11:e0156973. doi: 10.1371/journal.pone.0156973

Ludwig, N., Lavergne, C., and Sevathian, J. C. (2010). Notes on the Conservation Status of Mauritian Palms. *Palms* 54, 77–93.

Mounce, R., Smith, P., and Brockington, S. (2017). Ex situ conservation of plant diversity in the world's botanic gardens. *Nat. Plants* 3:795. doi: 10.1038/s41477-017-0019-3

Namoff, S., Husby, C. E., Francisco-Ortega, J., Noblick, L. R., Lewis, C. E., and Griffith, M. P. (2010). How well does a botanical garden collection of a rare palm capture the genetic variation in a wild population? *Biol. Conserv.* 143, 1110–1117. doi: 10.1016/j.biocon.2010.02.004

Oates, M. J., Abu-Khalaf, N., Molina-Cabrera, C., Ruiz-Canales, A., Ramos, J., and Bahder, B. W. (2020). Detection of Lethal Bronzing Disease in Cabbage Palms (*Sabal palmetto*) Using a Low-Cost Electronic Nose. *Biosensors* 10:188. doi: 10.3390/bios10110188

Oldfield, S. F. (2009). Botanic gardens and the conservation of tree species. *Trends Plant Sci.* 14, 581–583. doi: 10.1016/j.tplants.2009.08.013

Paiz, O., and Stuardo, H. (1999). *Distribución y usos de la palma de escoba (Sabal guatemalensis Beccari) en el municipio de Guastatoya, El Progreso*. Ph.D. thesis, Universidad de San Carlos de Guatemala, Guatemala.

Pautasso, M., and Parmentier, I. (2007). Are the living collections of the world's botanical gardens following species-richness patterns observed in natural ecosystems?. *Bot. Helv.* 117, 15–28. doi: 10.1007/s00035-007-0786-y

Peguero, B., Jiménez, F., Joseph, P. A., Cinea, W., Griffith, M. P., Francisco-Ortega, J., et al. (2015). *Coccothrinax jimenezii* – A Critically Endangered Palm from Hispaniola. *Palms* 59, 145–153.

Pence, V. C. (2013). In vitro methods and the challenge of exceptional species for Target 8 of the Global Strategy for Plant Conservation. *Ann. Mo. Bot. Gard.* 99, 214–220. doi: 10.3417/2011112

Perez, T. M., Valverde-Barrante, S. O., Bravo, C., Taylor, T. C., Fadrique, B., Hogan, J. A., et al. (2019). Botanic gardens are an untapped resource for studying the functional ecology of tropical plants. *Phil. Trans. R. Soc. B Biol. Sci.* 374:20170390. doi: 10.1098/rstb.2017.0390

Pérez-Harguindeguy, N., Diaz, S., Gamier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., et al. (2013). New handbook for standardized measurement of plant functional traits worldwide. *Aust. J. Bot.* 61, 167–234.

Pérez, H. E., Criley, R. A., and Baskin, C. C. (2008). Promoting germination in dormant seeds of *Pritchardia remota* (Kuntze) Beck., an endangered palm endemic to Hawaii. *Nat. Area. J.* 28, 251–260. doi: 10.3375/0885-8608(2008)28[251:pgidso]2.0.co;2

Porto, K. C. N., Nunes, Y. R. F., and Ribeiro, L. M. (2018). The dynamic of recalcitrant seed banks of *Mauritia flexuosa* (Arecaceae) reveal adaptations to marsh microenvironments. *Plant Ecol.* 219, 199–207. doi: 10.1007/s11258-017-0788-9

Quero, H. J. (1998a). *Sabal gretheriae. The IUCN Red List of Threatened Species 1998: e.T38692A10139282*. Gland: IUCN.

Quero, H. J. (1998b). *Sabal pumos. The IUCN Red List of Threatened Species 1998: e.T38693A10139394*. Gland: IUCN.

Quero, H. J. (1998c). *Sabal uresana. The IUCN Red List of Threatened Species 1998: e.T38694A10139483*. Gland: IUCN.

Shapcott, A. (1998). The genetics of *Ptychosperma bleeseri*, a rare palm from the Northern Territory, Australia. *Biol. Conserv.* 85, 203–209. doi: 10.1016/s0006-3207(97)00147-x

Shaw, K., and Hird, A. (2014). *Global Survey of Ex situ Conifer Collections*. Richmond: BGCI.

Small, J. K. (1926). A new palm from the Mississippi Delta. *Torreya* 26, 33–35.

Tomlinson, P. (1979). Systematics and Ecology of the Palmae. *Annu. Rev. Ecol. Syst.* 10, 85–107. doi: 10.1146/annurev.es.10.110179.000505

Tucker Lima, J. M., Reyes, J., and Salman, N. (2021). Flower Color Variation in *Attalea phalerata* (Arecaceae) Revisited. *Palms* 65, 27–33. doi: 10.15553/c2016v711a6

Valdes, I., Tucker Lima, J. M., and Noblick, L. R. (2021). Pollination of *Nypa fruticans* (Wurmb.) in a South Florida botanic garden. *J. Pollinat. Ecol.* 27, 57–64.

Verdecia, R. (2015). *Copernicia fallaensis León*. Available online at: https://www.iucn.org/sites/dev/files/import/downloads/psg_copernicia_fallaensis.pdf (Accessed August 10, 2020).

Vovides, A. P., Griffith, M. P., Stevenson, D. W., Li, N., Li, Y., Fang, S., et al. (2018). Botanic gardens cycad collections: 4th GBGC symposium report. *Mem. N. Y. Bot. Gard.* 117, 69–85.

Walter, K. S., and Gillett, H. J. (eds) (1998). *1997 IUCN red list of threatened plants*. Switzerland: IUCN.

Wang, H. C., Chen, J. T., Wu, S. P., Lin, M. C., and Chang, W. C. (2003). Plant regeneration through somatic embryogenesis from zygotic embryo-derived callus of *Areca catechu* L.(Arecaceae). *In Vitro Cell. Dev. Biol. Plant* 39, 34–36. doi: 10.1079/ivp2002373

Zona, S. (1985). A new species of *Sabal* (*Palmae*) from Florida. *Brittonia* 37, 366–368. doi: 10.2307/2806549

Zona, S. (1990). A monograph of *Sabal* (Arecaceae: Coryphoideae). *Aliso* 12, 583–666. doi: 10.5642/aliso.19901204.02

Zona, S., Verdecia, R., Sánchez, A. L., Lewis, C. E., and Maunder, M. (2007). The conservation status of West Indian palms (*Arecaceae*). *Oryx* 41, 300–305. doi: 10.1017/s0030605307000404

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

frontiers
in Forests and Global Change

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

Linking Plant Functional Traits to Demography in a Fragmented Landscape

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

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

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

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

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

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

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

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

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

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

INTRODUCTION

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

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

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

MATERIALS AND METHODS

Study Sites

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

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

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

Species Selected for the Study

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

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

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

Demographic Data

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

Demographic Analysis

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

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

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

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

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

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

Relative Diameter Growth Rate

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

Plant Functional Traits Data

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

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

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

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

Analysis of Plant Functional Traits

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

RESULTS

Deterministic Asymptotic Growth Rate (λ)

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

Lower-Level Vital Rates

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

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

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

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

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

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

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

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

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

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

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

Lower-Level Vital Rates Elasticities

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

Relative Diameter Growth Rate

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

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

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

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

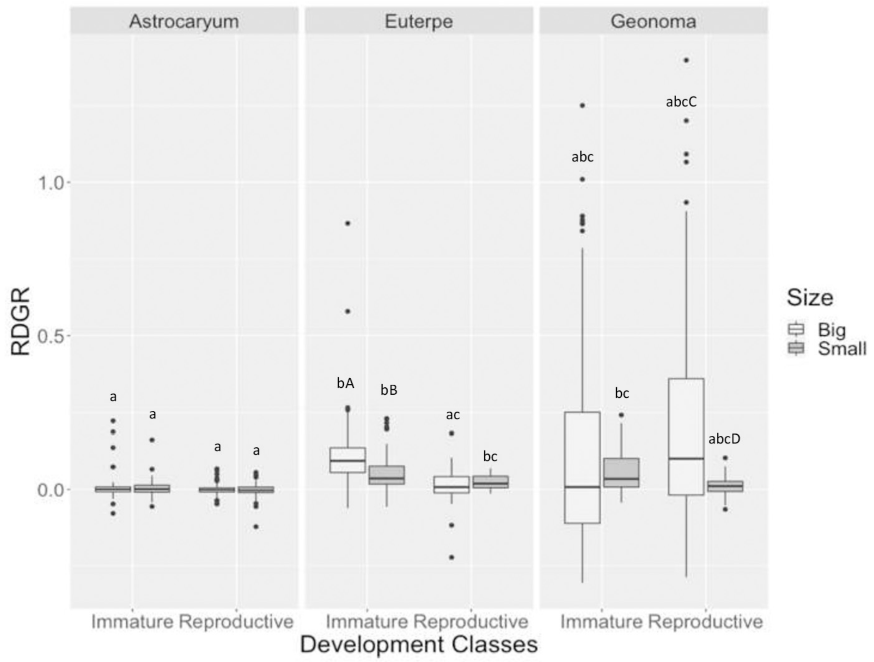


FIGURE 1 | Relative diameter growth rate (RDGR) of individuals of the demography plots (from year 2005 to 2007). The bootstrap confidence intervals were calculated for mean difference, lowercase letters indicate differences in the mean value of the attribute between species, and capital letters indicate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

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

Functional Traits

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

DISCUSSION

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

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

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

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

(Continued)

TABLE 5 | (Continued)

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

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

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

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

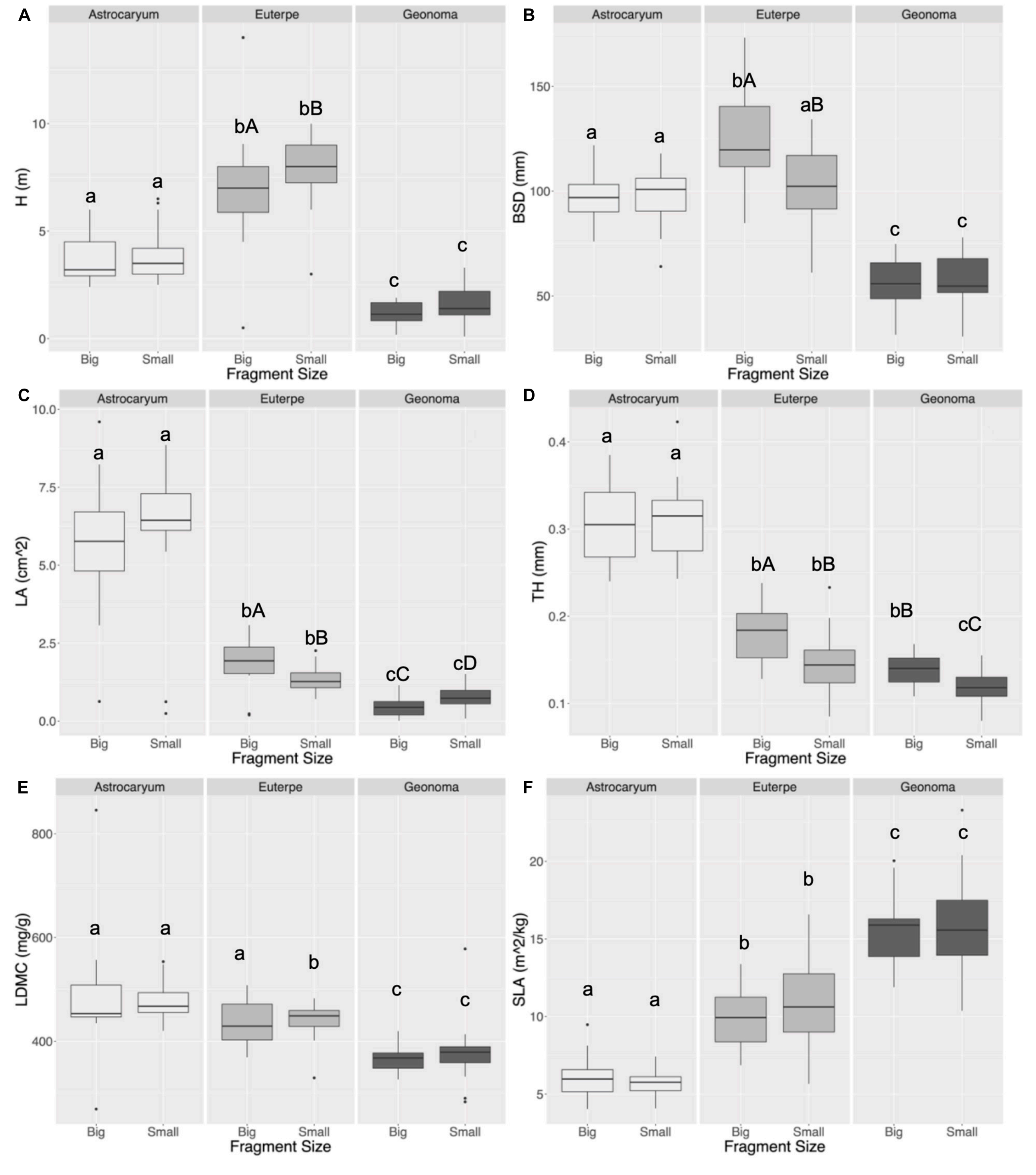


FIGURE 2 | (Continued)

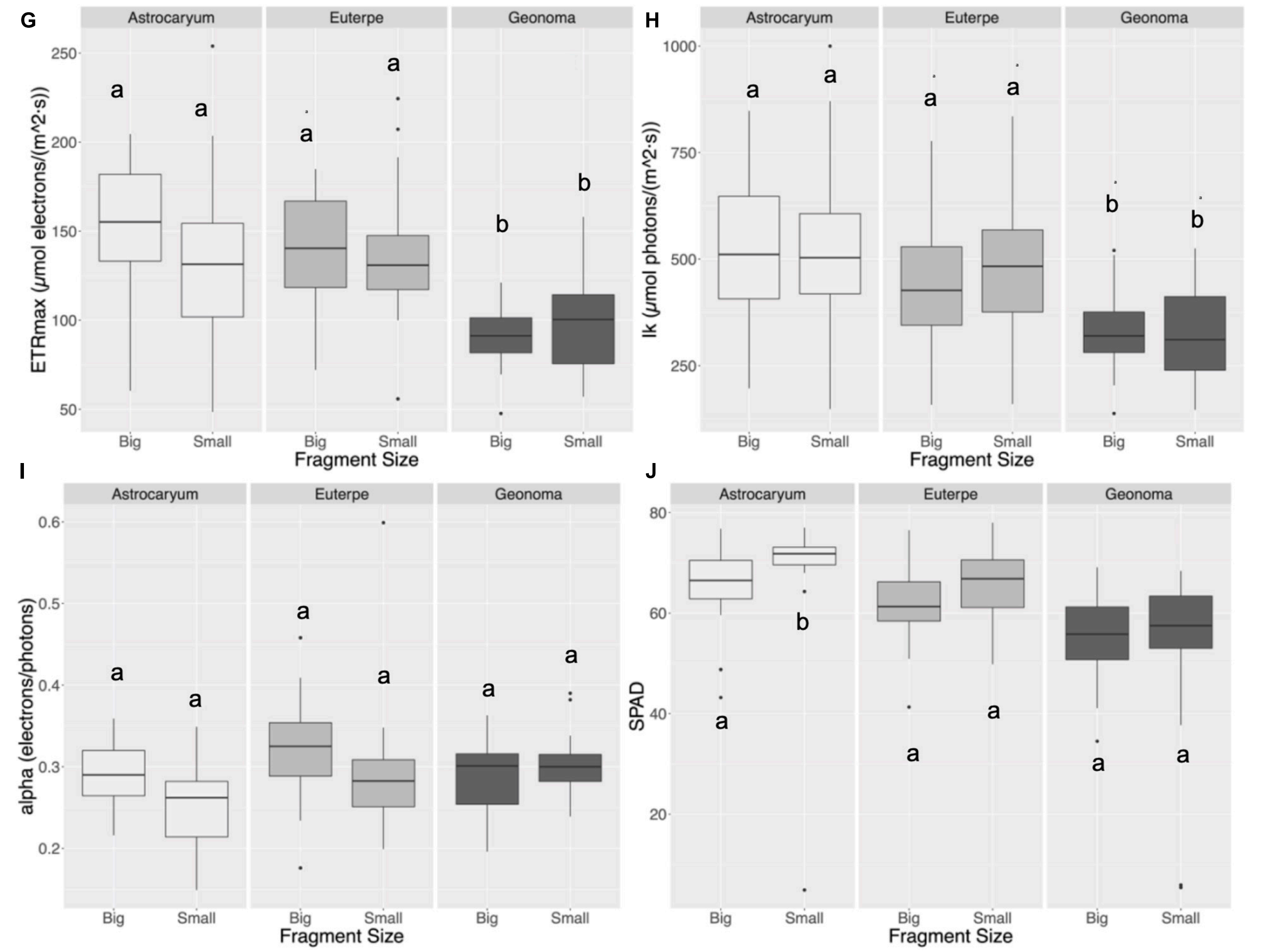


FIGURE 2 | Functional traits measured for each palm species in large and small fragments: height (H, cm – **A**), basal stem diameter (BSD, mm – **B**), leaf area (LA, cm^2 – **C**), leaf thickness (TH, mm – **D**), and leaf dry matter content (LDMC, mg·g^{-1} – **E**), specific leaf area (SLA, m^2·kg^{-1}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

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

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

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

CONCLUSION

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

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

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

FUNDING

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

ACKNOWLEDGMENTS

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

REFERENCES

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

frontiers | Frontiers in Ecology and Evolution

ORIGINAL RESEARCH
published: 27 April 2022
doi: 10.3389/fevo.2022.678125

Functional Traits, Species Diversity and Species Composition of a Neotropical Palm Community Vary in Relation to Forest Age

Sarah Lueder[1], Kaushik Narasimhan[1,2], Jorge Olivo[2], Domingo Cabrera[2], Juana G. Jurado[2], Lewis Greenstein[1] and Jordan Karubian[1,2]*

[1] Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA, United States, [2] Fundación Para la Conservación de los Andes Tropicales, Quito, Ecuador

Understanding the factors that shape the diversity and composition of biotic communities in natural and human-modified landscapes remains a key issue in ecology. Here, we evaluate how functional traits, species diversity and community composition of palm species vary in relation to biogeographic variables and forest age in northwest Ecuador. Functional traits capture essential aspects of species' ecological tradeoffs and roles within an ecosystem, making them useful in determining the ecological consequences of environmental change, but they have not been used as commonly as more traditional metrics of species diversity and community composition. We inventoried palm communities in 965 10 × 10 m plots arrayed in linear transects placed in forests of varying age. Adult palms in forests of younger regeneration stages were characterized by species with greater maximum stem height, greater maximum stem diameter, and solitary stems. The shift in functional features could indicate that shade tolerant palms are more common in old-growth forest. The shift could also reflect the legacy of leaving canopy palms as remnants in areas that were cleared and then allowed to regrow. Moreover, younger forest age was associated with decreased abundance and altered species composition in both juvenile and adult palms, and decreased species richness in adults. These results highlight the importance of retaining intact, old-growth forest to preserve functional and species diversity and highlight the importance of considering multiple aspects of diversity in studies of vegetation communities.

Keywords: Arecaceae, functional traits, community composition, abundance, diversity, Chocó, species richness, secondary forest

Edited by:
Kelly M Andersen,
Nanyang Technological University,
Singapore

Reviewed by:
Daisy Cárate Tandalla,
University of Göttingen, Germany
Gerardo Avalos,
University of Costa Rica, Costa Rica

****Correspondence:***
Jordan Karubian
jk@tulane.edu

Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

***Received:** 08 March 2021*
***Accepted:** 24 March 2022*
***Published:** 27 April 2022*

Citation:
Lueder S, Narasimhan K, Olivo J, Cabrera D, Jurado JG, Greenstein L and Karubian J (2022) Functional Traits, Species Diversity and Species Composition of a Neotropical Palm Community Vary in Relation to Forest Age. Front. Ecol. Evol. 10:678125. doi: 10.3389/fevo.2022.678125

INTRODUCTION

Tropical forests harbor most of the planet's terrestrial biodiversity, however, anthropogenic influences put these systems under increasing pressure (Laurance et al., 2006; Bradshaw et al., 2009; Gardner et al., 2010). Expanding human settlements, agriculture, and infrastructure development induce persistently high rates of deforestation (Achard et al., 2002). Deforested areas are often allowed to regenerate after exploitation (Rudel et al., 2009), and, consequently, over half of the planet's contemporary forest cover is regenerating (Food and Agriculture Organization of the United Nations [FAO], 2010). As the proportion of regenerating forests continues to increase (Wright, 2010), the ability of these regenerating (i.e., secondary) forests to retain diverse biota has emerged as an important research topic over the past several decades.

The relative ability of secondary forests to support biodiversity is controversial (Barlow et al., 2007; Gardner et al., 2007; Norden et al., 2009; Gibson et al., 2011; Melo et al., 2013; Rozendaal et al., 2019). Some studies suggest that succession will occur predictably, indicating secondary forest species will converge with old-growth forests and retain significant proportions of the original diversity in the process (Finegan, 1996; Letcher and Chazdon, 2009; Norden et al., 2009). Alternatively, secondary forests may have disrupted ecological processes, with negative implications for biodiversity retention and conservation (Tabarelli et al., 2010, 2012; Gibson et al., 2011). A myriad of factors may influence the biodiversity value of secondary forests, including landscape context (Tabarelli et al., 2010; Araia et al., 2019), successional pathways (Arroyo-Rodríguez et al., 2017), and stochasticity (Chazdon, 2008), with many studies emphasizing the resilience of secondary forests occurring under ideal conditions (e.g., proximity to old-growth forest, high levels of seed dispersal) (Letcher and Chazdon, 2009; Norden et al., 2009). Moreover, outcomes differ markedly based on study taxa; while secondary forests may provide appropriate habitat for many species, others are disadvantaged or excluded (Barlow et al., 2007; Tabarelli et al., 2012; Martin et al., 2013).

Another important consideration concerns how biodiversity is measured. Species richness is a fundamental metric of biodiversity (Su et al., 2004), but it may fail to capture important components of a habitat's value for conservation. For example, in a recent meta-analysis of longitudinal studies, Blowes et al. (2019) concluded that while local species richness is not changing on average worldwide, local change in community composition is pervasive. The decoupling of species richness and community composition may be due to differential speeds of recovery: in tropical tree communities, species richness is thought to recover more quickly, over the span of decades, while community composition may require centuries to recover (Finegan, 1996; Liebsch et al., 2008; Martin et al., 2013; Rozendaal et al., 2019).

Functional trait analyses may also provide important perspectives that complement those provided by species richness and community composition. Functional traits are a species' morphological, physiological, or phenological characteristics that influence growth, reproduction, or survival (Violle et al., 2007). These traits mediate species' responses to environmental changes, revealing how different ecological strategies are constrained in community assembly (Paine et al., 2011; Boukili and Chazdon, 2017). Moreover, changes within the functional composition of forest communities along environmental gradients may point to mechanisms behind alterations in ecosystem functioning and services (Dìaz and Cabido, 2001; Díaz et al., 2013). Studies that combine richness, community composition, and functional trait analysis are rare but have the potential to provide a more holistic understanding of how habitat characteristics impact biodiversity.

Palms (Arecaceae) are among the most abundant and diverse neotropical plant taxa (Goulding and Smith, 2007; ter Steege et al., 2013; Muscarella et al., 2020). As fundamental components of forest structure and function, palms influence plant recruitment (Wang and Augspurger, 2004), nutrient turnover (Villar et al., 2020), and the movement of dispersers and pollinators (Galetti et al., 2006; Muñoz et al., 2019; Sardeshpande and Shackleton, 2019). Furthermore, they are a keystone food resource for many frugivorous species (Galetti et al., 2006; Muñoz et al., 2019; Sardeshpande and Shackleton, 2019). Additionally, from an anthropogenic perspective, neotropical palms often provide crucial economic and cultural services (Bernal et al., 2011; Macía et al., 2011). Previous work has suggested palms are sensitive to anthropic disturbances and environmental gradients (Pintaud, 2006; Arroyo-Rodríguez et al., 2007; Baez and Balslev, 2007; Eiserhardt et al., 2011; Montúfar et al., 2011; Benchimol et al., 2017), highlighting the importance of understanding impacts of human activities on this key group.

As many palms are long-lived (Tomlinson, 2006), the contemporary mix of adults on the landscape may represent the recruitment, establishment, and persistence processes that occurred over the past several decades, whereas juveniles are more likely to reflect more recent assembly processes (Norden et al., 2009; Green et al., 2014). Differences between the two life stages can indicate demographic changes occurring in the community, pointing to trends in population growth and impending shifts in diversity and composition related to abiotic (e.g., light, moisture) or biotic (e.g., dispersal mutualisms) factors. Yet, how palm communities vary between relatively undisturbed vs. regenerating forests has not been widely studied (Montúfar et al., 2011). Those studies available have highlighted increasing species richness of juveniles (Capers et al., 2005), converging composition of canopy palm communities to those in old-growth forest during succession (Norden et al., 2009), and increased susceptibility of juveniles to distance to forest edge (Browne and Karubian, 2016).

Our goal in this study was to identify how patterns of Neotropical palm abundance, species richness, community composition, and functional trait composition vary in relation to forest age, in juvenile and adult life stages. We predicted that, after controlling for effects of elevation, abundance and richness will decrease in younger forests and community composition and functional trait composition will differ in relation to forest age. We also predicted that responses to forest age will be stronger in juvenile palms due to recent habitat loss and stronger responses to diversifying processes.

MATERIALS AND METHODS

Study Region

We conducted this study in the Chocó Biogeographic zone, a relatively poorly studied, increasingly modified conservation hotspot known for exceptional diversity of palms and other species (Gentry, 1986; Dodson and Gentry, 1991; Myers et al., 2000). Data were collected in and around the Mache-Chindul Ecological Reserve (REMACH, 0°47′N, 79°78′W), Esmeraldas Province, Ecuador, from June to August 2019. The most common forest types in REMACH are humid evergreen and sub-humid evergreen, with canopy height of primary forest typically ranging from 30–40 m. Dominant tree families include Arecaceae, Rubiaceae, Lauraceae, Moraceae, and Myristicaceae (Clark et al., 2006). REMACH is a mountainous area ranging from sea level to over 700 m asl. Previous work here by

Browne and Karubian (2016) showed that elevation was an important predictor of abundance and community composition of palms, across both adult and seedling life stages.

We sampled habitats within two privately owned reserves – Fundación para la Conservación de los Andes Tropicales (FCAT, 00°23′28″N, 79°41′05″W) and Bilsa Biological Station (BBS, 00°21′33″N, 79°42′02″W) – and in adjacent areas on privately owned lands (**Figure 1**). The study region receives approximately 2,500-3,500 mm of precipitation annually and the average temperature is between 23°C and 25.5°C (Clark et al., 2006). We sampled representative habitat types (forest, pasture, agricultural crops) covering nearly the full gradient of elevations (198-686 m.a.s.l., **Supplementary Table 1**) and range of regeneration (primary (undisturbed) forest and secondary (previously disturbed) forest) found in REMACH (**Supplementary Figure 1**). This area has been extensively deforested, reflecting the deforestation that has occurred in all of western Ecuador (Dodson and Gentry, 1991). Deforestation in our study area is relatively recent, beginning ca. 40 years ago (Browne and Karubian, 2016) and continuing into the present (Van der Hoek, 2017; Kleemann et al., 2022). The annual mean net change in forested area is dynamic, with the periods between 1990 to 2000 and 2000 to 2008 exhibiting the highest amount of forest lost (Tamayo et al., 2020). The landscape at the time of data collection was a dynamic agro-mosaic consisting of many isolated forest fragments, pasture, and agricultural crops. As several members of our team (JO, DC) have lived in the area for over 30 years, we had *a priori* knowledge of forest chronosequence. We were unable to obtain exact data on forest age from remotely sensed images or aerial photograph due to low image resolution and the persistence of cloud cover in the study area.

Palm Transect Sampling

To sample palm communities, we established nine, 10 × 1000-m long transects and one 10 × 650-m long transect in and around REMACH. Each transect was composed of a linear series of 10 × 10 m plots. Transect locations were selected to cover the full range of forest regeneration in the area, ranging from old-growth forest through those highly degraded, as well as agricultural and pasture lands (**Supplementary Figure 1**). At each plot, we classified the habitat as pasture, crop, or forest; the forest category represented forests of primary and secondary successional stages. Within each plot, we recorded all individuals of palms, assigning them to the lowest possible taxonomic level. We classified each individual into seedlings, juveniles, subadults, and adults following Browne and Karubian, 2016: seedlings have undivided leaves; juveniles, divided leaves but no signs of reproduction; subadults, a size near that of a reproductive adult but with no signs of reproductions; and adults, signs of current or past reproduction. We later collapsed seedlings and juveniles into a single 'juvenile' category and sub-adults and adults into a single 'adult' category. For clonal species (e.g., *Prestoea decurrens*), we classified each ramet as an individual.

We characterized the habitat of each 10 × 10 m plot in each transect. We recorded soil moisture (M0750 Soil Moisture Meter, Extech, Boston, MA, United States) and leaf litter at five points within the plot: once in the center and once in each cardinal direction at the plot boundaries. To record leaf litter, we inserted a sharp metal dowel (3 mm diameter) through the litter and into the humus layer. We then marked the dowel, pushed the litter aside, and measured between the two points to the nearest 0.1 cm (Kostel-Hughes et al., 1998). We measured canopy cover using a spherical crown densiometer (Concave – Mode C – Robert E. Lemon, Forest Densiometer – Bartlesville, OK, United States), standing in the center of the plot and recording measurements in the four cardinal directions. We measured understory density using a 1.9-meter-tall metal pole marked with sighting targets placed at 13 evenly spaced intervals. An individual held the pole upright in at the plot boundary in each of four cardinal directions and an individual standing at the center point of each plot counted how many sighting targets were completely unobstructed by vegetation. We recorded canopy height using a laser rangefinder to measure the height of the tallest tree. We counted the number of trees > 10 cm and > 50 cm diameter at breast height (DBH) and the number of *Cecropia* spp., a species of tree that can be used as a proxy for disturbance (Didham and Lawton, 1999). We recorded elevation using a handheld GPS device (Garmin Foretrex 601, Garmin International, Inc., Olathe, KS, United States). For all forest plots, to estimate the distance to the edge of the forest, we calculated the distance between plot center and the nearest forest edge using the most recent high resolution (5 m) imagery available (PlanetScope, Planet labs, San Francisco, CA, United States) in QGIS (QGIS Development Team, 2020).

Data Analysis

Principal Component Analysis

We used a Principal Component Analysis (PCA) to reduce the dimensionality of the environmental variables and avoid using correlated variables for the abundance, species richness, and community composition analyses. Because many variables were highly correlated with elevation (soil moisture, leaf litter, understory density), we excluded these from the PCA and conducted separate analyses on elevation (below). We treated each 10 × 10 m plot as an independent sampling unit. We conducted each set of analyses separately for juveniles (including seedlings) and adults (including sub-adults).

Species Abundance and Richness Models

We modeled species abundance and richness with generalized linear models to account for non-normal distributions in response variables. We used a Poisson distribution for species richness models (O'Hara and Kotze, 2010) and a negative binomial distribution for palm abundance models (O'Hara and Kotze, 2010). Both distributions model non-negative count data. The negative binomial distribution allows for more variance in the response variable and accordingly accounts for overdispersion. We tested these models against models with other distributions, plotting and comparing residuals and fitted values to check for residual patterns (Zuur et al., 2009). We used PC1, PC2, and elevation as fixed effects. We performed each regression analysis on each transect separately ($N = 10$). We then calculated the mean regression coefficients from the separate transect analyses, and, using a one-sample t-test,

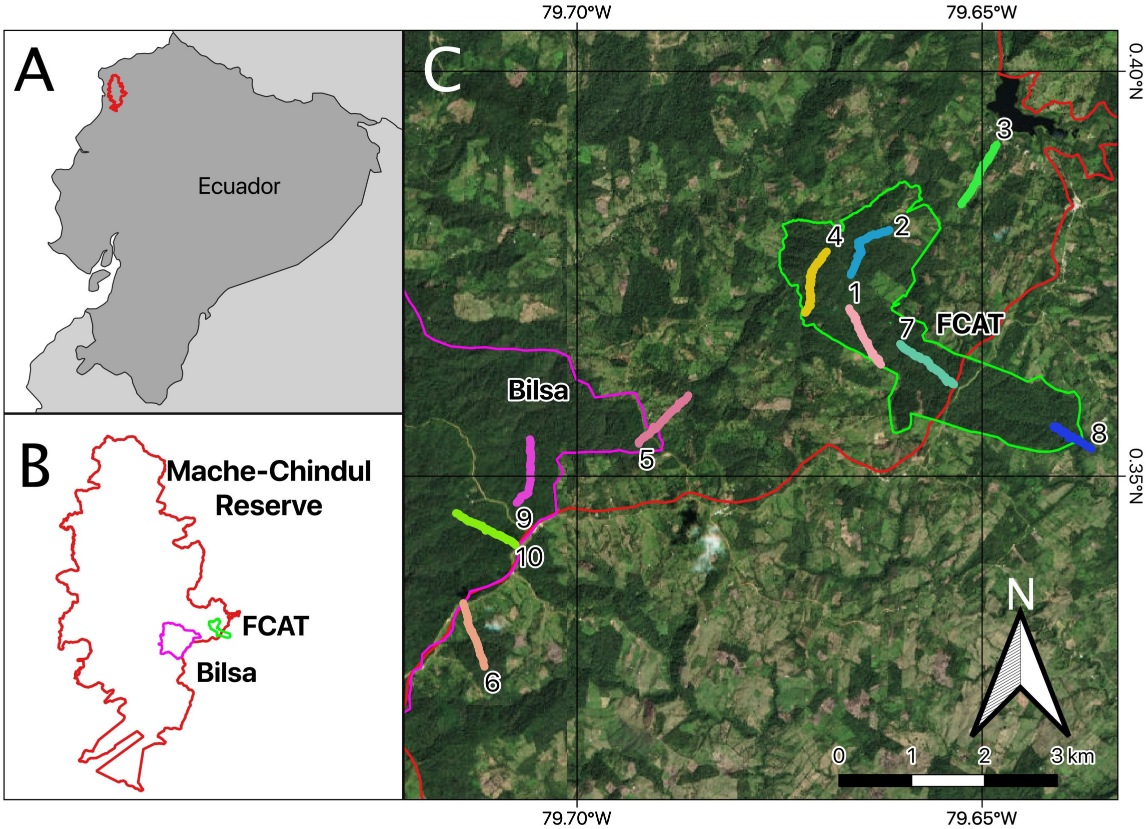


FIGURE 1 | (A): Map of Ecuador with the Mache-Chindul Ecological Reserve (REMACH) outlined in red. **(B)**: A close up of REMACH with the Fundación para la Conservación de los Andes Tropicales (FCAT, green) and the Bilsa Biological Station (Bilsa, purple) outlined. **(C)**: The study site, the transect locations, and associated ecological reserves. Transects, made of continuous 10 × 10 m plots, are distinguished by color.

determined if the means were different from zero (cf. Normand et al., 2006; Browne and Karubian, 2016). We quantified the variance around the mean estimated regression coefficients using standard deviation. Performing the regression analyses on transects separately allowed us to remove those that were spatially autocorrelated to ensure that our results were not pseudo-replicated. This method also allowed us to assess how patterns vary between transects by using the variance around the mean. To test for spatial autocorrelation within our models, we used Mantel tests with 999 permutations (Giraldo et al., 2018). We created a distance matrix from the geographical data of each plot, as well as a distance matrix from the residuals of each of the regression models for abundance and richness. Using these matrices, the Mantel test indicated whether there was a significant correlation between the two. The geographical distance matrix was $\log_{10}$-transformed, as logarithmic distance decay is expected to occur due to dispersal limitation (Condit et al., 2002) and based on Haversine distance. We detected significant levels of spatial autocorrelation for the model assessing juvenile richness in one transect, T5 (**Supplementary Table 2**) and subsequently removed this transect from our analysis. Removing the regression coefficient associated with this model from the one-sample t-test did not change the qualitative outcome of the results.

Community Composition Analysis

Partial Mantel tests assess the correlation between two distance matrices while controlling for a third, allowing us to analyze the effects of spatially independent environmental variables on species composition. Following Kristiansen et al. (2012), we conducted analyses for both juveniles and adults. In each we tested a species composition matrix, using data from all the transects combined, against each of the most informative Principal Components from the PCA as well as elevation while controlling for the geographical distance matrix. Controlling for geographical distance addresses the effect of spatial autocorrelation within the transect sample design. For the juvenile and adult species composition matrices, we used presence-absence data and computed dissimilarity using Sørensen distance (Legendre and Legendre, 1998). To estimate the distances between Principal Component scores as well as elevation, we used Euclidean distance.

To further assess the compositional patterns among juveniles and adults, we employed non-metric multidimensional scaling (NMDS). We removed species with <5 adult individuals or <10 juvenile individuals from the respective analyses, considering these rare species, to reduce noise in the multivariate analysis (McCune et al., 2002). NMDS ordinations were based on dissimilarity matrices generated from species abundance data and Bray–Curtis distance. To evaluate how species composition varied along principal components and elevation, we calculated multiple regression of environmental variables along the ordination axes with 999 permutations *post hoc*. To visualize the association between environmental variables and community composition, we overlayed these results on the NMDS axes.

Functional Trait Analyses

To assess how functional traits and environmental variables co-vary, we utilized RLQ (a multivariate analysis) and fourth-corner (a bivariate analysis) methods, carrying them out for adults and juveniles. Both analyses rely on information from three tables: R (environmental variable data), Q (functional trait data), and L (species distribution data) (Dray et al., 2014).

Environmental variables included were canopy cover, leaf litter depth, elevation, distance to forest edge, number of *Cecropia*, number of trees DBH > 10 cm, and number of trees DBH > 50 cm. We removed canopy height, soil moisture, and understory density from the analysis based on their high correlation with the remaining variables. We selected species functional traits based on which were available for all species in "PalmTraits 1.0, a species-level functional trait database of palms worldwide" (Kissling et al., 2019). Traits included were climbing habit, erect habit, solitary stem habit, stem armature, leaf armature, maximum stem height, maximum stem diameter, strata, average fruit length, fruit size, and fruit color conspicuousness (**Supplementary Material**, **Table 3**). The following were analyzed as binary variables: climbing habit, erect habit, solitary stem habit, stem and leaf armature, strata, and fruit color conspicuousness.

RLQ is a multivariate analysis that allows the qualitative assessment of the relationships between environmental variables and functional traits mediated by species abundances. The analysis is visualized in an ordination plot, with axes that explain functional trait and environmental variable cross-covariance. Before performing RLQ analysis, each table necessitates a separate ordination. For table L, we applied Correspondence Analysis; for table R, a Principal Component Analysis; and for table Q, a Hill-Smith analysis (Hill and Smith, 1976).

The fourth-corner method evaluates the association between pairs of single variables (i.e., one functional trait and one environmental variable) corresponding to a matrix containing trait-environment association measures. This means here we are testing bivariate associations as opposed to performing a multivariate analysis like the RLQ analysis (Legendre et al., 1997; Dray and Legendre, 2008; Dray et al., 2014). To control type I error, we combined outputs from two permutation models: model 2, which tests the null hypothesis that the environment does not influence the distribution of species with fixed functional traits and model 4, which tests the null hypothesis that the functional traits do not influence the distribution of species with fixed environmental conditions (ter Braak et al., 2012). We performed these tests sequentially, only performing the second test if we rejected the null hypothesis of the first, which further fixes type I error (ter Braak et al., 2012). Because the fourth-corner method deals with bivariate associations and our study considered many functional traits and environmental variables, the number of tests was high, necessitating adjusting p-values (Dray et al., 2014). Here, we used the false discovery rate method (Benjamini and Hochberg, 1995) to control for the error rate.

After performing RLQ analyses and fourth-corner methods separately, we combined the two approaches, addressing some of the issues that arise from the respective analyses (Dray et al., 2014). RLQ provides no significance tests, and our factorial maps were hard to interpret due to the large number of variables considered. Fourth-corner does not consider covariation among environmental variables and produced no significant results when p-values were adjusted. To remedy these issues, we used fourth-corner methods to test the associations between the RLQ axes and the functional traits/environmental variables. Here, we performed model 2 and model 4 permutation tests sequentially (ter Braak et al., 2012) and adjusted p-values using the false discovery rate method (Benjamini and Hochberg, 1995), as outlined above.

All data analyses were performed in R v3.5.2 (R Core Team, 2018). Poisson models and negative binomial models were performed with the 'glmmTMB' package (Brooks et al., 2017). Distance matrices, NMDS ordination, NMDS overlays, Mantel tests, and Partial Mantel tests were performed with the 'vegan' package (Oksanen et al., 2019). RLQ and fourth-corner analyses were performed with the 'ade4' package (Dray and Dufour, 2007).

RESULTS

Summary Data

The 9,750 m^2 sampled in our transects included 7,440 m^2 forest (76.3%), 1,590 m^2 pasture (16.3%), and 720 m^2 crop land (7.1%). Sixteen species of palms and 2,989 individuals were identified. Of the 2,989 individuals, 2949 (99%) were found in forest, with 17 found in pasture (all adults) and 23 found in crop land (11 adults, 12 juveniles). In pasture and crop land, *Iriartea deltoidea* was the most prevalent species, accounting for 64.3% of adults and 25% of juveniles (**Table 1**). Due to the low number of palms in the non-forested habitat types, we restricted remaining analyses to only forested habitat.

Of the 2,949 individuals found in forest, 2,219 (75%) were juveniles and 730 (25%) were adults. For adults, three abundant species accounted for 70% of individuals recorded: *I. deltoidea* (31%), *P. decurrens* (24%)*, and Geonoma cuneata* (16%). For juveniles, the three most abundant species (62% of individuals) were *I. deltoidea* (34%)*, Attalea colenda* (15%), and *P. decurrens* (13%) (**Table 1**).

PCA Results

The PCA analysis produced two axes that account for 49.6% of the variance in the six environmental variables used. PC1 accounted for 28.35% of the variance and is dominated by canopy cover, canopy height and density of the pioneer species *Cecropia.* Thus, we treated PC1 as an index of forest age, with higher values representing younger forests. PC2, which accounted for 21.25% of the variance, was associated with the tree density. High

TABLE 1 | Number of individuals of adults (adults and sub-adults) and juveniles (juveniles and seedlings) found in each habitat within the 965 plots in and around the Mache-Chindul Reserve, north-western Ecuador.

	Forest		Pasture		Crop		Total	%
	Adult	**Juvenile**	**Adult**	**Juvenile**	**Adult**	**Juvenile**		
Species								
Astrocaryum standleyanum	8	43	0	0	1	0	52	1.7
Attalea colenda	1	322	1	0	1	2	327	10.9
Bactris colorandonis	29	30	1	0	0	1	61	2
Bactris setulosa	12	6	0	0	0	0	18	0.6
Chamaedorea linearis	6	1	0	0	0	0	7	0.2
Desmoncus cirrhifer	14	3	0	0	0	0	17	0.6
Geonoma cuneate	115	60	0	0	0	0	175	5.8
Iriartea deltoidea	222	753	12	0	6	3	996	33.3
Oenocarpus bataua	10	192	1	0	1	1	205	6.9
Pholidostachys synanthera	0	1	0	0	0	0	1	0.03
Phytelephas aequatorialis	12	254	1	0	0	0	267	8.9
Prestoea decurrens	177	297	0	0	0	1	475	15.9
Prestoea ensiformis	4	0	0	0	0	0	4	0.1
Socratea exorrhiza	48	175	1	0	2	3	229	7.7
Synechanthus warscewiczianus	50	49	0	0	0	1	100	3.3
Wettinia aequalis	22	33	0	0	0	0	55	1.8

PC2 scores are associated with a higher density of small trees (DBH > 10 cm) and low scores are associated with a higher density of large trees (DBH > 50 cm) (**Table 2**).

Richness, Abundance, and Community Composition in Forest

Younger forests (as measured by PC1) were associated with decreased abundance of adults and juveniles, decreased adult species richness, and a change in community composition for adults and juveniles (**Tables 3**, **4**). PC1 dissimilarity was more strongly associated with compositional dissimilarity for the juvenile palm community compared to the adult palm community (**Table 4**). Changes in tree density, as measured by PC2, were not associated with abundance, species richness, or changes in community composition for either age class (**Tables 3**, **4**). As elevation increased, there was an associated decrease in juvenile abundance and a change in adult community composition, but no change in richness for either age class (**Tables 3**, **4**). The patterns of change in richness and abundance varied markedly between transects, as indicated by the variance around the mean regression coefficients (**Table 3**).

TABLE 2 | The loadings of the nine environmental variables on the first two axes of a Principal Component Analysis, the variance explained by each axis, and the eigenvalues of each axis.

Environmental variables	PC 1	PC 2
Canopy Cover%	– 2.1969	1.1343
Cecropia spp.	0.8406	1.7012
Trees above 50 cm DBH	−1.8593	−1.4872
Trees above 10 cm DBH	−1.3816	2.4700
Canopy Height (m)	– 2.5267	−0.6765
Variance explained	28.35%	21.25%
Eigenvalue	1.4177	1.0624

The above results on community composition are largely corroborated by NMDS ordination, which indicated that PC1 significantly affected composition in adults and nearly significantly affected juveniles (**Table 5**). Visualized in the NMDS plots, the second ordination axes reflected differences in species composition across forest age, as indicated by PC1 (**Table 5** and **Figure 2**). For adults, the younger sites and associated species are to the top of the ordination space. For juveniles, the younger sites and associated species are to the bottom of the ordination space. Neither PC2 nor elevation significantly affected composition in this analysis (**Table 5**).

Functional Trait Analysis

For juveniles, the first axis of the RLQ ordination indicates when trees DBH > 10 cm decrease and distance from edge increases (**Figure 3A**), palm species with armed stems decrease and species with non-solitary stems increase (**Figure 3C**). This is exemplified by *Astrocaryum standleyanum*, which has low scores on the axis (**Figure 3E**), and a solitary, armed stem. For adults, the first axis of the RLQ ordination revealed a positive relationship between elevation, distance to edge, trees DBH > 10 cm (**Figure 3B**) and palms species with non-solitary stems, non-erect stems, and climbing stems (**Figure 3D**). This is exemplified by *Desmoncus cirrhifer*, which has high scores on the axis (**Figure 3F**), and a stem with non-solitary, non-erect, and climbing habit. The fourth-corner analysis revealed no associations between individual traits and environmental variables when p-values were adjusted for multiple tests.

Combining the approaches, there were associations for adults between the second RLQ axis and three functional

TABLE 3 | Estimated regression coefficients ± standard deviation for the abundance and species richness of adult and juvenile palms.

	Adult abundance	Juvenile abundance	Adult species richness	Juvenile species richness
PC1	**−1.30 ± 1.15****	**−1.19 ± 1.23***	**−1.27 ± 1.44***	−0.695 ± 1.31
PC2	0.181 ± 0.760	−0.211 ± 0.803	−0.954 ± 2.94	−0.448 ± 0.716
Elevation	−0.00204 ± 0.0139	**−0.010 ± 0.0121***	−0.220 ± 0.567	−0.00866 ± 0.0155

Statistical significance is signified with bold text. $^{**}P < 0.01$; $^{*}P < 0.05$.

traits: maximum stem height (*p*-adjusted = 0.00667), maximum stem diameter (*p*-adjusted = 0.00667), and solitary stem habit (*p*-adjusted = 0.0145). The second RLQ axis represents forest maturity, as along it canopy cover and distance from edge of forest increase and trees DBH > 10 cm and leaf litter decrease (**Figure 3B**). Along this axis, the maximum stem height decreased, maximum stem diameter decreased, and solitarily stemmed palms became less common (**Figure 3D**). No other associations between the RLQ axes and functional traits were significant after *p*-values were adjusted, and no significant relationships were found between the axes and the environmental variables.

DISCUSSION

Because of their outsized importance for ecological processes and humans, identifying how Neotropical palm tree diversity, abundance, composition, and functional traits vary in relation to forest age sheds important light on the value of regenerating (i.e., secondary) forests for the conservation of biodiversity and the well-being of human residents. Working in a biodiversity hotspot in northwest Ecuador, we found that abundance decreased and community composition changed for both juveniles and adults in younger, regenerating forests relative to older, more intact forests. Adult species richness also decreased in younger forests, while juvenile species richness remained unaffected. We also documented decreased maximum stem height and diameter among adults, but not juveniles, in more mature forests and an impact of elevation on both juvenile abundance and adult community composition. These results suggest that secondary forests have less diverse palm communities in our study area, emphasizing the importance of undisturbed forests for these iconic components of the tropical flora and the associated food webs and other biotic processes they help to support.

TABLE 4 | Mantel r statistics according to partial Mantel tests of 10 transects (*n* = 16 species) located in northwestern Ecuador.

	Adult	Juvenile
PC1	**0.02726***	**0.08399*****
PC2	−0.001241	-0.009599
Elevation	**0.03354***	0.01893

Statistical significance is signified with bold text. $^{***}P < 0.001$; $^{*}P < 0.05$.

TABLE 5 | Correlation coefficients of environmental variables according to a non-metric multidimensional scaling ordination of 10 transects (*n* = 16 species) in northwestern Ecuador.

	NMDS1	NMDS2	R^2	*P*-value
Adults				
PC1	-0.07014	0.99754	0.0169	**0.027***
PC2	-0.55859	0.82945	0.0008	0.835
Elevation	0.96615	0.25800	0.0049	0.378
Juveniles				
PC1	−0.36303	−0.93178	0.0127	0.062
PC2	−0.91352	−0.40680	0.0084	0.164
Elevation	−0.14686	0.98916	0.0031	0.497

Statistical significance is signified with bold text. $^{*}P < 0.05$.

Contrasting patterns between juvenile and adult palms can be useful in inferring future trajectories of palm communities in secondary forests. Our results seem to imply that the palm community will recover in richness as forests age, but with a distinctive composition of species compared to more pristine old-growth forests. The projection of sustained compositional change points to a persistent presence of 'winners' and 'losers' (Tabarelli et al., 2012), shaped by tolerance to anthropogenic disturbance. In these recovering habitats, available species may be those that are robust against the altered biotic and abiotic factors associated with forest clearing secondary succession. Reduced abundance among juveniles in secondary forests may also point to these forests supporting fewer palms in addition to different subsets of species. For example, *Prestoea decurrens* is a species that is more abundant in mature forests as juveniles but is more abundant in younger forests as adults (**Figure 2**). This incongruency may lead to a decrease in *P. decurrens* in regenerating forests over time if they fail to reproduce in these areas. However, there was marked variation between transects in their responses to forest age, so this may depend on location context. It is also worth noting that the cumulative amount of forest at the landscape level has also been decreasing in the past few decades (Van der Hoek, 2017), which may impact contemporary regeneration processes vs. those occurring in the past.

In the current study, increased elevation affected adult community composition and was associated with a minor decrease in juvenile abundance. Alternatively, Browne and Karubian (2016)'s study in the same area found increased elevation changed community composition and increased abundance for both juvenile and adult palms. These differences between the two studies may be due to the highly variable nature of the effect of elevation on communities, indicating that palm communities respond to elevation in a location-dependent manner. This is supported by the high degree of variation we found between transects in their responses to elevation.

Within the adult palm community, three functional traits representing variation in light acquisition strategies (Chazdon, 1991; Westoby, 1998; Svenning, 2000) were associated with varied

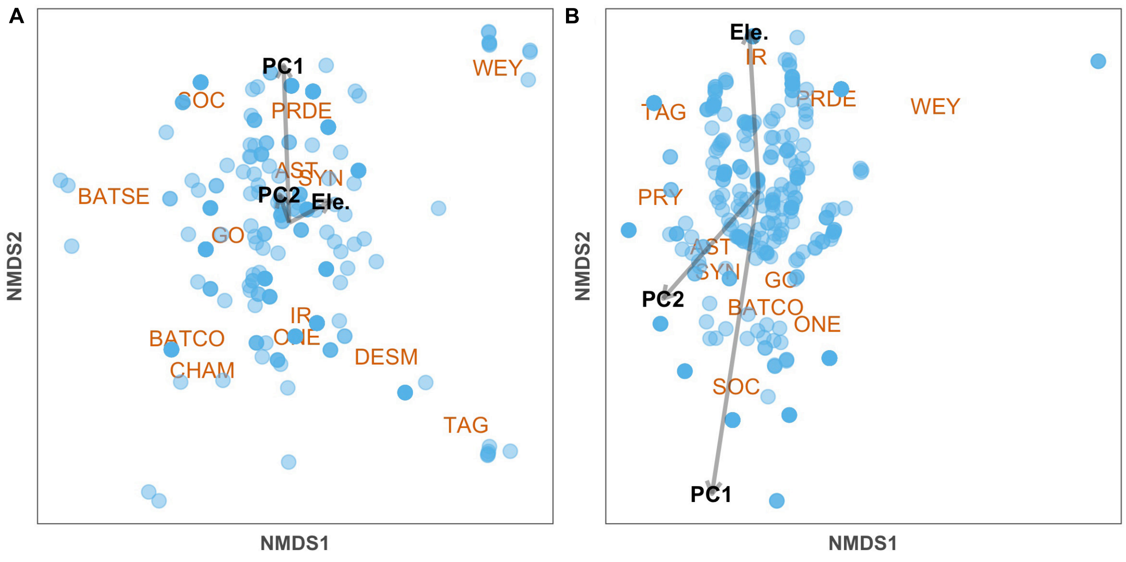


FIGURE 2 | Non-metric multidimensional scaling (NMDS) with projection of environmental variables in 10 transects in northwestern Ecuador, based on the dissimilarity of species abundance data and Bray-Curtis distance for **A** adults (Stress = 0.069) and **B** juveniles (Stress = 0.14).

regeneration stages: more mature forests were characterized by species with decreased (1) maximum stem height, (2) maximum stem diameter, and (3) solitary stem habit (Tabarelli et al., 2012). Functional traits related to light acquisition may be particularly sensitive to changes in microclimate, like those seen in forest regeneration (Zambrano et al., 2019). Palms of smaller stature, having greater shade tolerance (Chazdon, 1991; Svenning, 2002), may be replaced by species that occur preferentially in areas with increased light levels or species that occur irrespective of light availability in younger forests. For example, Craven et al. (2018) found evidence of functional convergence in light acquisition strategies during secondary succession in a wet tropical forest plant community. Along the successional gradient, trait variation was reduced due to the increased competitive advantage afforded to certain trait combinations. Our results suggest this may be occurring in our study area as well, indicating a potential functional shift in the biota. However, associations between traits and succession were found only in adults. Many palm species of all strata are able to remain in deep shade as acaulescent juveniles in their establishment phase (Kahn and de Granville, 1992; Charles-Dominique et al., 2003). When light availability is increased and reaches the acaulescent juveniles, either by natural or anthropogenic disturbance, taller, solitary palms may become common due to their ability to utilize the increased light, growing quickly and transitioning from a juvenile to an adult (Martínez-Ramos et al., 1988; de Granville, 1992; Cintra and Horna, 1997; Pintaud, 2006). This may explain why we only see the variation in stem height, diameter, and solitary stem habit in adult palms. In addition, our functional trait analyses did not include leaf traits, which may be more important in determining the shade tolerance of juveniles (Poorter et al., 2008).

The influence of shade tolerance on palm composition may be visualized by the abundance of the species *Socratea exorrhiza* and *Phytelephas aequatorialis* across a gradient of forest age. *S. exorrhiza* is a canopy palm that appears to be more abundant in younger forests (**Figure 2**) and is tolerant to a variety of environments. Other studies have found it to be dominant in regenerating secondary stands as well (Norden et al., 2009), potentially in part because of its ability to tolerate different light regimes. Conversely, *P. aequatorialis* (Escobar et al., 2022), an understory palm more abundant in older forests (**Figure 2**), regenerates best in shaded environments (Palacios and Jaramillo, 2005). This may limit the species' ability to thrive in younger forests.

Alternatively, differences in stem height, stem diameter, and solitary stem habit may reflect the fact that some canopy palms may be left standing in pastures or agricultural land as 'remnants', around which regenerating forests may grow when the lands are abandoned. Canopy palms often remain as isolated trees, while hardwoods and understory palms are cleared (Guevara et al., 1998; Harvey et al., 2004). The high abundance of remnants, and their presence as a seed source, may catalyze a proliferation of the remnant canopy species in regenerating forest patches (Aldrich and Hamrick, 1998). The abundant, limited subset of remnant canopy palms may be over-represented relative to other functional groups in younger, regenerating forests relative to mature, intact forests. Other studies have found an overrepresentation of remnant trees in nearby forest patches as well (Aldrich and Hamrick, 1998) and have found that remnant trees are able to influence the composition of a regenerating forest for decades (Schlawin and Zahawi, 2008; Sandor and Chazdon, 2014). The proliferation of remnant palms in regenerating habitats may be reflected by the abundance of *Oenocarpus bataua* juveniles in younger forest, as *O. bataua* are often left as remnants in the study area. The potential influence of remnant trees in this study highlights the need to consider remnant trees when

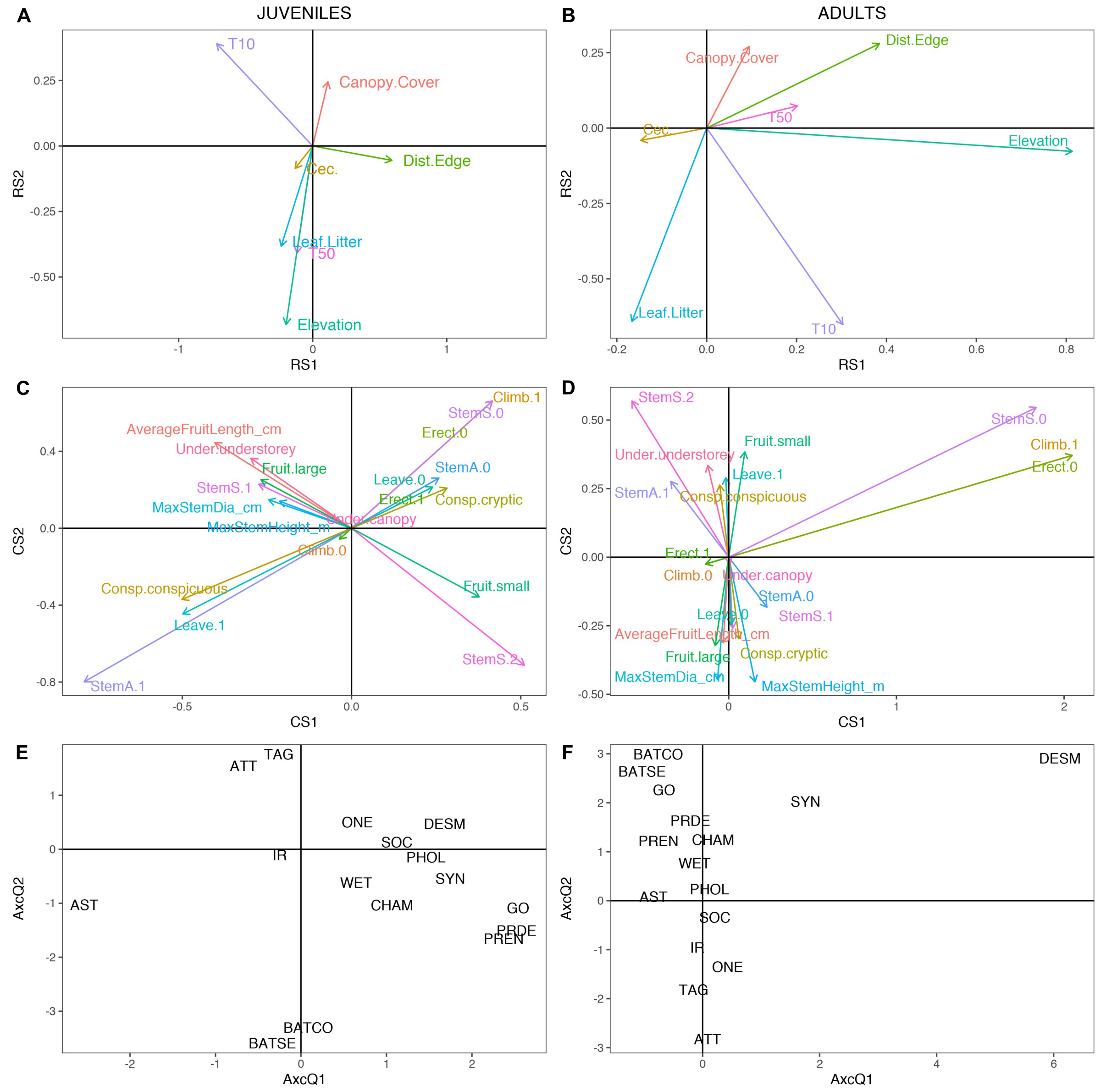


FIGURE 3 | Results of the first two axes of RLQ analysis for juveniles **(A,C,E)** and adults **(B,D,F)**. **(A,B)** visualize the coefficients of the environmental variables. **(C,D)** visualize the functional traits of palm species. **(E,F)** visualize the scores of the palm species. Codes for species, environmental variables, and traits are available in **Supplementary Tables 3–5**.

attempting to quantify patterns of biodiversity. It also points to a need to better understand the impacts of remnant palms on downstream ecological processes (e.g., frugivory) and on the abundance and diversity of species they support.

Utilizing species richness, community composition, and functional trait analysis in concert helped us to produce a more cohesive view of palm communities. Across a gradient of forest regeneration, the juvenile community changed in composition but not in species richness, pointing to the phenomenon of plant species richness recovering more quickly than species composition in tropical forests (Finegan, 1996; Liebsch et al., 2008; Martin et al., 2013; Rozendaal et al., 2019). As such, our study adds to global patterns of uncoupling between species richness and changes in community composition (Blowes et al., 2019) and stresses the importance of utilizing both species richness and community composition.

Our study is one of the first to address how functional traits vary along environmental axes within the palm community in the study area. Our results highlight how functional traits differ between adult and juvenile communities, both through the RLQ ordination (**Figure 3**) and through the fourth-corner analysis results. Utilizing functional trait composition pinpointed potential mechanisms for diversity loss, highlighting the value of combining trait analyses with traditional metrics of diversity.

Our results may be of particular value as palms are often removed in functional trait analyses of plant communities due to their differences in stem and leaf structure compared to dicot trees (Boukili and Chazdon, 2017), further restricting our understanding of functional trait patterns during succession.

Alongside evidence that secondary forest environments are selecting for different functional traits and contribute to shifts in diversity and composition, it is worth noting that other drivers are likely influencing the palm community. Species that may establish and survive in secondary habitats under ideal conditions may experience decreased success because of landscape-scale processes that can degrade forest habitat. In a highly degraded landscape like that of our study, these processes may include forest loss at the landscape scale (Rocha-Santos et al., 2016) and the intensity of previous land use (Karp et al., 2012; Jakovac et al., 2015). Both of these processes can independently affect palm diversity (Vandermeer et al., 2010; Benchimol et al., 2017). Forest loss can alter the diversity, density, and/or distance traveled by animal seed dispersers (Montúfar et al., 2011; Browne and Karubian, 2018) in addition to reducing proximity of regrowth to old-growth seed sources (Norden et al., 2009), with implications for dispersal outcomes of palm species. Intense previous land uses may alter abiotic factors vital to the regeneration of many palm species (Eiserhardt et al., 2011), like soil quality and nutrient availability (Lawrence et al., 2007; Runyan et al., 2012). The changes in the palm communities observed here are most likely due to multiple, potentially synergistic explanations (Benchimol et al., 2017). Moreover, our data were collected during one season, and the predictions on community change may change with a multi-year study. Future studies interested in palm communities, particularly when studies concern seedlings, should prioritize long-term data collection (Norden et al., 2009). Due to the site-specific and time-sensitive nature of the myriad factors that can influence community assembly processes, we caution the generalization of our results. We also caution interpretation of our results as general trends due to the possible effects of spatial autocorrelation, a longstanding issue in ecological survey data when transects are used.

Our results add to a line of evidence suggesting that palm communities are susceptible to changes caused by human-induced deforestation. Our study, to our knowledge, is the first to examine the effect of forest age on functional trait composition in palm communities. Our findings suggest that smaller palms, like *P. aequatorialis,* may be at greater risk in the palm community as undisturbed forest continues to disappear. While the juvenile community did not exhibit changes in functional trait composition, this may change over time. As the proportion of secondary forest increases, sensitive adult species may be limited to increasingly smaller areas and face increasing competition from remnant trees and less sensitive species. Over time, composition may continue to become more dissimilar and diversity lost.

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

JK and SL designed the research. SL, KN, JO, DC, and JJ contributed to data collection. SL and KN performed the statistical analyses. KN produced the figures. SL wrote the first draft of the manuscript. SL, KN, and JK contributed to revision. All authors contributed to the article and approved the submitted version.

FUNDING

Funding was provided by the Conservation Food and Health Foundation; Disney Conservation Fund; National Science Foundation (EAGER #1548548 and BEE # 2039842); Tulane University (Newcomb-Tulane College; Newcomb College Institute); and the United States Fish and Wildlife Service Neotropical Migratory Bird Act. We conducted work under permits from the Ecuadorian Ministry of the Environment (#010-2014-IC-FLO-FAU-DPE-MA).

ACKNOWLEDGMENTS

We thank the Ecuadorian Ministry of the Environment, the Jatun Sacha Foundation, and landowners in and around the Mache-Chindul Reserve for maintaining these forests and granting access. We also thank the Fundacion para la Conservacion de los Andes Tropicales (FCAT), particularly Margarita Baaquero, Luis Carrasco, Fernando Castillo and Nelson Gonzalez for logistical support.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.678125/full#supplementary-material

REFERENCES

Achard, F., Eva, H. D., Stibig, H. J., Mayaux, P., Gallego, J., Richards, T., et al. (2002). Determination of deforestation rates of the world's humid tropical forests. *Science* 297, 999–1002. doi: 10.1126/science.1070656

Aldrich, P. R., and Hamrick, J. L. (1998). Reproductive dominance of pasture trees in a fragmented tropical forest mosaic. *Science* 281, 103–105. doi: 10.1126/science.281.5373.103

Araia, M. G., Chirwa, P. W., and Assédé, E. S. P. (2019). Contrasting the effect of forest landscape condition to the resilience of species diversity in a human modified landscape: implications for the conservation of tree species. *Land* 9:4. doi: 10.3390/land9010004

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

Arroyo-Rodríguez, V., Melo, F. P. L., Martínez-Ramos, M., Bongers, F., Chazdon, R. L., Meave, J. A., et al. (2017). Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research: multiple successional pathways. *Biol. Rev.* 92, 326–340. doi: 10.1111/brv.12231

Baez, S., and Balslev, H. (2007). Edge effects on palm diversity in rain forest fragments in western Ecuador. *Biodiversity Conservation* 16, 2201–2211. doi: 10.1007/s10531-007-9159-5

Barlow, J., Gardner, T. A., Araujo, I. S., Avila-Pires, T. C., Bonaldo, A. B., Costa, J. E., et al. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proc. Natl. Acad. Sci. U S A.* 104, 18555–18560. doi: 10.1073/pnas.0703333104

Benchimol, M., Talora, D. C., Mariano-Neto, E., Oliveira, T. L. S., Leal, A., Mielke, M. S., et al. (2017). Losing our palms: the influence of landscape-scale deforestation on Arecaceae diversity in the Atlantic forest. *Forest Ecol. Manag.* 384, 314–322. doi: 10.1016/j.foreco.2016.11.014

Benjamini, Y., and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B Methodol.* 57, 289–300. doi: 10.1111/j.2517-6161.1995.tb02031.x

Bernal, R., Torres, C., García, N., Isaza, C., Navarro, J., Vallejo, M. I., et al. (2011). Palm management in South America. *Bot. Rev.* 77, 607–646. doi: 10.1007/s12229-011-9088-6

Blowes, S. A., Supp, S. R., Antão, L. H., Bates, A., Bruelheide, H., Chase, J. M., et al. (2019). The geography of biodiversity change in marine and terrestrial assemblages. *Science* 366, 339–345. doi: 10.1126/science.aaw1620

Boukili, V. K., and Chazdon, R. L. (2017). Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. *Perspect. Plant Ecol. Evol. Systemat.* 24, 37–47. doi: 10.1016/j.ppees.2016.11.003

Bradshaw, C. J., Sodhi, N. S., and Brook, B. W. (2009). Tropical turmoil: a biodiversity tragedy in progress. *Front. Ecol. Environ.* 7:79–87. doi: 10.1890/070193

Brooks, M., Kristensen, K., van Benthem, K., Magnusson, A., Berg, C., Nielsen, A., et al. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9, 378–400. doi: 10.32614/rj-2017-066

Browne, L., and Karubian, J. (2016). Diversity of palm communities at different spatial scales in a recently fragmented tropical landscape. *Botan. J. Linnean Soc.* 182, 451–464. doi: 10.1111/boj.12384

Browne, L., and Karubian, J. (2018). Habitat loss and fragmentation reduce effective gene flow by disrupting seed dispersal in a neotropical palm. *Mol. Ecol.* 27, 3055–3069. doi: 10.1111/mec.14765

Capers, R. S., Chazdon, R. L., Brenes, A. R., and Alvarado, B. V. (2005). Successional dynamics of woody seedling communities in wet tropical secondary forests: seedling dynamics in tropical secondary forests. *J. Ecol.* 93, 1071–1084. doi: 10.1111/j.1365-2745.2005.01050.x

Charles-Dominique, P., Chave, J., Dubois, M.-A., De Granville, J. J., Riera, B., and Vezzoli, C. (2003). Colonization front of the understorey palm *Astrocaryum sciophilum* in a pristine rain forest of French Guiana: spatial patterns of *Astrocaryum sciophilum*. *Global Ecol. Biogeography* 12, 237–248. doi: 10.1046/j.1466-822X.2003.00020.x

Chazdon, R. L. (2008). Chance and determinism in tropical forest succession. *Trop. For. Community Ecol.* 10, 384–408.

Chazdon, R. L. (1991). Plant size and form in the understory palm genus geonoma: are species variations on a theme? *Am. J. Botany* 78, 680–694. doi: 10.1002/j.1537-2197.1991.tb12592.x

Cintra, R., and Horna, V. (1997). Seed and seedling survival of the palm *Astrocaryum murumuru* and the legume tree *Dipteryx micrantha* in gaps in Amazonian forest. *J. Trop. Ecol.* 13, 257–277. doi: 10.1017/s0266467400010440

Clark, J. L., Neill, D. A., and Asanza, M. (2006). Floristic checklist of the mache-chindul mountains of Northwestern ecuador. *Contribut. U S Natl. Herb.* 54, 1–180.

Condit, R., Pitman, N., Leigh, E. G., Chave, J., Terborgh, J., Foster, R. B., et al. (2002). Beta-diversity in tropical forest trees. *Science* 295, 666–669. doi: 10.1126/science.1066854

Craven, D., Hall, J. S., Berlyn, G. P., Ashton, M. S., and van Breugel, M. (2018). Environmental filtering limits functional diversity during succession in a seasonally wet tropical secondary forest. *J. Veg. Sci.* 29, 511–520. doi: 10.1111/jvs.12632

de Granville, J. J. (1992). Life forms and growth strategies of Guianan palms as related to their ecology. *Bull. I. Fr. Étud. And.* 21, 533–548.

Dıìaz, S., and Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646–655. doi: 10.1016/s0169-5347(01)02283-2

Díaz, S., Purvis, A., Cornelissen, J. H. C., Mace, G. M., Donoghue, M. J., Ewers, R. M., et al. (2013). Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecol. Evol.* 3, 2958–2975. doi: 10.1002/ece3.601

Didham, R. K., and Lawton, J. H. (1999). Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments1. *Biotropica* 31, 17–30. doi: 10.1111/j.1744-7429.1999.tb00113.x

Dodson, C. H., and Gentry, A. H. (1991). Biological extinction in western ecuador. *Ann. Missouri Botan. Garden* 78:273. doi: 10.2307/2399563

Dray, S., and Dufour, A. B. (2007). The ade4 package: implementing the duality diagram for ecologists. *J. Statistical Software* 22, 1–20.

Dray, S., and Legendre, P. (2008). Testing the species traits-environment relationships: the fourth-corner problem revisited. *Ecology* 89, 3400–3412. doi: 10.1890/08-0349.1

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S., et al. (2014). Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95, 14–21. doi: 10.1890/13-0196.1

Eiserhardt, W. L., Svenning, J. C., Kissling, W. D., and Balslev, H. (2011). Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Ann. Bot.* 108, 1391–1416. doi: 10.1093/aob/mcr146

Escobar, S., Helmstetter, A. J., Montúfar, R., Couvreur, T. L., and Balslev, H. (2022). Phylogenomic relationships and historical biogeography in the South American vegetable ivory palms (Phytelepheae). *Mol. Phylogenet. Evol.* 166:107314. doi: 10.1016/j.ympev.2021.107314

Finegan, B. (1996). Pattern and process in neotropical secondary rain forests: the first 100 years of succession. *Trends Ecol. Evol.* 11, 119–124. doi: 10.1016/0169-5347(96)81090-1

Food and Agriculture Organization of the United Nations [FAO] (2010). *Global Forest Resources Assessment*. Rome: FAO. Main report. FAO Forestry Paper 163.

Galetti, M., Donatti, C. I., Pires, A. S., Guimarães, P. R., and Jordano, P. (2006). Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation. *Botan. J. Linnean Soc.* 151, 141–149. doi: 10.1111/j.1095-8339.2006.00529.x

Gardner, T. A., Barlow, J., Parry, L. W., and Peres, C. A. (2007). Predicting the uncertain future of tropical forest species in a data vacuum. *Biotropica* 39, 25–30. doi: 10.1111/j.1744-7429.2006.00228.x

Gardner, T. A., Barlow, J., Sodhi, N. S., and Peres, C. A. (2010). A multi-region assessment of tropical forest biodiversity in a human-modified world. *Biol. Conserv.* 143, 2293–2300. doi: 10.1016/j.biocon.2010.05.017

Gentry, A. H. (1986). Species richness and floristic composition of Chocó region plant communities. *Caldasia* 15, 71–91.

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., et al. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478, 378–381. doi: 10.1038/nature10425

Giraldo, R., Caballero, W., and Camacho-Tamayo, J. (2018). Mantel test for spatial functional data. *AStA Adv. Statistical Anal.* 102, 21–39. doi: 10.1007/s10182-016-0280-1

Goulding, M., and Smith, N. (2007). *Palms: Sentinels for Amazon Conservation*. St. Louis, MO: Missouri Botanical Garden Press.

Green, P. T., Harms, K. E., and Connell, J. H. (2014). Nonrandom, diversifying processes are disproportionately strong in the smallest size classes of a tropical forest. *Proc. Natl. Acad. Sci. U S A.* 111, 18649–18654. doi: 10.1073/pnas.1321892112

Guevara, S., Laborde, J., and Sánchez, G. (1998). Are isolated remnant trees in pastures a fragmented canopy? *Selbyana* 19, 34–43.

Harvey, C. A., Tucker, N. I., and Estrada, A. (2004). "Live fences, isolated trees, and windbreaks: tools for conserving biodiversity in fragmented tropical landscapes," in *Agroforestry and Biodiversity Conservation in Tropical Landscapes*, eds G. Schroth, G. A. B. Fonseca, C. A. Harvey, C. Gascon, H. L. Vasconcelos, and A. M. N. Izac (Washington, DC: Island Press).

Hill, M., and Smith, A. (1976). Principal component analysis of taxonomic data with multi-state discrete characters. *Taxon* 25, 249–255. doi: 10.2307/1219449

Jakovac, C. C., Peña-Claros, M., Kuyper, T. W., and Bongers, F. (2015). Loss of secondary-forest resilience by land-use intensification in the Amazon. *J. Ecol.* 103, 67–77. doi: 10.1111/1365-2745.12298

Kahn, F., and de Granville, J.-J. (1992). *Palms in Forest Ecosystems of Amazonia, Ecological Studies*. Berlin, NY.: Springer-Verlag.

Karp, D. S., Rominger, A. J., Zook, J., Ranganathan, J., Ehrlich, P. R., and Daily, G. C. (2012). Intensive agriculture erodes β-diversity at large scales. *Ecol. Lett.* 15, 963–970. doi: 10.1111/j.1461-0248.2012.01815.x

Kissling, W. D., Balslev, H., Baker, W. J., Dransfield, J., Göldel, B., Lim, J. Y., et al. (2019). PalmTraits 1.0, a species-level functional trait database of palms worldwide. *Sci. Data* 6:178. doi: 10.1038/s41597-019-0189-0

Kleemann, J., Zamora, C., Villacis-Chiluisa, A. B., Cuenca, P., Koo, H., Noh, J. K., et al. (2022). Deforestation in continental ecuador with a focus on protected areas. *Land* 11:268. doi: 10.3390/land11020268

Kostel-Hughes, F., Young, T. P., and Carreiro, M. M. (1998). Forest leaf litter quantity and seedling occurrence along an urban-rural gradient. *Urban Ecosystems* 2, 263–278.

Kristiansen, T., Svenning, J. C., Eiserhardt, W. L., Pedersen, D., Brix, H., Munch Kristiansen, S., et al. (2012). Environment versus dispersal in the assembly of western Amazonian palm communities: Amazonian palm community composition: inundation, soil and dispersal. *J. Biogeography* 39, 1318–1332. doi: 10.1111/j.1365-2699.2012.02689.x

Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A. C., Fearnside, P. M., Ribeiro, J. E. L., et al. (2006). Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87, 469–482. doi: 10.1890/05-0064

Lawrence, D., D'Odorico, P., Diekmann, L., DeLonge, M., Das, R., and Eaton, J. (2007). Ecological feedbacks following deforestation create the potential for a catastrophic ecosystem shift in tropical dry forest. *Proc. Natl. Acad. Sci. U S A.* 104, 20696–20701. doi: 10.1073/pnas.0705005104

Legendre, P., and Legendre, L. (1998). *Numerical Ecology*. Burlington: Elsevier.

Legendre, P., Galzin, R., and Harmelin-Vivien, M. L. (1997). Relating behavior to habitat: solutions to thefourth-corner problem. *Ecology* 78, 547–562. doi: 10.1890/0012-9658(1997)078[0547:rbthst]2.0.co;2

Letcher, S. G., and Chazdon, R. L. (2009). Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in Northeastern costa rica: rapid forest recovery in Costa Rica. *Biotropica* 41, 608–617. doi: 10.1111/j.1744-7429.2009.00517.x

Liebsch, D., Marques, M. C. M., and Goldenberg, R. (2008). How long does the Atlantic Rain Forest take to recover after a disturbance? changes in species composition and ecological features during secondary succession. *Biol. Conserv.* 141, 1717–1725. doi: 10.1016/j.biocon.2008.04.013

Macía, M. J., Armesilla, P. J., Cámara-Leret, R., Paniagua-Zambrana, N., Villalba, S., Balslev, H., et al. (2011). Palm uses in northwestern south america: a quantitative review. *Botan. Rev.* 77, 462–570. doi: 10.1007/s12229-011-9086-8

Martin, P. A., Newton, A. C., and Bullock, J. M. (2013). Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. *Proc. R. Soc. B.* 280:20132236. doi: 10.1098/rspb.2013.2236

Martínez-Ramos, M., Sarukhan, J., and Piñero, D. (1988). "The demography of tropical trees in the context of forest gap dynamics: the case of *Astrocaryum mexicanum* at Los Tuxtlas tropical rain forest," in *Plant Population Ecology: The 28th Symposium of the British Ecological Society*, eds A. J. Davy, MJ Hutchings, and AR Watkinson (Oxford: Blackwell).

McCune, B., Grace, J. B., and Urban, D. L. (2002). *Analysis of Ecological Communities*. Gleneden Beach, OR: MjM software design.

Melo, F. P. L., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., and Tabarelli, M. (2013). On the hope for biodiversity-friendly tropical landscapes. *Trends Ecol. Evol.* 28, 462–468. doi: 10.1016/j.tree.2013.01.001

Montúfar, R., Anthelme, F., Pintaud, J. C., and Balslev, H. (2011). Disturbance and resilience in tropical american palm populations and communities. *Bot. Rev.* 77, 426–461. doi: 10.1007/s12229-011-9085-9

Muñoz, G., Trøjelsgaard, K., and Kissling, W. D. (2019). A synthesis of animal-mediated seed dispersal of palms reveals distinct biogeographical differences in species interactions. *J. Biogeogr.* 46, 466–484. doi: 10.1111/jbi.13493

Muscarella, R., Emilio, T., Phillips, O. L., Lewis, S. L., Slik, F., Baker, W. J., et al. (2020). The global abundance of tree palms. *Global Ecol. Biogeogr.* 29, 1495–1514. doi: 10.1111/geb.13123

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858. doi: 10.1038/35002501

Norden, N., Chazdon, R. L., Chao, A., Jiang, Y.-H., and Vílchez-Alvarado, B. (2009). Resilience of tropical rain forests: tree community reassembly in secondary forests. *Ecol. Lett.* 12, 385–394. doi: 10.1111/j.1461-0248.2009.01292.x

Normand, S., Vormisto, J., Svenning, J.-C., Grández, C., and Balslev, H. (2006). Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. *Plant Ecol.* 186, 161–176. doi: 10.1007/s11258-006-9120-9

O'Hara, R., and Kotze, J. (2010). Do not log-transform count data. *Nat. Prec.* 1, 118–122. doi: 10.1111/j.2041-210x.2010.00021.x

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P.,McGlinn, D., et al. (2019). *vegan: Community Ecology Package. R package version 2.5–6*.

Paine, C. E. T., Baraloto, C., Chave, J., and Hérault, B. (2011). Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos* 120, 720–727. doi: 10.1111/j.1600-0706.2010.19110.x

Palacios, W., and Jaramillo, N. (2005). Ecological forest species groups in Northeastern Ecuador and their importance for the managenment of indigenous forest. *Lyonia* 6, 55–75.

Pintaud, J. (2006). The impact of forest disturbance on the palms of New Caledonia. *Palms-Lawrence* 50:123.

Poorter, L., Wright, S. J., Paz, H., Ackerly, D. D., Condit, R., Ibarra-Manríquez, G., et al. (2008). Are functional traits good predictors of demographic rates? *Evid. Five Neotrop. Forests Ecol.* 89, 1908–1920. doi: 10.1890/07-0207.1

QGIS Development Team (2020). *QGIS Geographic Information System*. QGIS Association.

R Core Team (2018). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rocha-Santos, L., Pessoa, M. S., Cassano, C. R., Talora, D. C., Orihuela, R. L. L., Mariano-Neto, E., et al. (2016). The shrinkage of a forest: landscape-scale deforestation leading to overall changes in local forest structure. *Biol. Conserv.* 196, 1–9. doi: 10.1016/j.biocon.2016.01.028

Rozendaal, D. M. A., Bongers, F., Aide, T. M., Alvarez-Dávila, E., Ascarrunz, N., Balvanera, P., et al. (2019). Biodiversity recovery of neotropical secondary forests. *Sci. Adv.* 5:eaau3114. doi: 10.1126/sciadv.aau3114

Rudel, T. K., Defries, R., Asner, G. P., and Laurance, W. F. (2009). Changing drivers of deforestation and new opportunities for conservation. *Conserv. Biol.* 23, 1396–1405. doi: 10.1111/j.1523-1739.2009.01332.x

Runyan, C. W., D'Odorico, P., and Lawrence, D. (2012). Effect of repeated deforestation on vegetation dynamics for phosphorus-limited tropical forests: coupled vegetation-phosphorus dynamics. *J. Geophys. Res.* 117:G001841. doi: 10.1029/2011JG001841

Sandor, M. E., and Chazdon, R. L. (2014). Remnant trees affect species composition but not structure of tropical second-growth forest. *PLoS One* 9:e83284. doi: 10.1371/journal.pone.0083284

Sardeshpande, M., and Shackleton, C. (2019). Wild edible fruits: a systematic review of an under-researched multifunctional NTFP (Non-Timber Forest Product). *Forests* 10:467. doi: 10.3390/f10060467

Schlawin, J. R., and Zahawi, R. A. (2008). 'Nucleating' succession in recovering neotropical wet forests: the legacy of remnant trees. *J. Veg. Sci.* 19, 485–492. doi: 10.3170/2008-8-18387

Su, J. C., Debinski, D. M., Jakubauskas, M. E., and Kindscher, K. (2004). Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. *Conserv. Biol.* 18, 167–173. doi: 10.1111/j.1523-1739.2004.00337.x

Svenning, J. C. (2000). Growth strategies of clonal palms (Arecaceae) in a neotropical rainforest, Yasuni, Ecuador. *Aust. J. Bot.* 48:167. doi: 10.1071/BT98048

Svenning, J. C. (2002). Crown illumination limits the population growth rate of a neotropical understorey palm (Geonoma macrostachys, Arecaceae). *Plant Ecol.* 159, 185–199. doi: 10.1023/A:1015520116260

Tabarelli, M., Aguiar, A. V., Ribeiro, M. C., Metzger, J. P., and Peres, C. A. (2010). Prospects for biodiversity conservation in the Atlantic Forest: lessons from aging human-modified landscapes. *Biol. Conserv.* 143, 2328–2340. doi: 10.1016/j.biocon.2010.02.005

Tabarelli, M., Peres, C. A., and Melo, F. P. L. (2012). The 'few winners and many losers' paradigm revisited: emerging prospects for tropical forest biodiversity. *Biol. Conserv.* 155, 136–140. doi: 10.1016/j.biocon.2012.06.020

Tamayo, F., Torres, B., Fischer, R., Lajones, A., Cervantes, R., Corozo, C., et al. (2020). "Characterization of forest landscapes in the ecuadorian Northwest: deforestation and sociocultural aspects," in Deforestación En Paisajes Forestales Tropicales Del Ecuador: Bases Científicas Para Perspectivas Políticas, ed. Universidad Estatal Amazo'nica - Instituto Johann Heinrich von Thünen (Puyo: Universidad Estatal Amazónica - Instituto Johann Heinrich von Thüen).

ter Braak, C. J., Cormont, A., and Dray, S. (2012). Improved testing of species traits-environment relationships in the fourth-corner problem. *Ecology* 93, 1525–1526. doi: 10.1890/12-0126.1

ter Steege, H., Pitman, N. C. A., Sabatier, D., Baraloto, C., Salomao, R. P., Guevara, J. E., et al. (2013). Hyperdominance in the Amazonian tree Flora. *Science* 342:1243092. doi: 10.1126/science.1243092

Tomlinson, P. B. (2006). The uniqueness of palms. *Botan. J. Linnean Soc.* 151, 5–14. doi: 10.1111/j.1095-8339.2006.00520.x

Van der Hoek, Y. (2017). The potential of protected areas to halt deforestation in Ecuador. *Environ. Conserv.* 44, 124–130. doi: 10.1017/S037689291700011X

Vandermeer, J., Perfecto, I., and Schellhorn, N. (2010). Propagating sinks, ephemeral sources and percolating mosaics: conservation in landscapes. *Landscape Ecol.* 25, 509–518. doi: 10.1007/s10980-010-9449-2

Villar, N., Paz, C., Zipparro, V., Nazareth, S., Bulascoschi, L., Bakker, E. S., et al. (2020). Frugivory underpins the nitrogen cycle. *Funct. Ecol.* 35, 357–368. doi: 10.1111/1365-2435.13707

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., et al. (2007). Let the concept of trait be functional! *Oikos* 116, 882–892. doi: 10.1111/j.0030-1299.2007.15559.x

Wang, Y. H., and Augspurger, C. (2004). Dwarf palms and cyclanths strongly reduce neotropical seedling recruitment. *Oikos* 107, 619–633. doi: 10.1111/j.0030-1299.2004.13328.x

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199, 213–227. doi: 10.1023/A:1004327224729

Wright, J. S. (2010). The future of tropical forests. *Ann. N. Y. Acad. Sci.* 1195, 1–27. doi: 10.1111/j.1749-6632.2010.05455.x

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

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., and Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R, Statistics for Biology and Health*. New York, NY: Springer. doi: 10.1007/978-0-387-87458-6

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

frontiers | Frontiers in Ecology and Evolution

ORIGINAL RESEARCH
published: 11 May 2022
doi: 10.3389/fevo.2022.790883

Worldwide Distribution of Antagonistic-Mutualistic Relationships Between Parrots and Palms

Martina Carrete[1], Fernando Hiraldo[2], Pedro Romero-Vidal[1,2], Guillermo Blanco[3], Dailos Hernández-Brito[2], Esther Sebastián-González[4], José A. Díaz-Luque[5] and José L. Tella[2]*

[1] Department of Physical, Chemical and Natural Systems, Universidad Pablo de Olavide, Seville, Spain, [2] Department of Conservation Biology, Estación Biológica de Doñana (CSIC), Seville, Spain, [3] Department of Evolutionary Ecology, Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain, [4] Department of Ecology, Universidad de Alicante, Alicante, Spain, [5] Endangered Conservation Consultancy, Málaga, Spain

OPEN ACCESS

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

Reviewed by:
Cibele De Cássia Silva,
Universidade Federal de Goiás, Brazil
Mauro Galetti,
São Paulo State University, Brazil

***Correspondence:**
Martina Carrete
mcarrete@upo.es

Specialty section:
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

Received: *07 October 2021*
Accepted: *19 April 2022*
Published: *11 May 2022*

Citation:
Carrete M, Hiraldo F, Romero-Vidal P, Blanco G, Hernández-Brito D, Sebastián-González E, Díaz-Luque JA and Tella JL (2022) Worldwide Distribution of Antagonistic-Mutualistic Relationships Between Parrots and Palms. Front. Ecol. Evol. 10:790883. doi: 10.3389/fevo.2022.790883

Palms, like all plants, show coevolutionary relationships with animals that have been traditionally categorized as mutualistic (seed dispersers and pollinators) or antagonistic (seed predators). This dual perspective, however, has prevented a full understanding of their true interactions with some animal groups, mainly those that do not ingest entire fruits. One clear example is parrots, which have been described to use palm species as feeding resources, while their role as seed dispersers has been largely neglected. Here, we combined fieldwork data with information from the literature and citizen science (i.e., naturalists and nature photographers) on parrot foraging ecology worldwide to evaluate the spatial and taxonomic extent of parrot-palm interactions and to identify the eco-evolutionary factors involved. We identified 1,189 interactions between 135 parrots and 107 palm species in more than 50 countries across the six realms where palms are present as natives or introduced. Combining this information, we identified 427 unique parrot-palm interacting pairs (i.e., a parrot species interacting with a palm species). Pure antagonistic interactions (i.e., parrots just preying on seeds or eating or destroying their non-reproductive parts) were less common (5%) than mutualistic ones (i.e., parrots benefiting by partially preying on the seed or fruit or consuming the pulp of the fruit or the flower but also contributing to seed dispersal and, potentially, pollination; 89%). After controlling for phylogeny, the size of consumed seeds and parrot body mass were positively related. Seed dispersal distances varied among palm species (range of estimated median dispersal distances: 9–250 m), with larger parrots dispersing seeds at greater distances, especially large fruits commonly categorized as megafauna anachronisms (>4 cm length). Although parrot-palm interactions are widespread, several factors (e.g., social behavior, predation fear, food availability, or seasonality) may affect the actual position of parrots on the antagonism-mutualism continuum for different palm species and regions, deserving further research. Meanwhile, the pervasiveness of parrot-palm mutualistic interactions, mainly involving seed dispersal and pollination, should not be overlooked in studies of palm ecology and evolution.

Keywords: pollination, seed dispersal, seed predation, dispersal distances, megafaunal fruits, defleshing, introduced species

INTRODUCTION

Plant-animal interactions are ubiquitous and can range from relationships that benefit both participating species (mutualisms) to interactions where only one is benefited while the other is negatively affected (antagonisms) (Mougi, 2020). However, categorizing plant-animal interactions as purely mutualistic or antagonistic is sometimes unclear. For instance, seed or pollen eaters can be considered as predators (antagonism) but also as dispersers if they move viable seeds after ingesting them or pollen further away from the mother plants (mutualism), promoting gene flow within and among plant populations (e.g., Rousset, 2004; Pérez-Méndez et al., 2016; Wandrag et al., 2018) and the colonization of new microhabitats (e.g., Janzen, 1970; Howe and Smallwood, 1982; Cousens et al., 2008). Therefore, plant-animal interactions, which have evolved over geological time and have driven both biodiversity patterns and species adaptations, should be studied considering all potential costs and benefits for both animals and plants (Montesinos-Navarro et al., 2017).

The life history of tropical trees is intimately connected to vertebrates through seed dispersal and seed predation (Levey et al., 1994). Palms (Arecaceae) are among the most abundant tree groups in tropical and sub-tropical ecosystems around the world (Pitman et al., 2001; Dransfield et al., 2008; Muscarella et al., 2020). With more than 2,400 species (Govaerts and Dransfield, 2005; Dransfield et al., 2008), palms exhibit large geographic variations in species richness, phylogenetic composition, and life forms, and serve as keystone resources for pollinators and frugivores (Terborgh, 1986; Zona and Henderson, 1989; Henderson, 2002; Onstein et al., 2017; Muñoz et al., 2019; Lim et al., 2020) but also for people by providing construction materials, fabrics, fuel, food, medicine, and ornamentals (Cámara-Leret et al., 2017). Thus, understanding factors driving palm recruitment, diversity, and distribution, which are all tightly linked to predation, dispersal, and plant regeneration, is pivotal not only to ensure their long-term persistence but also the structuring and functioning of tropical ecosystems (Eiserhardt et al., 2011).

Palms are predominantly animal dispersed (Zona and Henderson, 1989; Zona, 2006; Andreazzi et al., 2009; Muñoz et al., 2019; Dracxler and Kissling, 2021), so frugivory plays a special role in their population dynamics and evolution (Dracxler and Kissling, 2021). Although most vertebrates can disperse palm seeds, several studies provide evidence of dispersal limitations at broad and local scales among palms (Svenning, 2001, 2002; Sunderland and Morakinyo, 2002; Boll et al., 2005; Svenning and Wright, 2005; Blach-Overgaard et al., 2009, 2010). Mammals and birds have been listed as the principal dispersers for palms, in particular, tapirs, peccaries, toucans, cracids, and oilbirds, which disperse palm seeds by endozoochory (reviews in Zona and Henderson, 1989; Zona, 2006; Andreazzi et al., 2009; Muñoz et al., 2019; Dracxler and Kissling, 2021). However, palm seeds can also be effectively dispersed by stomatochory (i.e., animals flying or moving over the canopy with fruits in their beaks, mouths, or feet), such as large-fruited palm species dispersed by monkeys, rodents, or bats (e.g., Adler and Kestell, 1998; Chapman and Russo, 2007; Jansen et al., 2012; Abedi-Lartey et al., 2016; Blanco et al., 2019; Dracxler and Kissling, 2021).

Parrots (order Psittaciformes) are among those species potentially dispersing palms by stomatochory. While parrots have been traditionally considered as seed predators (Toft and Wright, 2015), recent studies have described multiple examples across the world of parrots legitimately dispersing several plant species through epizoochory, endozoocory, and stomatochory (Tella et al., 2015; Blanco et al., 2018; Hernández-Brito et al., 2021) as well as transferring pollen (i.e., acting as pollinators) after feeding on conifer cones or flowers (Fleming and Muchhala, 2008; Gleiser et al., 2017), thus challenging this paradigm. Parrots are among the richest avian orders (c. 400 extant species) and, although several species have decreasing populations in their native ranges (e.g., Olah et al., 2016; Berkunsky et al., 2017), they are still rather abundant compared with other taxa (Callaghan et al., 2021; but see Robinson et al., 2022 for caution on population estimates). This, in addition to their generalist diets and plastic feeding behaviors (Renton et al., 2015; Toft and Wright, 2015), may explain the pervasiveness of parrot-plant interactions, involving not only native but also exotic parrot and plant species. In the case of palms, a few studies have demonstrated that parrots predate on palm seeds or consume the pulp of the fruit but are also legitimate long-distance dispersers of some Neotropical species (Sazima, 2008; Prada Villalobos and Araújo Bagno, 2012; Baños-Villalba et al., 2017; Luna et al., 2018; Blanco et al., 2019; Tella et al., 2020; Silva et al., 2021). However, the large overlap between palm and parrot distributions (Provost et al., 2018; Reichgelt et al., 2018) suggests that this avian order may play a major —though overlooked— role in palm ecology worldwide (Zona and Henderson, 1989; Muñoz et al., 2019; Dracxler and Kissling, 2021).

Here, we combine fieldwork with published data and information gathered from citizen science (i.e., naturalists and nature photographers) to assess the nature of parrot-palm interactions (mutualistic or antagonistic), the eco-evolutionary factors involved, and their spatial extent across the ice-free realms of the world (*sensu* Olson et al., 2001), namely Nearctic, Palaearctic, Afrotropic, Indomalaya, Neotropic, Australasia, and Oceania (hereafter, these last two realms will be referred to as Australasia). As previously suggested (Montesinos-Navarro et al., 2017), we expect most interactions to be mutualistic. Moreover, given that the maximum number of interactions in an area depends on the number of interacting species (Jordano, 2016), regions with more palms (Kissling et al., 2007), and parrot species (Davies et al., 2007) such as the Neotropic, will show more interactions than regions with low numbers of species. However, although parrots may interact with palms in multiple ways, some interactions such as seed predation, defleshing, or dispersal may be limited by parrot morphology (mainly beak and body size) and palm fruit/seed size, as has been seen in other plant-frugivore pairs (Onstein et al., 2017). Thus, we predict a functional match between palm fruit size (used as a surrogate of palm seed size, see **Supplementary Material**) and parrot body size in all realms, regardless of whether palms were native or introduced. However, parrots can consume unripe fruits (Sebastián-González et al., 2019) and this may dismantle the functional trait matching by allowing small-sized parrots to interact with large-sized fruit palms. Moreover, as large-sized parrots are less constrained in consuming small or large fruits, they will be able to interact with more palm species than small-sized parrots, which can only interact with palms with small fruits. Accordingly, palms with smaller fruits will be able to interact with more parrot species than large-fruited palms, which will only interact with large-sized parrots. As for dispersal, since large-sized parrots are able to flight over larger areas and disperse heavier palm fruits (e.g., Tella et al., 2020) than smaller parrot species (e.g., Luna et al., 2018), we expect large-fruited palms to show longer parrot-mediated dispersal distances than small-fruited ones. Finally, despite differences in features linked to competitive ability, fecundity, and dispersal between native and introduced palms (Fehr et al., 2020), we do not expect differences in their interactions with parrots due to the generalist feeding behavior of these birds (Toft and Wright, 2015; **Table 1**).

MATERIALS AND METHODS

Parrot-Palm Interactions

Parrot-palm interactions were obtained by combining field data, bibliographic information, and citizen science. Depending on the parrot behavior, interactions were classified as seed predation (i.e., seeds or entire fruits, usually a single-seeded drupe although some genera may contain two or more seeds in each fruit; Henderson, 2002), flowers, or non-reproductive parts (i.e., bark, leaves, or petioles), defleshing (i.e., consumption of the pulp surrounding the seed, usually sweet and highly nutritive; Henderson, 2002), or dispersal (i.e., flying parrots observed carrying fruits or seeds in their beaks or feet). In all cases, both palms and parrots were identified to the species level, discarding data when this was not possible. The taxonomic names of palms and parrots, when needed, were updated following the World Checklist of palms (WFO, 2021), the World Checklist of Selected Plant Families,[1] and the BirdLife Taxonomic Checklist (BirdLife International, 2020), respectively. We classified the interaction based on whether a native or introduced palm was observed using the information on botanical countries provided by the Taxonomic Databases Working Group (2001), which mostly represents countries except for some of the largest ones which are subdivided into states or provinces (Kissling et al., 2012).

Field Data

Parrot-palm interactions were collected in different fieldwork campaigns performed in 17 countries and five continents between 2012 and 2020. We actively looked for foraging groups of parrots both through roadside surveys (98 roadside surveys covering c. 57,250 km of transects, Tella et al., 2021) and a large, but unquantified, number of walking transects across a variety of biomes and habitats (Sebastián-González et al., 2019; Hernández-Brito et al., 2021). When we located parrots

TABLE 1 | Summary of the hypotheses and details about the models used in each case.

Hypothesis	Library used	Dependent variable (error distribution, link function)	Explanatory variables (f: fixed factor; c: continuous variable)	Random terms
• The number of parrot-palm interactions differs among realms but not in areas where the palm species involved was native or introduced	glmmTMB	Number of parrot-palm interactions (log-transformed) (normal, identity)	Realm (f) Palm range (f)	
	glmmTMB	Number of parrot species interacting with each palm species (Negative binomial-truncated, logarithm)	Realm (f) Palm range (f) Realm*Palm range	palm species
	glmmTMB	Number of palm species interacting with each parrot species (Negative binomial-truncated, logarithm)	Realm (f) Palm range (f) Realm*Palm range	parrot species
• Interactions (seed predation, defleshing, and dispersal) are limited by functional trait relationships between palms and parrots	phyloglmm	Fruit length[1] (normal, identity)	Parrot body mass (c) Realm (f) Parrot body mass*Realm Palm range (f)	parrot species
• Palm fruit or parrot size are related to the ripeness of preyed, defleshed, or dispersed fruits	glmmTMB	Number of ripe fruits/Total number of fruits	Parrot body mass (c) Fruit length (c) Realm (f) Palm range (f)	
• The number of parrot species interacting with each palm species is related to its fruit size	phyloglmm	Number of parrot species (Poisson-truncated, logarithm)	Fruit length (c) Realm (f) Palm range (f)	palm species
• The number of palm species with which each parrot species interacts is related to parrot body size	phyloglmm	Number of palm species (Poisson-truncated, logarithm)	Parrot body mass (c) Realm (f) Palm range (f)	parrot species
• Dispersal distances are affected by palm fruit and parrot size	MCMCglmm	Dispersal distances[1,2](Gaussian)		parrot species palm species

[1] log-transformed; [2] right-censored data.

---

[1] https://wcsp.science.kew.org

feeding on palm trees, we observed them with telescopes and binoculars from a distance to avoid disturbing the birds. We recorded the parrot and the palm species involved, and whether parrots were preying on the seeds and/or fruits, flowers, or non-reproductive parts, consuming the pulp of the fruits (defleshing), or dispersing them (fruits and/or seeds). When good visibility was possible, we recorded the distance from the mother tree to the perching site where the fruit or seed was dropped (exact dispersal distance) or up to where the parrot went out of sight (minimum dispersal distance) using a laser rangefinder incorporated into the binoculars (Leica Geovid 10 × 42 ×, range: 10–1,300 m). Some of these data have been previously published (Baños-Villalba et al., 2017; Luna et al., 2018; Blanco et al., 2019, Tella et al., 2020).

Bibliographic Search

We compiled interactions from a literature search of the Web of Science (WoS; July 10, 2020) including the terms: "palm*" and "comportam* aliment*" or aliment* or "ecolog* forra*" or "forra*" or feed* or forag* or food* or aliment* or diet* or "resource use" and parrot* or psittaci* or ara or parak* or macaw* or cockato* or amazon* or guacamay* or loro* or cotorr* or peri* or papagay* or periqu* or arara*. From the first list obtained (N = 9,160 papers), we discarded articles that did not include explicit information on parrot-palm interactions. Selected articles (n = 180 papers; **Supplementary Table 1**) were manually and meticulously screened to obtain information on the parrot and the palm species involved, the interaction type (predation of fruits or seeds, flowers, or non-reproductive parts of the palm, defleshing, or dispersal), and the location to identify the realm and whether the palm was native or introduced. We complemented this search using Academia.edu. We considered an observation as a dispersal interaction when parrots were recorded as consuming the pulp or fruits (seeds) of equal or smaller size than those previously recorded as dispersed by each species by stomatochory, following the same criterion used for palms dispersed by endozoochory (Muñoz et al., 2019). When possible, we established if the palm fruit was ripe or unripe (i.e., based on fruit color and size). Interactions cited in a paper were checked in the original study to avoid potential errors associated with misinterpretations.

Citizen Science Data

We complemented our dataset with information from wildlife naturalists and photographers. Information from wildlife naturalists was compiled from acquaintances who sent data on a non-systematic basis. Data from wildlife photographers were collected making a non-exhaustive review of several photo galleries publicly available on the internet, namely: eBird,[2] WikiAves,[3] The Cornell Lab of Ornithology,[4] Flickr,[5] Instagram,[6] and Facebook.[7] All the information was carefully examined and interactions were classified as predation of fruits and/or seeds, flowers, or non-reproductive parts, defleshing, or dispersal, following previous criteria. When interactions were not easy to interpret (mainly when dealing with pictures), we asked the authors for clarifications or discarded the observation. Plant and parrot species were identified when possible or the photographers were contacted for assistance in identification. The location of the sighting was recorded to assess whether the palm was native or introduced.

Statistical Analysis

We compared the number of parrot-palm interactions (log-transformed) across realms and in areas where the palm species involved were native or introduced using Generalized Linear Models (package *glmmTMB*; Brooks et al., 2017), applying Tukey *post hoc* tests (package *lsmeans*; Lenth, 2016). Similarly, we assessed whether the number of parrot species interacting with each palm species and *vice versa* varied across realms through Generalized Linear Mixed Models (palm or parrot species were used as random terms, respectively), considering if the palm was in its native or introduced range. As seed predation, defleshing, and dispersal can be limited by palm fruit size but also by parrot size, we considered whether these two variables were related (dependent variable: fruit length, log-transformed; normal error distribution, identity link function; parrot species as a random term) and if they affected the number of interacting species (dependent variables: number of parrot or palm species; truncated Poisson error distribution, log-link function; palm or parrot species as random terms, respectively). As palm fruit and parrot sizes are similar among closely related species (see Phylogenetic signal, **Supplementary Figures 1, 2**), we used phylogenetic generalized linear mixed models (PGLMMs) implemented in the *phyloglmm* package (Li and Bolker, 2019). For parrots, we used the resolved phylogeny of Jetz et al. (2012) while for palms we employed those published by Faurby et al. (2016). All models included the interaction between palm fruit and parrot sizes, the realm and whether the palm was native or introduced. We used GLM to assess whether palm fruit or parrot sizes were related to the ripeness of fruits (ripe or unripe) when they were preyed, defleshed, or dispersed, considering potential differences among realms and native and introduced palms (response variable: ripe fruits/total, binomial error distribution, logit link function; 282 parrot-palm pairs, 2,092 fruits classified as ripe or unripe). We exclusively focused on our field data to estimate the dispersal distances at which parrots dropped palm fruits or seeds, and did not include bibliographic data to avoid methodological differences. As our dispersal distances were right-censored (i.e., some corresponded to exact distances at which fruits or seeds were dropped, whereas, for others, the true distance was outside the observed sample range), we estimated the median distance at which parrots dispersed the fruits or seeds of each palm species using Kaplan–Meier survival curves. This statistical procedure, commonly used for survival analysis, does not assume underlying probability distributions and allows the inclusion of categorical variables. The low number of exact dispersal distances compared to minimum dispersal distances for most parrot species precludes the inclusion of this variable (i.e., parrot species) in the models.

---

[2] https://ebird.org/

[3] https://www.wikiaves.com

[4] https://www.macaulaylibrary.org/

[5] https://www.flickr.com/

[6] https://www.instagram.com/

[7] https://www.facebook.com/

Thus, we estimated dispersal distances for each palm species after pooling information from all parrots dispersing them. Finally, we used MCMCglmm (Hadfield, 2010) to relate dispersal distances (log-transformed, right-censored data, cengaussian distribution) to palm fruit and parrot sizes, including fruit length and parrot body mass as covariates, and parrot and palm species as random terms. All models included the phylogenetic relationships between species (parrots or palms; Garamszegi, 2014), and were run for 100,000 iterations, preceded by a burn-in of 10,000 iterations. Estimates of parameters were stored every 25th iteration to reduce autocorrelation. The inclusion of the palm and parrot species in MCMCglmm allowed us to estimate how repeatable dispersal distances were for each group (palm or parrot species) as $\sigma_{\text{parrot}}/(\sigma_{\text{parrot}} + \sigma_{\text{palm}} + \sigma_{\text{residual}})$ and $\sigma_{\text{palm}}/(\sigma_{\text{parrot}} + \sigma_{\text{palm}} + \sigma_{\text{residual}})$, respectively. Data on body mass, as an indicator of parrot body size, and palm fruit size were taken from the literature (Burgio et al., 2019; Kissling et al., 2019). The use of fruit length (the variable with more data across palm species) as an overall indicator of fruit and seed size was supported by its strong positive correlations across palm species with other descriptors of fruit and seed size (**Supplementary Figure 3**). **Table 1** summarizes hypotheses tested and statistical details.

GLMs, GLMMs, and PGLMMs were compared using the Akaike Information Criteria corrected for small sample sizes (AICc), and models within 2 AICc units of the best one were considered as alternatives. Variables were considered as significant based on their associated *p*-value. For MCMCglmm, we tested the statistical support of the fixed effect by evaluating whether their posterior distributions (95% credible interval) overlapped with zero. Statistical analyses were conducted in R 4.1.0 (R Core Team, 2021).

RESULTS

We recorded a total of 1,189 interactions between 135 parrots and 107 palm species around the world (**Figure 1**), including parrots eating or destroying the non-reproductive parts (4%), consuming flowers (11%), preying on fruits and seeds (30%), consuming the pulp (25%), and dispersing fruits or seeds (30%) (**Table 2**). We combined these interactions (*n* = 427 unique parrot-palm interacting pairs, some of them repeated in different realms; **Table 2**), balancing the costs and benefits for each species involved. Antagonistic interactions in which only parrots benefited while causing harm to the palm (i.e., parrots preying on seeds or eating or destroying the non-reproductive parts) totaled 20 cases (5%), while mutualist interactions (i.e., parrots benefiting by preying on the seed or consuming the pulp of the fruit or the flower but also contributing to seed dispersal and, potentially, pollination) were much more common (89%, *n* = 381 parrot-palm interacting pairs). The other 26 parrot-palm interacting

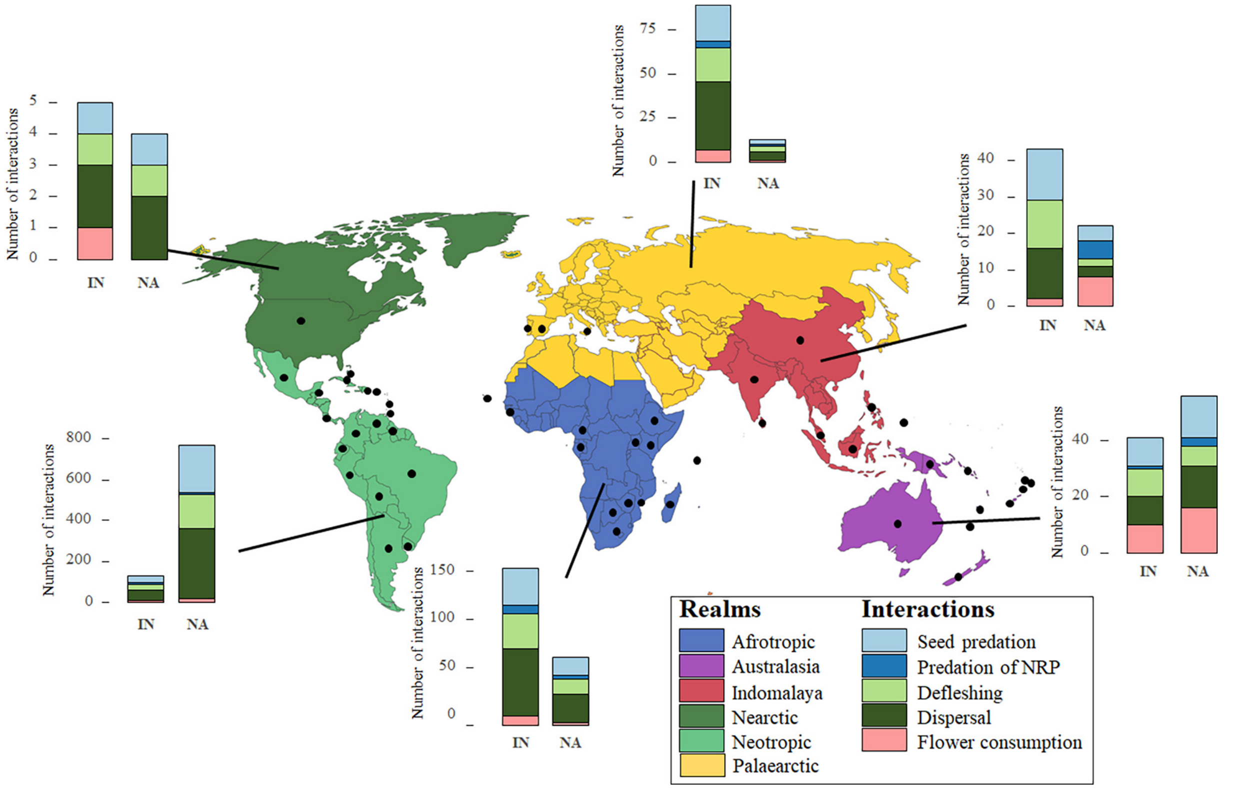


FIGURE 1 | Number of interactions between parrots and palms across the main biogeographic realms of the world (Olson et al., 2001), considering whether the palm species was in its native (NA) or introduced (IN) range. Black points show the country of parrot-palm interactions. NRP: non-reproductive parts (bark, leaves, etc.).

TABLE 2 | Number of parrot and palm species (N parrots and N palms, respectively), mean (±SD) number of palms involved in interactions per parrot species and *vice versa* (N interacting palms/parrot sp. and N interacting parrots/palm sp. respectively) and total number of interactions recorded across realms, considering whether the palm species were native **(A)** or introduced **(B)**.

(A) Native palms

Realm	N interacting pairs	N parrots	N interacting palms/parrot sp.	Npalms	N interacting parrots/palm sp.	Seed predation	Defleshing	Dispersal	Flower consumption	Predation NRP
Afrotropic	20	16	2.25 ± 0.77	11	1.82 ± 2.09	19	16	17	2	5
Australasia	28	19	2.42 ± 1.22	13	2.08 ± 2.78	15	7	10	24	2
Indomalaya	8	5	2.6 ± 0.89	5	1.6 ± 0.55	3	1	2	3	3
Nearctic	1	1	2	1	1	1	1	1	0	0
Neotropic	240	69	4.48 ± 3.57	66	3.64 ± 4.34	208	159	217	25	13
Palaearctic	3	3	2 ± 0	2	1.5 ± 0.71	3	3	3	1	0

(B) Introduced palms

Realm	N interacting pairs	N parrots	N interacting palms/parrot sp.	Npalms	N interacting parrots/palm sp.	Seed predation	Defleshing	Dispersal	Flower consumption	Predation NRP
Afrotropic	40	17	3.35 ± 1.77	9	4.44 ± 3.21	37	35	38	11	10
Australasia	24	18	2.33 ± 0.77	9	2.67 ± 2.87	9	9	6	33	3
Indomalaya	22	15	2.47 ± 0.64	5	4.4 ± 4.28	14	13	9	13	2
Nearctic	1	1	2	1	1	1	1	1	1	0
Neotropic	45	27	2.67 ± 1	11	4.09 ± 4.68	35	31	31	13	8
Palaearctic	20	6	4.33 ± 2.07	8	2.5 ± 1.69	20	19	20	2	0

NRP, non-reproductive parts (leaves, bark).

pairs (6%) correspond to parrots defleshing and predating on palm fruits but without confident information on potential fruit dispersal. Parrot species interacting with palms ranged in body mass between 28 and 1,565 g, while the fruit size of palms interacting with parrots ranged between 0.6 and 22.5 cm.

The number of interactions significantly differed among realms ($\chi^2 = 145.20$, df = 5, $p < 0.0001$) but not between native and introduced palms ($\chi^2 = 3.32$, df = 1, p = 0.0683; **Figure 1** and **Supplementary Table 2**). As predicted, parrot-palm interactions were more numerous in the Neotropic (comparison of the number of interactions per realm: native palms: Neotropic > Afrotropic = Australasia > Indomalaya = Nearctic = Palaearctic; introduced palms: Neotropic > Afrotropic = Australasia = Indomalaya > Palaearctic > Nearctic; **Supplementary Table 3**). However, the number of parrots interacting with each palm species was similar among realms and for native and introduced palms ($\chi^2 = 7.79$, df = 5, $p = 0.1679$, and $\chi^2 = 3.74$, df = 1, $p = 0.0531$, respectively; **Supplementary Table 4**), whereas the number of palms interacting with each parrot species did not differ in their association with the palm range ($\chi^2 = 2.68$, df = 1, $p = 0.1019$) but rather with the realms ($\chi^2 = 17.25$, df = 5, $p = 0.0041$; **Supplementary Table 5**). Thus, partially following our predictions, more palm species interact with each parrot species in the Neotropic while the pattern for the number of parrots interacting with each palm species was more heterogeneous (**Table 2** and **Figure 2**).

Seed Predation and Defleshing

Seed predation and defleshing totaled 660 interactions and were mainly recorded in the Neotropic, in native palms (**Figure 1** and **Table 2**). Despite differences between native and introduced palms (estimate for native palms: −0.25, SE = 0.10, $\chi^2 = 7.14$, df = 1, $p = 0.0076$), the proportion of ripe fruits predated were not affected by the parrot or palm fruit size (**Supplementary Tables 6, 7**). The ripeness of defleshed fruits did not show any significant pattern (**Supplementary Tables 6, 7**).

After controlling for phylogenetic relationships among species and differences among realms and for palms in their native and introduced ranges, we found a general positive relationship between palm fruit size and parrot body size (**Supplementary Tables 8, 9**), so that large-sized parrots predate and deflesh more large than small palm fruits while smaller parrots do the same with palms with smaller fruits (seed predation: estimate for parrot body size: 0.13, SE = 0.02, $\chi^2 = 47.65$, df = 1, $p < 0.0001$; defleshing: estimate for parrot body size: 0.07, SE = 0.02, $\chi^2 = 13.60$, df = 1, $p = 0.0002$; **Figure 3** and **Supplementary Figures 4, 5**). Although there was no significant relationship between fruit size and the number of parrots eating or defleshing them (**Supplementary Tables 10, 11** and **Supplementary Figures 6, 7**), only a few, large-sized parrot species were observed preying on palm species with the largest fruits (**Figure 4**). For instance, the mean body mass (±SD) of parrots preying on palms with fruits smaller or larger than 4 cm (the threshold to consider a fruit as megafaunal; Guimarães et al., 2008) was 567.49 g (±500.30 g) and 333.11 g (±347.46 g), respectively; Kruskal–Wallis test: $p < 0.0001$]. Regarding the number of palms with which each parrot species interacted, results show that, partially coinciding with our predictions, large parrots prey upon more palm species than small-sized parrots (seed predation: estimate for parrot body size: 0.23, SE = 0.10, $\chi^2 = 4.95$, df = 1, $p = 0.0261$; **Supplementary Tables 12, 13**, **Figure 5**, and **Supplementary Figure 8**). There

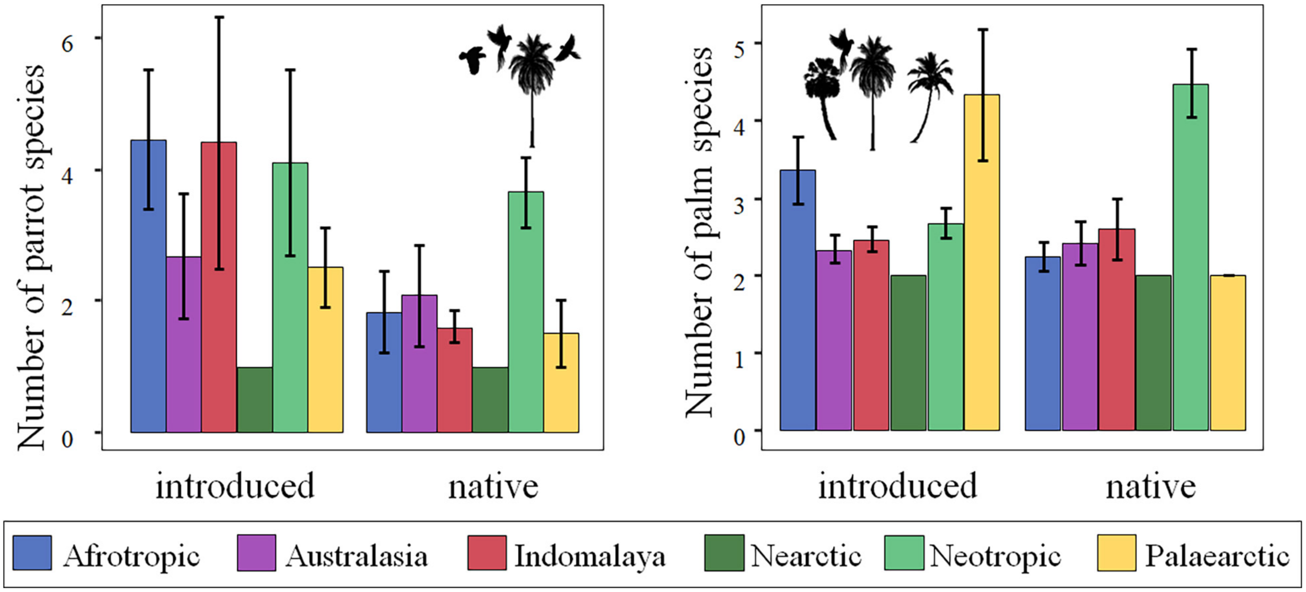


FIGURE 2 | Mean number of parrots (±95% confidence interval) interacting with palms and number of palms interacting with parrots across the main biogeographic realms of the world, considering whether the palm species was in its native or introduced range.

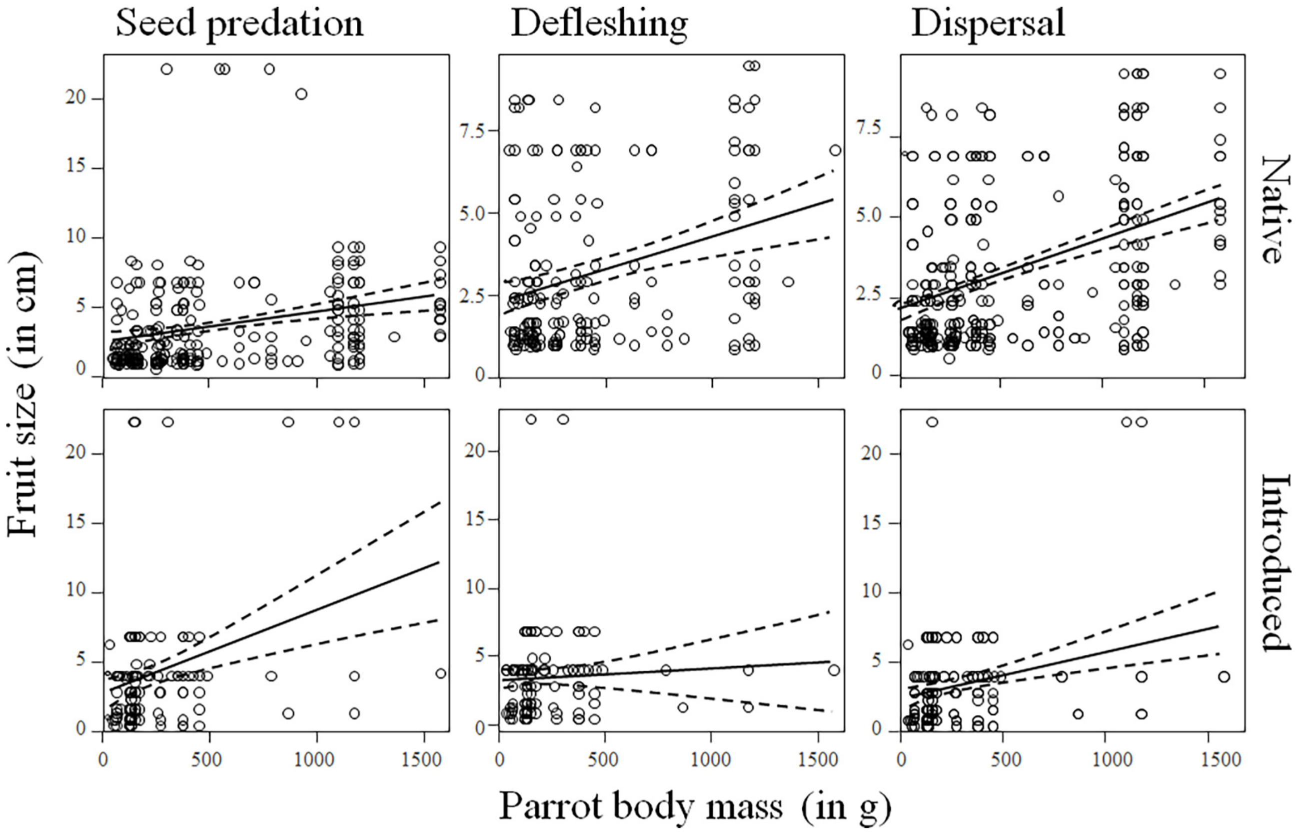


FIGURE 3 | Relationship between palm fruit size (measured as fruit length, in cm) and the size of the parrot (measured as body mass, in g) predating, defleshing, and dispersing them. See **Supplementary Figures 2, 3**, and **4** for more detailed plots within each realm considered. The solid line represents the general trend across regions (dashed line: 95% confidence interval).

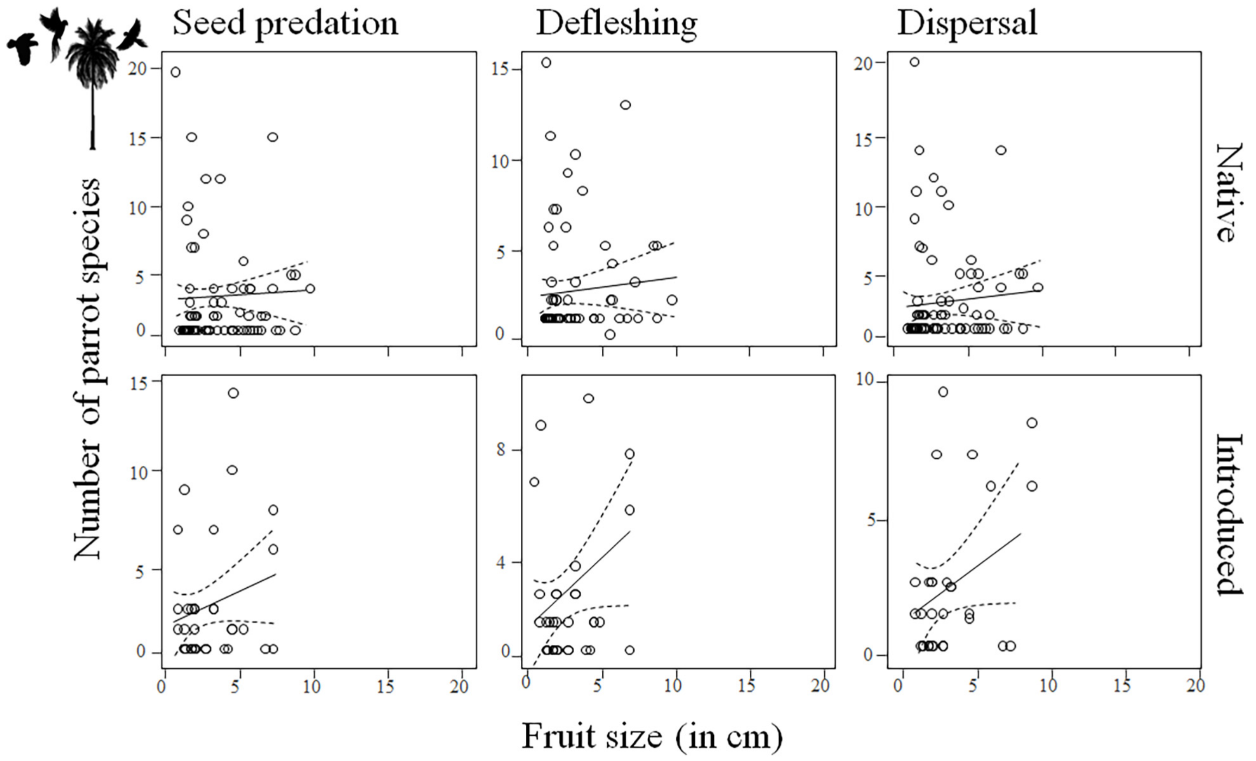


FIGURE 4 | Number of parrot species interacting with palms (i.e., seed predation, defleshing, and dispersal) differing in fruit size (measured as fruit length, in cm) across six main realms of the world and in areas where palms were native and introduced.

was no relationship between parrot body mass and the number of palm species defleshed (**Supplementary Tables 12, 13**, **Figure 5**, and **Supplementary Figure 9**).

Dispersal

Our dataset included 176 specific parrot-palm interactions corresponding to seed dispersal. However, when considering previous data from the same parrot species dispersing fruits of similar size after preying on or defleshing them, interactions involving parrots dispersing palm fruits or seeds increased to 355. Like predation, parrots tend to disperse unripe fruit of native palms more often than those of introduced palms (estimate for the proportion of ripe fruits dispersed in the native area of palms: −0.26, SE = 0.07, $\chi^2 = 12.77$, df = 1, $p = 0.0004$; **Supplementary Tables 6, 7**).

Despite the larger size of fruits in the introduced range of palms (estimate for native range: −0.07, SE = 0.04; $\chi^2 = 3.09$, df = 1, $p = 0.0787$) and after controlling for the phylogenetic relationship among species and potential differences among realms where dispersal events were recorded, we found a positive relationship between palm fruit and parrot size, so that large-sized parrots tend to disperse larger fruits than small-sized parrots (estimate for parrot size: 0.12, SE = 0.02, $\chi^2 = 53.45$, df = 1, $p < 0.0001$; **Figure 3**, **Supplementary Figure 10**, and **Supplementary Tables 8, 9**). Fruit size, however, did not affect the number of parrot species dispersing each palm species (**Supplementary Tables 10, 11** and **Figure 4**), with some parrot species being able to disperse even palms with the largest fruits. We also found that large parrots dispersed more palm species than small-sized parrots in the native range of palms, but not when palms were introduced (estimate for parrot size: 0.23, SE = 0.11, $\chi^2 = 4.01$, df = 1, $p = 0.0454$; **Supplementary Tables 12, 13**, **Figure 5**, and **Supplementary Figure 11**).

During our fieldwork, we recorded 4,983 dispersal distances involving 32 parrot species and 29 palm species (20 palm species classified as native and 10 palm species classified as introduced in the area where the observation was made). Using raw data of exact and minimum dispersal distances, we obtained a median dispersal distance of 41 m (range: 1–1620 m). However, as most distances were right-censored (73%), estimated mean dispersal distances obtained using Kaplan–Meier Survival Curves were larger and rather variable among palm species (range of mean dispersal distances for the different palm species: 9–250 m; **Table 3**). In general, larger palm fruits were dispersed by larger parrot species (estimate for parrot size: 0.15, SE = 0.07, $\chi^2 = 4.39$, df = 1, $p = 0.0362$; **Figure 6**), although the variability was very high, and small-sized parrots were also able to move fruits up to 7 cm in length. Moreover, independent of whether palms were in their native or introduced range (95% credible interval: −0.33 to 0.27), larger parrots also dispersed larger fruits at greater distances than smaller ones (MCMCglmm, interaction parrot size*fruit size: posterior mean: −0.21, 95% credible interval: −0.35 to −0.10). The inclusion of the palm and parrot species in models allowed us to estimate how repeatable dispersal distances

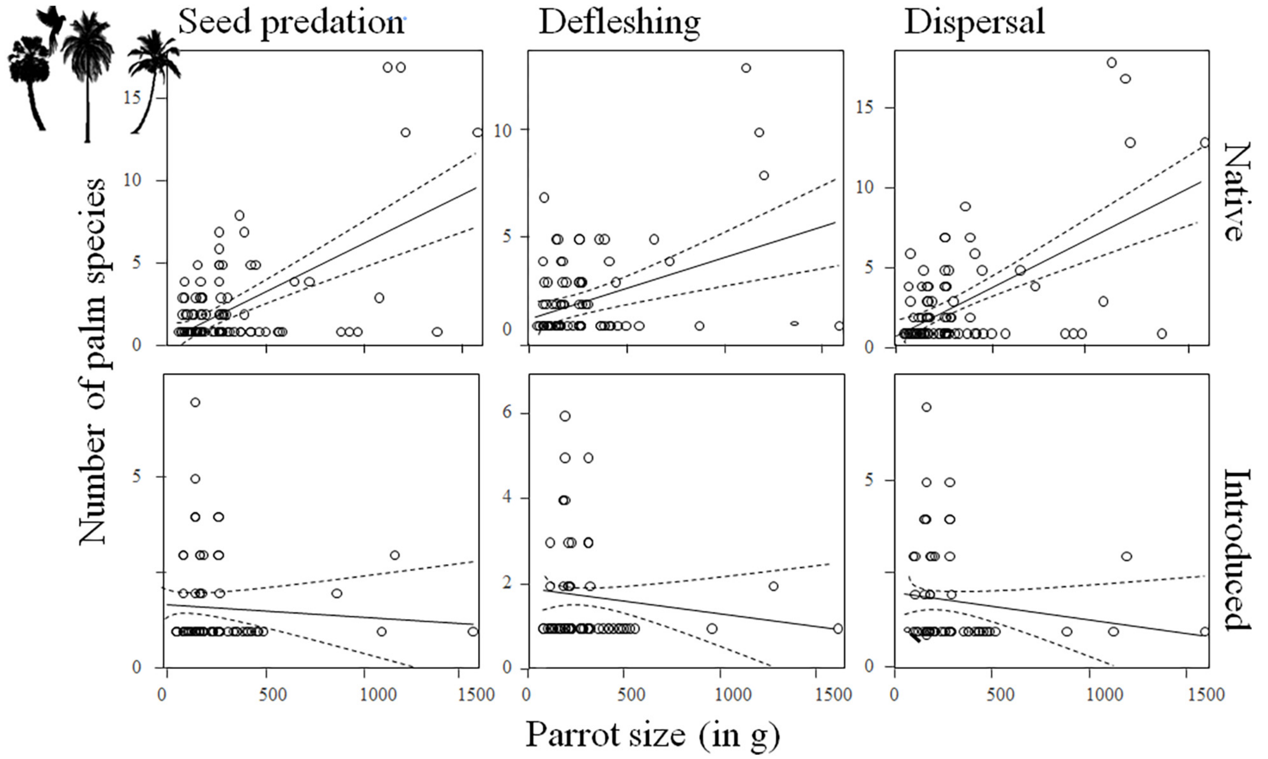


FIGURE 5 | Number of palm species interacting with parrots (i.e., seed predation, defleshing, and dispersal) differing in size (measured as body mass) across the main biogeographic realms of the world, considering whether the palm species was in its native or introduced range.

were for each group, indicating that repeatability for palms was high ($r = 0.89$, 95% credible interval: 0.68–0.96) but negligible for parrot species ($r = 0.03$, 95% credible interval: 0–0.24).

DISCUSSION

Parrots have traditionally been considered as seed predators and thus plant antagonists (Toft and Wright, 2015). However, evidence has been accumulating to suggest that this role may ultimately represent a mutualistic relationship (Montesinos-Navarro et al., 2017) as, typically, a relevant proportion of seeds are viable and successfully recruited following parrot dispersal events (Blanco et al., 2016, 2020, 2021; Tella et al., 2016, 2020; Speziale et al., 2018; Bravo et al., 2020). After performing the most comprehensive compilation on parrot-palm interactions on a global scale, we show how interactions between these taxonomic groups rarely involve pure antagonistic relationships. Conversely, parrots develop mainly mutualistic interactions with palms across the world, especially when, at the same time they eat their fruits and seeds, they also disperse them. Although the overall generalist diet of parrots suggests no specificity in these interactions (but see Baños-Villalba et al., 2017 and Tella et al., 2020 for some specific macaw-palm species interactions), we found a positive relationship between fruit and parrot size (i.e., large-sized parrots predate, deflesh, and disperse larger fruits than small-sized parrots) after controlling for phylogenies. This pattern suggests that some interactions can be constrained because of morphological matching between parrots and palms, while others are favored. However, the large variability around this relationship is likely due to the flexibility in the feeding strategies of parrots, so even small species can disperse rather large fruits and vice-versa.

Although the most widely assumed interaction among parrots and palms has been seed predation (where parrots crush palm fruits and seeds with the bill), parrots can feed on fruits using strategies that may have costs but also benefits for palms (**Figure 7**). In most cases, parrots only consume the pulp of the fruits, without consuming the seeds (Baños-Villalba et al., 2017; Luna et al., 2018), or consume the seeds but leave a number of them undamaged and viable (Tella et al., 2020). There is increasing evidence on the viability of seeds dispersed by parrots (Blanco et al., 2016; Baños-Villalba et al., 2017; Tella et al., 2020), and even on the enhanced germination of seeds partially consumed by them (Tella et al., 2016; Speziale et al., 2018). In general, larger parrots deflesh larger fruits than smaller ones, perhaps due to the difficulty of handling small fruits while the opposite is true for small-sized parrots or simply because the beak of all parrot species is prepared to obtain pulp fragments regardless of their size. Interestingly, more parrot species consume the pulp of palms with larger fruits, maybe because the smaller ones easily ingested as a whole. Parrots are social species that usually feed in flocks. Intraspecific interactions, combined with predation fear (Howe, 1979; Laundré et al., 2010),

TABLE 3 | Median distances (and 95% credible intervals) at which parrots of different sizes (mean body mass ± SD of individuals dispersing each palm species; in g) can disperse different palm species varying in their fruit size (estimated as fruit length; in cm).

Palm species	*n*	events	Dispersal distance	Fruit size	Parrot size	Parrot species
Acrocomia totai	536	182	81 (81–110)	3	1404.74 ± 381.36	Ahy (427), Aar (48), Ach (15), Mmo (15), Tac (12), Aae (8), Ase (7), Agl (2), Bch (1), Pma (1)
Adonidia merrillii	2	0	–	2.5	146	Pch (2)
Aiphanes minima	3	3	60 (50–Inf)	1.4	275	Avi (3)
Archontophoenix alexandrae	1429	0	–	1.1	245	Cga (1429)
Attalea barreirensis	244	116	115 (115–115)	5.25*	1565	Ahy (244)
Attalea butyracea	3	1	–	8.25*	857 ± 530.01	Aar (2), Aoc (1)
Attalea eichleri	386	369	9 (9–10)	7.5*	1561.98 ± 59.3	Ahy (385), Aae (1)
Attalea maripa	5	3	50 (45–Inf)	5*	284.2 ± 53.68	Aam (3), Ase (2)
Attalea phalerata	146	48	90 (70–Inf)	8.5*	1562.4 ± 31.45	Ahy (145), Ach (1)
Attalea princeps	366	351	13.5 (10–18)	7*	784.9 ± 370.24	Aar (168), Ase (130), Agl (67), Aae (1)
Attalea speciosa	171	4	290	9.55*	1163.26 ± 2.37	Aar (169), Ach (2)
Carpentaria acuminata	13	0	–	2	245	Cga (13)
Chamaerops humilis	1	1	15	1.3	128	Pkr (1)
Dypsis lutescens	176	0	–	1.5	146	Pch (176)
Elaeis guineensis	7	2	126 (66–Inf)	4.25*	269.43 ± 64.63	Cga (6), Aau (1)
Livistona chinensis	48	48	30 (30–35)	3	135.42 ± 29.19	Pkr (39), Mmo (4), Aam (3), Ane (1), Tac (1)
Mauritia flexuosa	67	5	–	7	1042.49 ± 406.95	Aar (30), Oma (13), Ahy (11), Ach (10), Aae (2), Prma (1),
Phoenix canariensis	595	45	95 (85–Inf)	1.75	121.49 ± 11.53	Mmo (557), Pkr (32), Aam (3), Aoc (1), Ane (1), Pma (1)
Phoenix dactylifera	109	109	30 (25–40)	7*	142.09 ± 48.1	Pkr (71), Mmo (20), Aam (4), Pse (3), Pmi (3), Ane (3), Aae (2), Aoc (2), Pma (1)
Prestoea acuminata	9	4	55 (55–Inf)	1.4	203.33 ± 67.99	Pch (5), Avi (4)
Roystonea borinquena	76	7	250 (230–Inf)	1.3	239.07 ± 281.23	Pch (61), Aar (6), Aam (4), Bve (2), Cal (2), Eca (1)
Sabal domingensis	3	0	–	1.25	146	Pch (3)
Saribus rotundifolius	1	1	30	1.8	128	Pkr (1)
Socratea exorrhiza	3	0	–	3	1091.5	Amac (3)
Syagrus coronata	362	2	–	2.75	940	Ale (362)
Syagrus romanzoffiana	2	1	35	2.5	182.5 ± 88.39	Aam (1), Mmo (1)
Syagrus sancona	15	15	15 (12–35)	3.25	336.47 ± 25.3	Ase (14), Pau (1)
Washingtonia filifera	191	17	20 (20–Inf)	0.6	121.12 ± 9.2	Mmo (179), Pkr (11), Aam (1)
Washingtonia robusta	14	14	27.5 (20–Inf)	1	177.57 ± 60.63	Pkr (7), Aam (2), Ape (1), Aro (1), Mun (1), Mmo (1), Pma (1)

Sample sizes (n: number of dispersal distances measured; events: number of exact dispersal distances, i.e., uncensored data) are shown. Inf, value not calculated but tending toward infinity due to the skewness of the data. Parrot species: Aae: Amazona aestiva, Aam: Amazona amazonica, Aar: Ara ararauna, Aau: Amazona autumnalis, Ach: Ara chloropterus, Agl: Ara glaucogularis, Ahy: Anodorhynchus hyacinthinus, Ale: Anodorhynchus leari, Amac: Ara macao, Ane: Aratinga nenday, Aoc: Amazona ochrocephala, Ape: Agapornis personatus, Aro: Agapornis roseicollis, Ase: Ara severus, Avi: Amazona vittata, Bch: Brotogeris chiriri, Bve: Brotogeris versicolurus, Cal: Cacatua alba, Cga: Cacatua galerita, Eca: Eupsittula canicularis, Mmo: Myiopsitta monachus, Mun: Melopsittacus undulatus, Oma: Orthopsittaca manilatus, Pau: Primolius auricollis, Pch: Psittacara chloropterus, Pkr: Psittacula krameri, Pma: Pionus maximiliani, Pmi: Psittacara mitratus, Prma: Primolius maracana, Pse: Poicephalus senegalus, Tac: Thectocercus acuticaudatus. The brackets next to the abbreviations of the parrot names indicate the number of individuals of each parrot species dispersing fruits of each palm species. The asterisk highlights megafaunal fruits (>4 cm width; Guimarães et al., 2008; see ***Supplementary Figure 1*** *for the relationship between fruit width and length).*

may cause some feeding individuals to fly away to finish eating on perches located at variable distances. On these occasions, parrots carry in their feet or beaks the fruits or seeds they were eating, dispersing them by stomatochory (e.g., Sazima, 2008; Baños-Villalba et al., 2017; Blanco et al., 2019; Tella et al., 2020; Silva et al., 2021). Stomatochory allows the transportation of larger fruits than endozoochory (Blanco et al., 2016). However, there is still a constraint in the size of fruits moved (i.e., the weight of the fruit, which is related to its size), and larger parrots disperse by stomatochory larger fruits than small-sized parrots. Although more research is needed, previous work has shown that the proportion of palm fruits picked from the mother palm and dispersed by some macaw species ranges among palm species from 5% (*Acrocomia totai*) to 13% (*Attalea phalerata*) and 100% of the fruits (*Attalea barreirensis, Attalea eichleri,* and *Acrocomia aculeata*) (Tella et al., 2020; Silva et al., 2021). For smaller parrot species, these proportions are also highly variable (Sist and Puig, 1987). Moreover, parrots can accidentally or, as observed for this and other plant taxa, purposely discard a large proportion of undamaged palm fruits (11–75%) while feeding at perches distant from the mother plant (Tella et al., 2020) but also under the mother tree (Sebastián-González et al., 2019). Once on the ground, fruits can become available to other animals (e.g., insects, fish, reptiles, or mammals), which may disperse them through secondary dispersal (Blanco et al., 2019; Mittelman et al., 2021). Otherwise, if fruits remain under the mother tree or conspecifics, they can experience a high mortality rate (Janzen-Connell effect; Song et al., 2021) through

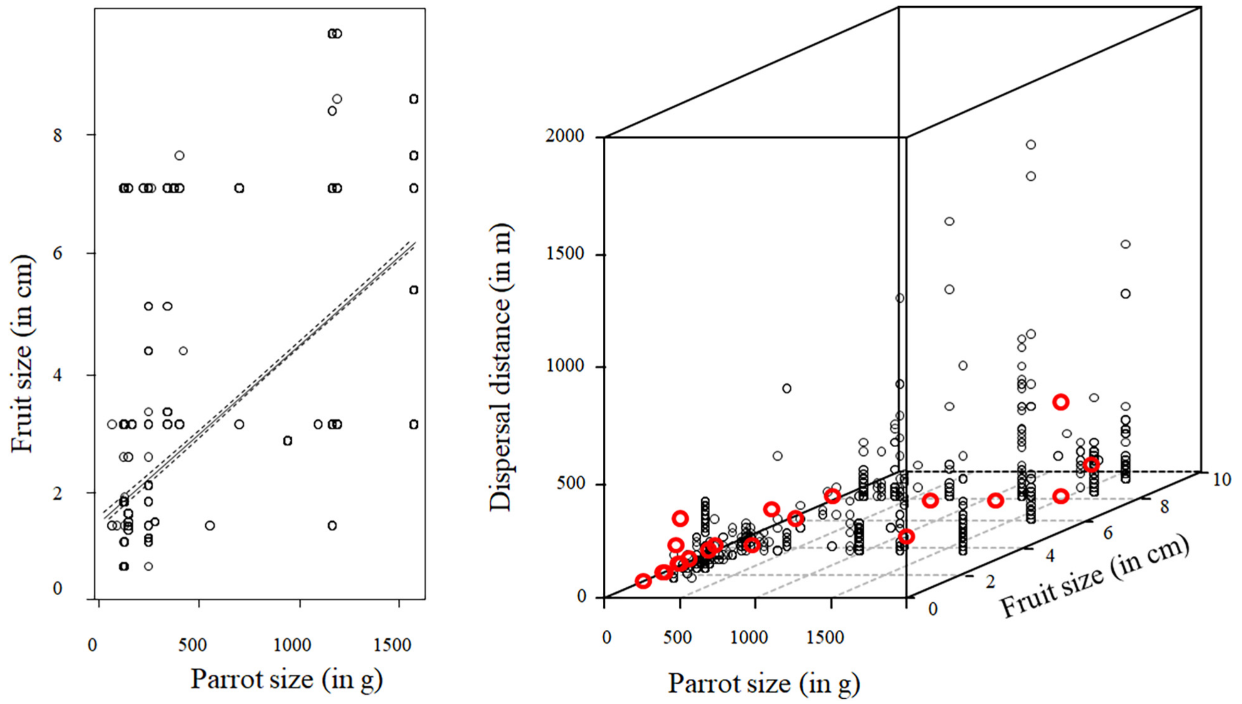


FIGURE 6 | Relationship between the size of palm fruits (in cm) dispersed by parrots and their size (in g), and how these variables affect observed dispersal distances. Red points show the relationship among the mean dispersal distances estimated for each palm species considering the right-censored nature of data (through Kaplan Meier Survival Curves), the size of the palm fruits, and the mean size of parrots moving them (for details, see **Table 3**).

parasitization by invertebrates, mainly bruchines (Fragoso et al., 2003; Dracxler et al., 2011). The pulp of palm fruits has adaptive functions such as defense against seed predators (invertebrates) and pathogens (Silvius and Fragoso, 2002; Pereira et al., 2014), so undamaged fruits may last longer under the mother tree and increase their chances of being dispersed. However, some studies show that palm fruits with injuries in the epicarp can be easily colonized by decomposing fungi, which reduces the selection of the egg-laying site by insects (Pereira et al., 2014). Moreover, defleshing facilitates germination (Nascimento et al., 2019), with dispersers removing the pulp of the fruits being more effective than those regurgitating them (Loayza and Knight, 2010; de Barros Leite et al., 2012). Thus, if defleshed fruits are moved by stomatochory far from the mother palm —under which the risk of invertebrate infection is the highest— or by other animal species, they have a higher probability of survival and germination (Fragoso et al., 2003; Comita et al., 2014; Song et al., 2021). In this sense, the large numbers of viable seeds and saplings below a high proportion of trees (31–100%) used by parrots as perching sites at variable distances from mother palms confirm their role not only as legitimate but also as frequent palm seed dispersers (Sist and Puig, 1987; Baños-Villalba et al., 2017; Tella et al., 2020). Although poorly understood, parrots could, at least theoretically, swallow the whole palm fruit directly, dispersing palm seeds by endozoochory. A few studies have shown that parrots can defecate and/or regurgitate viable seeds of different plant species including palms (Lieberman and Lieberman, 1986; Henderson, 2002; Blanco et al., 2016, 2020; Buitron-Jurado and Sanz, 2016; Bravo et al., 2020; Buitron-Jurado in Litt, unpublished). However, compared to stomatochory, endozoocory is a rather infrequent strategy (only 30 out of 11,274 records of parrots dispersing different plant species corresponded to endozoochory, and none of them were for palms; authors' unpublished results) and deserves more research to understand its relevance for palm ecology.

Parrots can disperse seeds at large distances (i.e., >100 m; Cain et al., 2000), especially large fruits commonly categorized as megafaunal (i.e., >4 cm width; Guimarães et al., 2008). Obtaining reliable dispersal distances is challenging, though many studies have found different approaches to directly or indirectly estimate them. The maximum dispersal distance obtained for palms was provided by Jansen et al. (2012), who recorded the movement of *Astrocaryum standleyanum* palm seeds over distances greater than 100 m from the source after secondary dispersal by several individuals of agoutis *Dasyprocta punctata* stealing each other's seeds after burying them. However, large rodents (*Dasyprocta* sp. and *Cuniculus* sp.) usually hide or bury seeds at distances rarely exceeding 20 m from the mother tree (Franco-Quimbay and Rojas Robles, 2015; Mendieta-Aguilar et al., 2015). These seeds can be dug up and subsequently consumed by the same rodents (Janzen, 1970) or by other species such as peccaries (family Tayassuidae; Kiltie, 1981; Silman et al., 2003), or secondarily dispersed by con- or heterospecifics (Jansen et al., 2012). Our data, representing primary dispersal distances, surpass these values for some palm species (range of median dispersal distances: 9–250 m), in particular, large-fruited

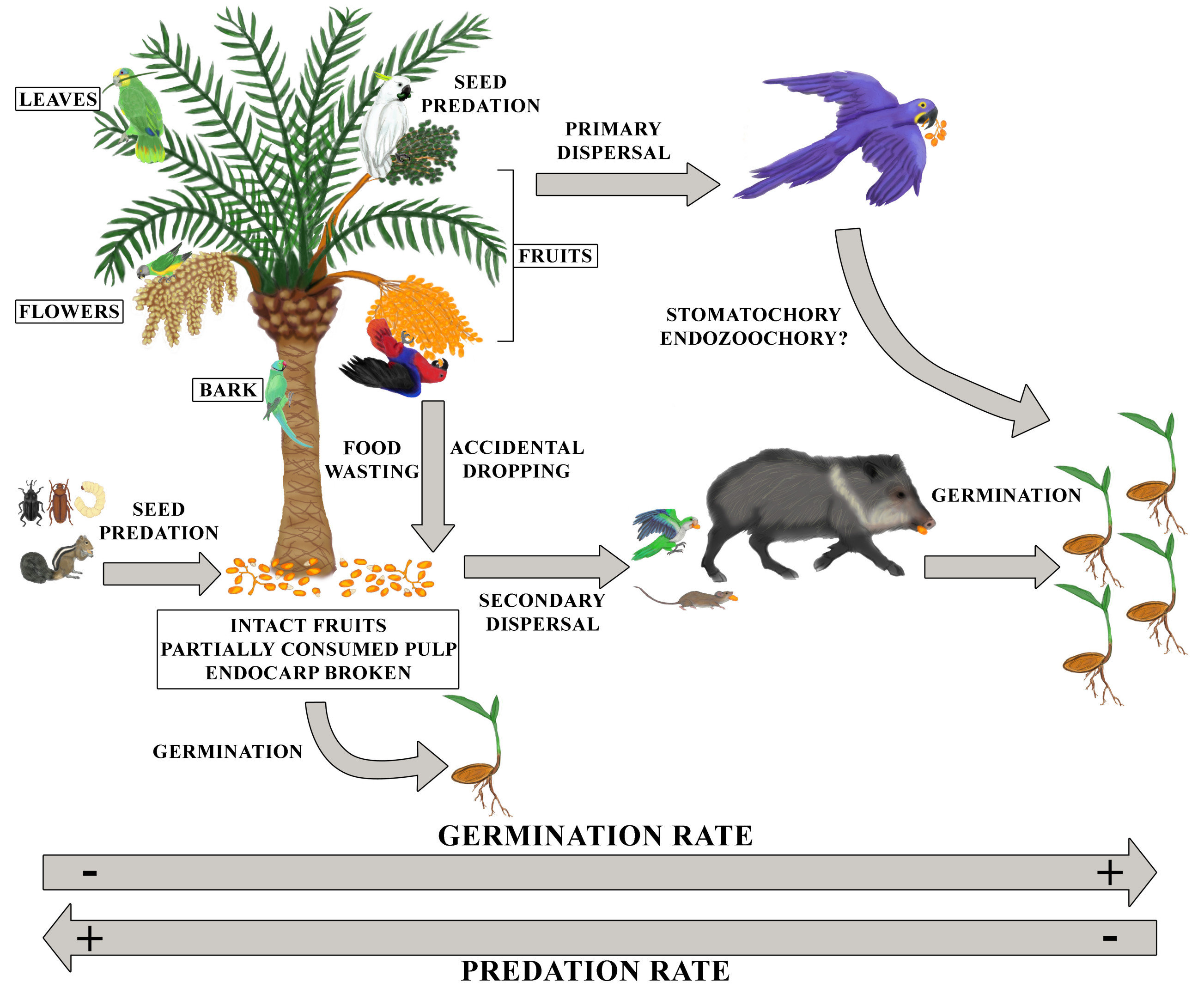


FIGURE 7 | Although most known interactions between parrots and palms have been seed predation and consumption of vegetative parts such as leaves or bark (antagonistic interactions), parrots can also feed using strategies that favor palms (mutualistic interactions). When parrots consume only the pulp of the fruits (defleshing), without consuming the seeds or leaving some undamaged and viable, they can favor the germination of seeds that fall to the ground accidentally or when the individual wastes them (food wasting). In many cases, parrots carry the fruits or seed with their feet or beaks to consume them on perches, dispersing them (stomatochory) and favoring germination in areas far from the mother plant, where predation rates are lower. In addition, these fruits and seeds that fall to the ground, either under the mother palm or under a perch, may then be secondarily dispersed by other species. Although it is possible that parrots also swallow palm fruits and disperse them by endozoochory, this dispersal mechanism has not been described for parrots and palms. Finally, parrots may also consume palm flowers, possibly contributing to pollination. Illustrations by Dailos Hernández-Brito.

ones (up to at least 1,620 m for *Anodorhynchus hyacinthinus* dispersing *Attalea barreirensis* in Brazil). Importantly, dispersal distances vary among parrot species, maybe depending on the dispersed palm species, but are similar (e.g., repeatable) at the palm level. This suggests that although parrot-palm interactions are not species-specific (Blanco et al., 2019), with some exceptions like bush-layer *Attalea* palms (Tella et al., 2020), the ability to disperse certain palm fruits —mainly the largest ones— is restricted to a few, rather large-sized parrot species. Parrots are known for their flying abilities (i.e., they can make long-distance daily, seasonal, altitudinal, and regional movements by tracking their food resources; Renton et al., 2015) that allow them to perform movements far superior to those of large terrestrial mammals (from 10 km for medium-sized species to several tens of kilometers per day, in the case of large macaws; Adamek, 2011; Brightsmith et al., 2021), making them long-distance dispersers of the plants they use (e.g., Tella et al., 2015, 2019; Baños-Villalba et al., 2017; Blanco et al., 2021; present results). Thus, although extinct megafauna might have played a pivotal role in the dispersal of palms with large fruits, these species with presumably anachronic fruits —the so-called "megafaunal" fruits— are in fact dispersed at rather large distances by extant mammals and birds (Jansen et al., 2012; Blanco et al., 2019), such as parrots as evidenced here. Importantly, the fact that large parrots prey upon and disperse more palm species than small-sized parrots supports the primary role that this avian order can play in the structure, organization, and functioning of tropical ecosystems (Blanco et al., 2015, 2018).

Palms are mainly insect-pollinated (mainly by beetles, bees, and flies), even though they can also be pollinated by other invertebrates (e.g., crabs) and by mammals (e.g., bats and marsupials) (Barfod et al., 2011). Our data show several cases of parrots consuming palm flowers, suggesting a potential role as palm pollinators. Data on parrots consuming palm flowers are neither numerous nor detailed enough to adequately understand their significance for pollination. However, parrot feeding behavior (i.e., individuals feeding on palm flowers and moving from inflorescence to inflorescence and between different palms) may facilitate pollination through the transportation of pollen in their feathers and beaks. Indeed, lories and lorikeets have been recognized as important pollinators in Australian and Southeast Asian rainforests (Brown and Hopkins, 1995; Gelis, 2011), while species of the genera *Pionites*, *Brotogeris*, *Psittacara*, and *Enicognathus* are effective pollinators of Neotropical phanerogams and gymnosperms (Maués and Venturieri, 1997; Vicentini and Fischer, 1999; Gleiser et al., 2017). Importantly, while less frequent visitors to palm flowers than insects, parrots may make a unique contribution to palm population structure because of their capacity to move significant pollen loads per individual (Bezemer et al., 2016) and at large distances (Southerton et al., 2004; Byrne et al., 2007; Bezemer et al., 2016). This line of research deserves more attention to properly understand the relevance of parrots as palm pollinators.

Although not very frequent, parrots can develop entirely antagonistic interactions with palms when consuming their non-reproductive structures, causing fitness costs in repairing tissues (Blanco et al., 2015) and, sometimes, the death of individuals (Costion et al., 2013; Brightsmith and Cáceres, 2017; Gilardi in Litt., unpublished; authors unpublished). Palms are known to bioaccumulate sodium (Arnason et al., 1984; Brightsmith and Cáceres, 2017), a vital nutrient for vertebrates (Randall et al., 1997). Animals are regularly confronted with sodium limitations, which are usually overcome through geophagy (i.e., the deliberate consumption of clay or soil by an animal; Diamond et al., 1999). In the case of parrots, different studies show not only geophagy (Emmons and Stark, 1979; Brightsmith and Aramburu, 2004; Brightsmith and Villalobos, 2011) but also palm consumption (mainly leaves and bark; Brightsmith and Cáceres, 2017) as a source of sodium. Parrots are known consumers of plant parts rich in toxic chemicals (Gilardi and Toft, 2012), whose detoxification promotes a negative sodium balance in animals (Pehrson, 1983; Reichardt et al., 1984; Freeland et al., 1985; Jakubas et al., 1995). Therefore, parrots may have particularly high sodium requirements, which, in part, could be met by consuming the vegetative parts of palms.

Palms have been widely introduced elsewhere for ornamental purposes, food, and other uses (Byg and Balslev, 2001; Campos and Ehringhaus, 2003; Byg et al., 2006; Sosnowska and Balslev, 2009; Martins et al., 2014), resulting in the establishment and spread of many palm species into new areas (Fehr et al., 2020; Bello et al., 2021). We found that, in general, parrots interact similarly with native and introduced palms, maybe due to the generalist habits of these avian species (Christianini, 2006). Moreover, the human-induced movement of several parrot species out of their native ranges (Calzada Preston and Pruett-Jones, 2021) has allowed parrot-palm interactions for palm species introduced in the Palaearctic and Nearctic realms. Although more research is needed, these interactions may facilitate palm invasion through the dispersal of fruits, not only across human-modified but also in more natural areas across the world.

As predicted, most parrot-palm interactions have been recorded in the Neotropic, where the richness of both taxa is very high and, more importantly, the mean number of parrot and palm species overlapping their distributions is the highest (see **Supplementary Figure 12**). However, the scientific literature on palm ecology is also skewed toward studies performed in Neotropical countries (**Supplementary Figure 12**) so this result should be more deeply investigated. Muñoz et al. (2019) recently highlighted that knowledge on palm-frugivore interactions in this realm as well as in the Afrotropic is largely incomplete. Part of this gap has been filled here, by focusing on understanding the interactions that one of the most diverse and abundant avian groups has with palms. Data for Africa, Australia, and Asia are still scarce, and more research should be carried out to fully understand the role of parrots in palm ecology in these areas.

CONCLUSION

Parrots are undisputed seed predators. However, as we have demonstrated in this study, they frequently develop mutualistic interactions, including effective seed dispersal, facilitation of secondary dispersal and, quite possibly, pollination. The distinction between disperser and predator is not always immediately evident, and the position of parrots on the antagonist-mutualist continuum may change depending on several factors (e.g., social behavior, predation fear, food availability, seasonality), which are expected to vary among the enormous range of ecosystems they inhabit. All of these aspects should be more deeply investigated to properly comprehend how palms would respond to habitat transformations, fragmentation, and defaunation. Meanwhile, the pervasiveness of parrot-palm mutualistic interactions should not be overlooked in studies of palm ecology and evolution. This would help us to better understand the history of this plant lineage and ensure its long-term conservation. In an era where human impacts are reducing overall plant regeneration by affecting processes early in the regeneration cycle, conserving pollination and seed dispersal, to a large extent by conserving the animal species that provide these ecological functions, should become a priority in forest conservation efforts globally.

DATA AVAILABILITY STATEMENT

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

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because ethical approval not request for observational data on foraging animal.

AUTHOR CONTRIBUTIONS

MC, FH, PR-V, GB, DH-B, ES-G, and JT conceived the ideas for this study. MC, FH, PR-V, GB, DH-B, JD-L, and JT collected the data. FH compiled the data. MC analyzed the data. MC, FH, and JT wrote the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

This research was funded by Severo Ochoa Program (SVP-2014-068732), Action COST "ParrotNet" (ES1304), and Loro Parque Fundación (PP-146-2018-1). ES-G was funded by a Ramón y Cajal contract (RYC-2019-027216I) from the Spanish Ministry of Science and Innovation.

ACKNOWLEDGMENTS

We would like to acknowledge all naturalists and photographers as well as researchers who help us to identify and complete information on parrot-palm interactions, especially G. Buitrón-Jurado, J. Gilardi, L. Ortiz-Catedral, and Y. Takahatato for their kind comments and information shared. N. Cunha, M. Paniw, and R. Rodríguez helped with the phylogenetic analysis. S. Young revised the English and two reviewers and editor have contributed with very useful comments that have improved the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.790883/full#supplementary-material

REFERENCES

Abedi-Lartey, M., Dechmann, D. K. N., Wikelski, M., Scharf, A. K., and Fahr, J. (2016). Long-distance seed dispersal by straw-coloured fruit bats varies by season and landscape. *Global Ecol. Cons.* 7, 12–24. doi: 10.1016/j.gecco.2016.03.005

Adamek, K. (2011). *Temporal Variation in Space and Resource Use of Macaws in the Southeastern Peruvian Amazon*. Ph.D. Thesis. Austin, TX: Texas University.

Adler, G. H., and Kestell, D. W. (1998). Fates of neotropical tree seeds influenced by Spiny Rats (*Proechimys semispinosus*). *Biotropica* 30, 677–681. doi: 10.1111/j.1744-7429.1998.tb00109.x

Andreazzi, C. S., Pires, A. S., and Fernandez, F. A. S. (2009). Mamíferos e palmeiras neotropicais: interações em paisagens fragmentadas. *Oecol. Bras.* 13, 554–574. doi: 10.4257/oeco.2009.1304.02

Arnason, J. T., Lambert, J. D., and Gale, J. (1984). Mineral cycling in a tropical palm forest. *Plant Soil* 79, 211–225. doi: 10.1007/bf02182343

Baños-Villalba, A., Blanco, G., Díaz-Luque, J. A., Dénes, F. V., Hiraldo, F., and Tella, J. L. (2017). Seed dispersal by macaws shapes the landscape of an Amazonian ecosystem. *Sci. Rep.* 7:7373. doi: 10.1038/s41598-017-07697-5

Barfod, A. S., Hagen, M., and Borchsenius, F. (2011). Twenty-five years of progress in understanding pollination mechanisms in palms (Arecaceae). *Ann. Bot.* 108, 1503–1516. doi: 10.1093/aob/mcr192

Bello, C., Cintra, A. L. P., Elisa Barreto, E., Vancine, M. H., Sobral-Souza, T., Graham, C. H., et al. (2021). Environmental niche and functional role similarity between invasive and native palms in the Atlantic Forest. *Biol. Invas.* 23, 741–754. doi: 10.1007/s10530-020-02400-8

Berkunsky, I., Quillfeldt, P., Brightsmith, D. J., Abbud, M. C., Aguilar, J. M. R. E., Alemán-Zelaya, U., et al. (2017). Current threats faced by neotropical parrot populations. *Biol. Conserv.* 214, 278–287.

Bezemer, N., Krauss, S. L., Phillips, R. D., Roberts, D. G., and Hopper, S. D. (2016). Paternity analysis reveals wide pollen dispersal and high multiple paternity in a small isolated population of the bird-pollinated *Eucalyptus caesia* (Myrtaceae). *Heredity* 117, 460–471. doi: 10.1038/hdy.2016.61

BirdLife International (2020). *Handbook of the Birds of the World and BirdLife International Digital Checklist of the Birds of the World. Version 5*. Available online at: http://datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife_Checklist_v5_Dec20.zip (accessed January 12, 2022).

Blach-Overgaard, A., Svenning, J. C., and Balslev, H. (2009). Climate change sensitivity of the African ivory nut palm, *Hyphaene petersiana* Klotzsch ex Mart. (Arecaceae) – a keystone species in SE Africa. *IOP Conf. Ser. Earth Environ. Sci.* 8:012014. doi: 10.1088/1755-1315/8/1/012014

Blach-Overgaard, A., Svenning, J. C., Dransfield, J., Greve, M., and Balslev, H. (2010). Determinants of palm species distributions across Africa: the relative roles of climate, non-climatic environmental factors, and spatial constraints. *Ecography* 33, 380–391.

Blanco, G., Bravo, C., Chamorro, D., Lovas-Kiss, A., Hiraldo, F., and Tella, J. L. (2020). Herb endozoochory by cockatoos: is "foliage the fruit"? *Austr. Ecol.* 45, 122–126. doi: 10.1111/aec.12835

Blanco, G., Bravo, C., Pacífico, E., Chamorro, D., Speziale, K., Lambertucci, S., et al. (2016). Internal seed dispersal by parrots: an overview of a neglected mutualism. *PeerJ* 4:e1688. doi: 10.7717/peerj.1688

Blanco, G., Hiraldo, F., Rojas, A., Dénes, F. V., and Tella, J. L. (2015). Parrots as key multilinkers in ecosystem structure and functioning. *Ecol. Evol.* 18, 4141–4160. doi: 10.1002/ece3.1663

Blanco, G., Hiraldo, G., and Tella, J. L. (2018). Ecological functions of parrots: an integrative perspective from plant life cycle to ecosystem functioning. *Emu* 118, 36–49. doi: 10.1080/01584197.2017.1387031

Blanco, G., Romero-Vidal, P., Carrete, M., Chamorro, D., Bravo, C., Hiraldo, F., et al. (2021). Burrowing parrots *Cyanoliseus patagonus* as long-distance seed dispersers of keystone Algarrobos, Genus *Prosopis*, in the Monte desert. *Diversity* 13:204. doi: 10.3390/d13050204

Blanco, G., Tella, J. L., Díaz-Luque, J. A., and Hiraldo, F. (2019). Multiple external seed dispersers challenge the megafaunal syndrome anachronism and the surrogate ecological function of livestock. *Front. Ecol. Evol.* 7:328. doi: 10.3389/fevo.2019.00328

Boll, T., Svenning, J. C., Vormisto, J., Normand, S., Grandez, C., and Balslev, H. (2005). Spatial distribution and environmental preferences of the piassaba palm *Aphandra natalia* (Arecaceae) along the Pastaza and Urituyacu rivers in Peru. *For. Ecol. Manage.* 213, 175–183. doi: 10.1016/j.foreco.2005.03.020

Bravo, C., Chamorro, D., Hiraldo, F., Speziale, K., Lambertucci, S. A., Tella, J. L., et al. (2020). Physiological dormancy broken by endozoochory: austral parakeets as legitimate dispersers of Calafate (*Berberis microphylla*) in the Patagonian Andes. *J. Plant Ecol.* 13, 538–544. doi: 10.1093/jpe/rtaa041

Brightsmith, D. J., and Aramburu, R. (2004). Avian geophagy and soil characteristics in southeastern Peru. *Biotropica* 36, 534–543. doi: 10.1111/j.1744-7429.2004.tb00348.x

Brightsmith, D. J., and Cáceres, A. (2017). Parrots consume sodium-rich palms in the sodium-deprived landscape of the Western Amazon Basin. *Biotropica* 49, 921–931. doi: 10.1111/btp.12479

Brightsmith, D. J., and Villalobos, E. (2011). Parrot behavior at a Peruvian clay lick. *Wilson J. Ornithol.* 123, 595–602. doi: 10.1676/09-109.1

Brightsmith, D. J., Boyd, J. D., Hobson, E. A., and Randel, C. J. (2021). Satellite telemetry reveals complex migratory movement patterns of two large macaw species in the western Amazon basin. *Avian Cons. Ecol.* 16:14.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., et al. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9, 378–400. doi: 10.32614/rj-2017-066

Brown, E. D., and Hopkins, M. J. G. (1995). A test of pollinator specificity and morphological convergence between nectarivorous birds and rainforest tree flowers in New Guinea. *Oecologia* 103, 89–100. doi: 10.1007/BF00328429

Buitron-Jurado, G., and Sanz, V. (2016). Notes on the diet of endemic Red-eared parakeet Pyrrhura hoematotis and other Venezuelan montane parrots. *Ardeola* 63, 357–367. doi: 10.13157/arla.63.2.2016.sc2

Burgio, K. R., Davis, K. E., Dreiss, L. M., Cisneros, L. M., Klingbeil, B. T., Presley, S. J., et al. (2019). Phylogenetic supertree and functional trait database for all extant parrots. *Data Brief* 24:103882. doi: 10.1016/j.dib.2019.103882

Byg, A., and Balslev, H. (2001). Diversity and use of palms in Zahamena, eastern Madagascar. *Biodiv. Cons.* 10, 951–970.

Byg, A., Vormisto, J., and Balslev, H. (2006). Using the useful: characteristics of used palms in south-eastern Ecuador. *Environ. Dev. Sustain.* 8, 495–506. doi: 10.1007/s10668-006-9051-6

Byrne, M., Elliott, C. P., Yates, C. J., and Coates, D. J. (2007). Extensive pollen dispersal in a bird-pollinated shrub, *Calothamnus quadrifidus*, in a fragmented landscape. *Mol. Ecol.* 16, 1303–1314. doi: 10.1111/j.1365-294X.2006.03204.x

Cain, M. L., Milligan, B. G., and Strand, A. E. (2000). Long-distance seed dispersal in plant populations. *Ann. Bot.* 87, 1217–1227. doi: 10.2307/2656714

Callaghan, C. T., Nakagawa, S., and Cornwell, W. K. (2021). Global abundance estimates for 9,700 bird species. *Proc. Natl. Acad. Sci. U.S.A.* 118:e2023170118. doi: 10.1073/pnas.2023170118

Calzada Preston, C. E., and Pruett-Jones, S. (2021). The number and distribution of introduced and naturalized parrots. *Diversity* 13:412. doi: 10.3390/d13090412

Cámara-Leret, R., Faurby, S., Macía, M. J., Balslev, H., Göldel, B., Svenning, J. C., et al. (2017). Fundamental species traits explain provisioning services of tropical American palms. *Nat. Plants* 3:16220. doi: 10.1038/nplants.2016.220

Campos, M. T., and Ehringhaus, C. (2003). Plant virtues are in the eyes of the beholders: a comparison of known palm uses among indigenous and folk communities of Southwestern Amazonia. *Econ. Bot.* 57:324. doi: 10.1663/0013-0001(2003)057[0324:pvaite]2.0.co;2

Chapman, C., and Russo, S. (2007). "Primate seed dispersal. Linking behavioral ecology with forest community structure," in *Primates in Perspective*, eds C. Campbell, A. Fuentes, K. Mackinnon, M. Panger, and S. Bearder (Oxford: Oxford University Press), 510–525.

Christianini, A. V. (2006). Fecundidade, dispersão e predação de sementes de Archontophoenix cunninghamiana H. Wendl. and Drude, uma palmeira invasora da Mata Atlântica. *Rev. Brasil. Bot.* 29, 587–594.

Comita, L. S., Queenborough, S. A., Murphy, S. J., Eck, J. L., Xu, K., Krishnadas, M., et al. (2014). Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance and density-dependent seed and seedling survival. *J. Ecol.* 102, 845–856. doi: 10.1111/1365-2745.12232

Costion, C. M., Hillmann-Kitalong, A., Perlman, S., and Edwards, W. (2013). Palau's rare and threatened palm *Ponapea palauensis* (Arecaceae): population density, distribution, and threat assessment. *Pac. Sci.* 67, 599–607. doi: 10.2984/67.4.10

Cousens, R., Dytham, C., and Law, R. (2008). *Dispersal in Plants: A Population Perspective*. Oxford: Oxford University Press.

Davies, R. G., Orme, C. D. L., Webster, A. J., Jones, K. E., Blackburn, T. M., and Gaston, K. J. (2007). Environmental predictors of global parrot (Aves: Psittaciformes) species richness and phylogenetic diversity. *Glob. Ecol. Biogeogr.* 16, 220–233. doi: 10.1111/j.1466-8238.2007.00282.x

de Barros Leite, A., Brancalion, P. H. S., Guevara, R., and Galetti, M. (2012). Differential seed germination of a keystone palm (*Euterpe edulis*) dispersed by avian frugivores. *J. Trop. Ecol.* 28, 615–618. doi: 10.1017/s0266467412000594

Diamond, J., Bishop, K. D., and Gilardi, J. D. (1999). Geophagy in New Guinea birds. *Ibis* 141, 181–193. doi: 10.1111/j.1474-919x.1999.tb07540.x

Dracxler, C. M., and Kissling, W. D. (2021). The mutualism–antagonism continuum in Neotropical palm–frugivore interactions: from interaction outcomes to ecosystem dynamics. *Biol. Rev.* 97, 527–553. doi: 10.1111/brv.12809

Dracxler, C. M., Pires, A. S., and Fernandez, F. A. S. (2011). Invertebrate seed predators are not all the same: seed predation by bruchine and scolytine beetles affects palm recruitment in different ways. *Biotropica* 43, 8–11. doi: 10.1111/j.1744-7429.2010.00723.x

Dransfield, J., Uhl, N. W., Asmussen, C. B., Baker, W. J., Harley, M. M., and Lewis, C. E. (2008). *Genera Palmarum – The Evolution and Classification of Palms*. Kew, VIC: Royal Botanic Gardens.

Eiserhardt, W. L., Svenning, J. C., Kissling, W. D., and Balslev, H. (2011). Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Ann. Bot.* 108, 1391–1416. doi: 10.1093/aob/mcr146

Emmons, L. H., and Stark, M. N. (1979). Elemental composition of a natural mineral lick in Amazonia. *Biotropica* 11, 311–313. doi: 10.2307/2387925

Faurby, S., Eiserhardt, W. L., Baker, W. J., and Svenning, J. C. (2016). An all-evidence species-level supertree for the palms (Arecaceae). *Mol. Phylogenet. Evol.* 100, 57–69. doi: 10.1016/j.ympev.2016.03.002

Fehr, V., Buitenwerf, R., and Svenning, J. C. (2020). Non-native palms (Arecaceae) as generators of novel ecosystems: a global assessment. *Div. Dist.* 26, 1523–1538. doi: 10.1111/ddi.13150

Fleming, T. H., and Muchhala, N. (2008). Nectar-feeding bird and bat niches in two worlds: pantropical comparisons of vertebrate pollination systems. *J. Biogeogr.* 35, 764–780. doi: 10.1111/j.1365-2699.2007.01833.x

Fragoso, J. M. V., Silvius, K. M., and Correa, J. A. (2003). Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. *Ecology* 84, 1998–2006. doi: 10.1890/01-0621

Franco-Quimbay, J., and Rojas Robles, R. (2015). Frugivory and seed dispersal of the palm *Oenocarpus bataua* in two regions with different conservation status. *Actual. Biol.* 37, 273–285.

Freeland, W. J., Calcott, P. H., and Geiss, D. P. (1985). Allelochemicals, minerals and herbivore population size. *Biochem. Syst. Ecol.* 13, 195–206. doi: 10.1016/0305-1978(85)90079-1

Garamszegi, L. Z. (ed.) (2014). *Modern Phylogenetic Comparative Methods and their Application in Evolutionary Biology*. Berlin: Springer.

Gelis, S. (2011). "A review of the nutrition of lories and lorikeets," in *Proceedings of AVES International Parrot Convention*.

Gilardi, J. D., and Toft, C. A. (2012). Parrots eat nutritious foods despite toxins. *PLoS One* 7:e38293. doi: 10.1371/journal.pone.0038293

Gleiser, G., Lambertucci, S. A., Speziale, K. L., Hiraldo, F., Tella, J. L., and Aizen, M. A. (2017). The southernmost parakeet might be enhancing pollination of a dioecious conifer. *Ecology* 98, 2969–2971. doi: 10.1002/ecy.1938

Govaerts, R., and Dransfield, J. (2005). *World Checklist of Palms*. Richmond: Royal Botanic Gardens, 223.

Guimarães, P. R. Jr, Galetti, M., and Jordano, P. (2008). Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. *PLoS One* 3:e1745. doi: 10.1371/journal.pone.0001745

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Soft.* 33, 1548–7660.

Henderson, A. (2002). *Evolution and Ecology of Palms*. Bronx, NY: The New York Botanical Garden Press.

Hernández-Brito, D., Romero-Vidal, P., Hiraldo, F., Blanco, G., Díaz-Luque, J. A., Barbosa, J. M., et al. (2021). Epizoochory in parrots as an overlooked yet widespread plant–animal mutualism. *Plants* 10:760. doi: 10.3390/plants10040760

Howe, H. F. (1979). Fear and frugivory. *Am. Nat.* 114, 925–931. doi: 10.1086/283540

Howe, H. F., and Smallwood, J. (1982). Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13, 201–228.

Jakubas, W. J., Guglielmo, C. G., Vispo, C., and Karasov, W. H. (1995). Sodium-balance in ruffed grouse as influenced by sodium levels and plant secondary metabolites in quaking aspen. *Can. J. Zool.* 73, 1106–1114. doi: 10.1139/z95-132

Jansen, P. A., Hirsch, B. T., Emsens, W. J., Zamora-Gutierrez, V., Wikelski, M., and Kays, R. (2012). Rodents as dispersers of megafaunal seeds. *Proc. Natl. Acad. Sci. U.S.A.* 109, 12610–12615. doi: 10.1073/pnas.1205184109

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104, 501–528. doi: 10.1086/282687

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., and Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature* 491, 444–448. doi: 10.1038/nature11631

Jordano, P. (2016). Sampling networks of ecological interactions. *Funct. Ecol.* 30, 1883–1893. doi: 10.1111/1365-2435.12763

Kiltie, R. A. (1981). Distribution of palm fruits on a rain forest floor: why white-lipped peccaries forage near objects. *Biotropica* 13, 141–145. doi: 10.2307/2387716

Kissling, W. D., Baker, W. J., Balslev, H., Barfod, A. S., Borchsenius, F., Dransfield, J., et al. (2007). Quaternary and pre-quaternary historical legacies in the global distribution of a major tropical plant lineage. *Glob. Ecol. Biogeogr.* 16, 220–233.

Kissling, W. D., Balslev, H., John Baker, W., Dransfield, J., Göldel, B., Lim, J. Y., et al. (2019). Data from: PalmTraits 1.0, a species-level functional trait database for palms worldwide. *Sci. Data* 6, 1–13. doi: 10.1038/s41597-019-0189-0

Kissling, W. D., Eiserhardt, W. L., Baker, W. J., Borchsenius, F., Couvreur, T. L. P., Balslev, H., et al. (2012). Phylogenetic assemblage structure in palms. *Proc. Natl. Acad. Sci. U.S.A.* 109, 7379–7384.

Laundré, J. W., Hernandez, L., and Ripple, W. J. (2010). The landscape of fear: ecological implications of being afraid. *Open Ecol. J.* 3, 1–7. doi: 10.2174/1874213001003030001

Lenth, R. V. (2016). Least-squares means: the R package lsmeans. *J. Stat. Softw.* 69, 1–33.

Levey, D. J., Moermond, T. C., and Denslow, J. S. (1994). "Frugivory: an overview," in *La Selva: Ecology and Natural History of a Neotropical Rainforest*, eds L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (Chicago, IL: University of Chicago Press), 282–294. doi: 10.1002/ajp.22246

Li, M., and Bolker, B. (2019). *Wzmli/Phyloglmm: First Release of Phylogenetic Comparative Analysis in lme4-verse (Version v1.0.0)*. Zenodo. doi: 10.5281/zenodo.2639887

Lieberman, M., and Lieberman, D. (1986). An experimental study of seed ingestion and germination in plant-animal assemblage in Ghana. *J. Trop. Ecol.* 2, 113–126. doi: 10.1017/s0266467400000717

Lim, J. Y., Svenning, J. C., Göldel, B., Faurby, S., and Kissling, W. D. (2020). Frugivore-fruit size relationships between palms and mammals reveal past and future defaunation impacts. *Nat. Commun.* 11:4904. doi: 10.1038/s41467-020-18530-5

Loayza, A. P., and Knight, T. (2010). Seed dispersal by pulp consumers, not "legitimate" seed dispersers, increases *Guettarda viburnoides* population growth. *Ecology* 91, 2684–2695. doi: 10.1890/09-0480.1

Luna, A., Romero-Vidal, P., Hiraldo, F., and Tella, J. L. (2018). Cities may save some threatened species but not their ecological functions. *PeerJ* 6:e4908. doi: 10.7717/peerj.4908

Martins, R. C., Filgueiras, T. S., and Albuquerque, U. P. (2014). Use and diversity of palm (Arecaceae) resources in Central Western Brazil. *Sci. World J.* 2:942043. doi: 10.1155/2014/942043

Maués, M. M., and Venturieri, G. C. (1997). Pollination ecology of platonia insignis mart. (Clusiaceae), a fruit tree from Eastern Amazon region. *Acta Hortic.* 437, 255–260. doi: 10.17660/actahortic.1997.437.29

Mendieta-Aguilar, G., Pacheco, L. F., and Roldán, A. I. (2015). Dispersión de semillas de *Mauritia flexuosa* (Arecaceae) por frugívoros terrestres en Laguna Azul, Beni, Bolivia. *Acta Amaz.* 45, 45–56. doi: 10.1590/1809-4392201400283

Mittelman, P., Dracxler, C. M., Santos-Coutinho, P. R. O., and Pires, A. S. (2021). Sowing forests: a synthesis of seed dispersal and predation by agoutis and their influence on plant communities. *Biol. Rev.* 96, 2425–2445. doi: 10.1111/brv.12761

Montesinos-Navarro, A., Hiraldo, F., Tella, J. L., and Blanco, G. (2017). Network structure embracing mutualism-antagonism continuums increases community robustness. *Nat. Ecol. Evol.* 1:1661. doi: 10.1038/s41559-017-0320-6

Mougi, A. (ed.) (2020). *Diversity of Functional Traits and Interactions. Perspectives on Community Dynamics*. Singapore: Springer.

Muñoz, G., Trøjelsgaard, K., and Kissling, W. D. (2019). A synthesis of animal-mediated seed dispersal of palms reveals distinct biogeographical differences in species interactions. *J. Biogeogr.* 46, 466–484. doi: 10.1111/jbi.13493

Muscarella, R., Emilio, T., Phillips, O. L., Lewis, S. L., Slik, F., Baker, W. J., et al. (2020). The global abundance of tree palms. *Glob. Ecol. Biogeogr.* 29, 1495–1514.

Nascimento, L. M., Vendruscolo, E. P., Campos, L. F. C., Garcia, L. G. C., Pires, L. L., and Seleguini, A. (2019). Pre-depulping and depulping treatments and the emergence of queen palm seeds (*Syagrus romanzoffiana* [Cham.] Glassman). *Rev. Colomb. Ciencias Hortíc.* 13, 466–472. doi: 10.17584/rcch.2019v13i3.8363

Olah, G., Butchart, S. H. M., Symes, A., Medina Guzmán, I., Cunningham, R., Brightsmith, D. J., et al. (2016). Ecological and socio-economic factors affecting extinction risk in parrots. *Biodivers. Conserv.* 25, 205–223. doi: 10.1007/s10531-015-1036-z

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., et al. (2001). Terrestrial ecoregions of the world: a new map of life on earth. *Bioscience* 51, 933–938. doi: 10.1641/0006-3568(2001)051[0933:teotwa]2.0.co;2

Onstein, R. E., Baker, W. J., Couvreur, T. L. P., Faurby, S., Svenning, J.-C., Daniel Kissling, W., et al. (2017). Frugivory-related traits promote speciation of tropical palms. *Nat. Ecol. Evol.* 1, 1903–1911. doi: 10.1038/s41559-017-0348-7

Pehrson, A. (1983). Digestibility and retention of food components in caged mountain hares *Lepus timidus* during winter. *Holarct. Ecol.* 6, 395–403. doi: 10.1111/j.1600-0587.1983.tb01235.x

Pereira, A. C. F., Fonseca, F. S. A., Mota, G. R., Fernandes, A. K. C., Fagundes, M., Reis-Júnior, R., et al. (2014). Ecological interactions shape the dynamics of seed predation in *Acrocomia aculeata* (Arecaceae). *PLoS One* 9:e98026. doi: 10.1371/journal.pone.0098026

Pérez-Méndez, N., Jordano, P., García, C., and Valido, A. (2016). The signatures of Anthropocene defaunation: cascading effects of the seed dispersal collapse. *Sci. Rep.* 6:24820. doi: 10.1038/srep24820

Pitman, N. C. A., Terborgh, J. W., Silman, M. R., Núñez, P., Neill, D. A., Cerón, C. E., et al. (2001). Dominance and distribution of tree species in upper amazonian terra firme forests. *Ecology* 82, 2101–2117. doi: 10.1890/0012-9658(2001)082[2101:dadots]2.0.co;2

Prada Villalobos, M., and Araújo Bagno, M. (2012). Avian frugivores feeding on *Mauritia flexuosa* (Arecaceae) fruits in Central Brazil. *Rev. Brasil. Ornitol.* 20, 26–29.

Provost, K. L., Joseph, L., and Tilston Smith, B. (2018). Resolving a phylogenetic hypothesis for parrots: implications from systematics to conservation. *Emu* 118, 7–21. doi: 10.1080/01584197.2017.1387030

R Core Team (2021). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Randall, D., Burggren, W., and French, K. (1997). *Eckert Animal Physiology: Mechanisms and Adaptations*, 4th Edn. New York, NY: W. H. Freeman and Company.

Reichardt, P. B., Bryant, J. P., Clausen, T. P., and Wieland, G. D. (1984). Defense of winter-dormant Alaska paper birch against snowshoe hares. *Oecologia* 65, 58–69. doi: 10.1007/BF00384463

Reichgelt, T., West, C. K., and Greenwood, D. R. (2018). The relation between global palm distribution and climate. *Sci. Rep.* 8:4721. doi: 10.1038/s41598-018-23147-2

Renton, K., Salinas-Melgoza, A., De Labra-Hernández, M. Á, and de la Parra-Martínez, S. M. (2015). Resource requirements of parrots: nest site selectivity and dietary plasticity of Psittaciformes. *J. Ornithol.* 156, 73–90. doi: 10.1007/s10336-015-1255-9

Robinson, O. J., Socolar, J. B., Stuber, E. F., Auer, T., Berryman, A. J., Boersch-Supan, P. H., et al. (2022). Extreme uncertainty and unquantifiable bias do not inform population sizes. *Proc. Natl. Acad. Sci. U.S.A.* 119:e2113862119. doi: 10.1073/pnas.2113862119

Rousset, F. (2004). *Genetic Structure and Selection in Subdivided Populations*. Princeton, NJ: Princeton University Press.

Sazima, I. (2008). The parakeet *Brotogeris tirica* feeds on and disperses the fruits of the palm *Syagrus romanzoffiana* in Southeastern Brazil. *Biota Neotrop.* 8, 231–234. doi: 10.1590/s1676-06032008000100026

Sebastián-González, E., Hiraldo, F., Blanco, G., Hernández Brito, D., Romero-Vidal, P., Carrete, M., et al. (2019). The extent, frequency and ecological functions of food wasting by parrots. *Sci. Rep.* 9:15280. doi: 10.1038/s41598-019-51430-3

Silman, M. R., Terborgh, J. W., and Kiltie, R. A. (2003). Population regulation of a dominant rain forest tree by a major seed predator. *Ecology* 84, 431–438. doi: 10.1890/0012-9658(2003)084[0431:proadr]2.0.co;2

Silva, L. B., Pereira, G. A., Passos, P. B., and Almeida, N. M. (2021). Seed dispersal of the palm *Acrocomia aculeata* by the blue-and-yellow macaw (*Ara ararauna*). *Braz. J. Biol.* 83:e244697. doi: 10.1590/1519-6984.244697

Silvius, K. M., and Fragoso, J. M. V. (2002). Pulp handling by vertebrate seed dispersers increases palm seed predation by bruchid beetles in the northern Amazon. *J. Ecol.* 90, 1024–1032. doi: 10.1046/j.1365-2745.2002.00728.x

Sist, P., and Puig, H. (1987). Régénération, dynamique des populations et dissémination d'un palmier de Guyane française: Jessenia bataua (Mart.) Burret subsp. oligocarpa (Griseb. and H. Wendl.) Balick. *Bull. Mus. Nat. Hist. Nat. B* 9, 317–336.

Song, X., Lim, J. Y., Yang, J., and Luskin, M. S. (2021). When do Janzen-Connell effects matter? A phylogenetic meta-analysis of conspecific negative distance and density dependence experiments. *Ecol. Lett.* 24, 608–620. doi: 10.1111/ele.13665

Sosnowska, J., and Balslev, H. (2009). American palm ethnomedicine: a meta-analysis. *J. Ethnobiol. Ethnomed.* 5:43. doi: 10.1186/1746-4269-5-43

Southerton, S. G., Birt, P., Porter, J., and Ford, H. A. (2004). Review of gene movement by bats and birds and its potential significance for eucalypt plantation forestry. *Aust. For.* 67, 44–53. doi: 10.1080/00049158.2004.10676205

Speziale, K. L., Lambertucci, S. A., Gleiser, G., Tella, J. L., Hiraldo, F., and Aizen, M. A. (2018). An overlooked plant-parakeet mutualism counteracts human overharvesting on an endangered tree. *R. Soc. Open Sci.* 5:171456. doi: 10.1098/rsos.171456

Sunderland, T. C. H., and Morakinyo, T. (2002). Nypa fruticans, a weed in West Africa. *Palms* 46, 154–155.

Svenning, J. C. (2001). On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (Arecaceae). *Bot. Rev.* 67, 1–53. doi: 10.1007/bf02857848

Svenning, J. C. (2002). Crown illumination limits the population growth rate of a Neotropical understorey palm (*Geonoma macrostachys*, Arecaceae). *Plant Ecol.* 159, 185–199.

Svenning, J. C., and Wright, S. J. (2005). Seed limitation in a Panamanian forest. *J. Ecol.* 93, 853–862. doi: 10.1111/j.1365-2745.2005.01016.x

Taxonomic Databases Working Group (2001). *World Geographic Scheme for Recording Plant Distributions Standard. Biodiversity Information Standards (TDWG)*. Available online at: http://www.tdwg.org/standards/109 (accessed January 12, 2022).

Tella, J. L., Baños-Villalba, A., Hernández-Brito, D., Rojas, A., Pacífico, E., Díaz-Luque, J. A., et al. (2015). Parrots as overlooked seed dispersers. *Front. Ecol. Environ.* 13:338–339. doi: 10.1890/1540-9295-13.6.338

Tella, J. L., Blanco, G., Dénes, F. V., and Hiraldo, F. (2019). Overlooked parrot seed dispersal in Australia and South America: insights on the evolution of dispersal syndromes and seed size in Araucaria trees. *Front. Ecol. Evol.* 7:82. doi: 10.3389/fevo.2019.00082

Tella, J. L., Dénes, F. V., Zulian, V., Prestes, N. P., Martínez, J., Blanco, G., et al. (2016). Endangered plant–parrot mutualisms: Seed tolerance to predation makes parrots pervasive dispersers of the Parana pine. *Sci. Rep.* 6:31709. doi: 10.1038/srep31709

Tella, J. L., Hiraldo, F., Pacífico, E., Díaz-Luque, J. A., Dénes, F. V., Fontoura, F. M., et al. (2020). Conserving the diversity of ecological interactions: the role of two threatened macaw species as legitimate dispersers of "megafaunal" fruits. *Diversity* 12:45. doi: 10.3390/d12020045

Tella, J. L., Romero-Vidal, P., Dénes, F. V., Hiraldo, F., Toledo, B., and Rossetto, F. (2021). Roadside car surveys: methodological constraints and solutions for estimating parrot abundances across the world. *Diversity* 13:300. doi: 10.3390/d13070300

Terborgh, J. (1986). "Community aspects of frugivory in tropical forests," in *Frugivores and Seed Dispersal*, eds A. Estrada and T. H. Fleming (Dordrecht: Dr. W. Junk Publishers), 371–384. doi: 10.1007/978-94-009-4812-9_32

Toft, C. A., and Wright, T. F. (2015). *Parrots of the Wild: A Natural History of the World's Most Captivating Birds*. Oakland, CA: University of California Press.

Vicentini, A., and Fischer, E. (1999). Pollination of Moronobea coccinea (Clusiaceae) by the Golden-winged Parakeet in the central Amazon. *Biotropica* 31, 692–696. doi: 10.1111/j.1744-7429.1999.tb00419.x

Wandrag, E. M., Dunham, A. E., Duncan, R. P., and Rogers, H. S. (2018). Seed dispersal increases local species richness and reduces spatial turnover of tropical tree seedlings. *Proc. Natl. Acad. Sci. U.S.A.* 114, 10689–10694. doi: 10.1073/pnas.1709584114

WFO (2021). *World Flora Online*. Available online at: http://www.worldfloraonline.org (accessed July 19, 2021)

Zona, S. (2006). *Additions to a Review of Animal-Mediated Seed Dispersal of Palms*. Available online at: http://www.virtualherbarium.org/ (accessed January 12, 2022).

Zona, S., and Henderson, A. (1989). A review of animal mediated seed dispersal of palms. *Selbyana* 11, 6–21.

Conflict of Interest: JD-L was employed by Endangered Conservation Consultancy.

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

Frontiers in Forests and Global Change

ORIGINAL RESEARCH
published: 19 May 2022
doi: 10.3389/ffgc.2022.733636

Palm Species Traits Determine Soil Nutrient Effects on Seedling Performance

Colton Collins*, David A. Wardle and Kelly M. Andersen*

Asian School of the Environment, Nanyang Technological University, Singapore, Singapore

Environmental gradients influence plant establishment, survival, and functional traits. Along the Panama Canal Isthmus there is a strong rainfall gradient with an underlying mosaic of soil types ranging in soil nutrient availability. In this region, tree species distribution patterns are correlated with soil phosphorus availability and rainfall patterns, but how understory plant species such as palms relate to these factors is less clear. We hypothesized that due to greater resource use efficiency and optimal biomass allocation, specialist species will have greater seedling performance growing in home soil and sites compared to species not occurring there. To test this hypothesis, we used two specialist species (*Chamaedorea tepejilote* and *Geonoma congesta*) and two generalist species (*Geonoma cuneata* var. *cuneata* and *Chamaedorea pinnatifrons*), and for these four species we measured traits on seedlings and assessed their performance in shade house and field transplant experiments using five soils. Soils were sourced from five sites which varied in nutrient availability and rainfall, and were distributed along lowland tropical forests of the Panama Canal Isthmus. In the shadehouse experiment, leaf functional traits were determined by species rather than soil nutrient availability. However, in the shadehouse experiment, seedling biomass allocation, and relative growth rate were determined by interactions between species and soil, with weak support for home-site advantage for one of the species. In the field transplant experiment, seedling survival was strongly related to dry season water availability. However, species tended to have high survival at home sites and other sites with higher dry season rainfall. Together, results from these experiments suggest that understory palm species seedling performance are determined by species-specific responses to the combination of soil nutrient and water availability. This indicates that while soil nutrients influence seedling biomass allocation, dry season water availability determines both specialist and generalist seedling survival and therefore distributions along the soil nutrient and moisture gradient.

Keywords: biomass allocation, functional traits, home-site advantage, lowland tropical forest, seedling performance, understory palms

Edited by:
Sanna Sevanto,
Los Alamos National Laboratory (DOE), United States

Reviewed by:
Kelsey R. Carter,
Los Alamos National Laboratory (DOE), United States
Joseph Yavitt,
Cornell University, United States

****Correspondence:***
Colton Collins
coltonla001@e.ntu.edu.sg
Kelly M. Andersen
kelly.andersen@ntu.edu.sg

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

Received: *30 June 2021*
Accepted: *25 April 2022*
Published: *19 May 2022*

Citation:
Collins C, Wardle DA and Andersen KM (2022) Palm Species Traits Determine Soil Nutrient Effects on Seedling Performance. Front. For. Glob. Change 5:733636. doi: 10.3389/ffgc.2022.733636

INTRODUCTION

Abiotic environmental factors, including climate, soil nutrients, and light are drivers of seedling performance, including their survival, growth, and functional traits, and consequently influence species distribution patterns (Grubb, 1977; Grime, 2006; Engelbrecht et al., 2007). These abiotic factors do not operate independently of each other. For example, in lowland tropical forests, high mean annual precipitation (MAP) and temperatures leads to high rates of leaching of labile cations and phosphorous from the parent material during soil formation (Vitousek and Sanford, 1986; Sollins, 1998), and therefore result in nutrient limitation of rock-derived nutrients necessary for successful seedling regeneration (Alvarez-Clare et al., 2013). In addition to nutrient limitation, dry season soil moisture availability can also impose a filter on seedling regeneration and species composition (Baltzer et al., 2005; Engelbrecht et al., 2007; Condit et al., 2013). However, disentangling the effects of different abiotic drivers such as soil nutrient availability and dry season water deficit on seedling performance may reveal different mechanisms that drive habitat associations and ultimately species distribution patterns along environmental gradients (Fortunel et al., 2016).

Plants show trade-offs between "acquisitive" strategies aimed at rapid resource uptake driving fast growth rates, and "conservative" strategies aimed at the retention of resources and longer life spans (Diaz et al., 2004; Wright et al., 2004; Díaz et al., 2016). The traits underpinning these strategies are responsive to environmental gradients, including soil nutrient (Richardson et al., 2004; Peltzer et al., 2010), and moisture availability (Maharjan et al., 2011; Pollock et al., 2012; McLean et al., 2014). For example, plants growing in fertile soils allocate biomass aboveground and are associated with high relative growth rates (RGR), leaf-area ratios (LAR), specific leaf area (SLA; Aerts and Chapin, 2000; Palmiotto et al., 2004; Dent and Burslem, 2009), and height (Yavitt and Wright, 2008; Ali and Yan, 2017), whereas those growing in low-nutrient soils allocate more biomass belowground and are associated low RGR and SLA (Tilman and Wedin, 1991; Aerts and Chapin, 2000). Together, plant functional traits govern how species both influence and respond to their environment (Diaz et al., 2004) and can drive community assembly (Laughlin and Laughlin, 2013; Kumordzi et al., 2015). Among plant groups, monocots and particularly, palms, produce leaves with high leaf toughness (Dominy et al., 2008) and lignin (Santiago, 2007), slow decomposition rates, and low SLA and nutrient content compared to dicots, suggesting palms may have conservative plant economic strategies. However, despite the high species diversity and abundance of palm species in lowland tropical forests, we know little about how functional traits vary among palm species or the ecological significance of this variation compared to the breadth of information for their woody counterparts.

Understanding drivers of palm species distributions is central to understanding whole forest community ecology in lowland tropical forests because palms act as filters that affect tree seedling growth and survival (Farris-Lopez et al., 2004; Wang and Augspurger, 2004). Palms reduce seedling establishment by modifying microsite conditions through increasing leaf litter depth and decreasing light availability (Farris-Lopez et al., 2004). Therefore, it is important to better understand drivers of palm species distribution patterns. Palm species distribution patterns, phylogenetic structure, and ecological interactions are all influenced by soil conditions, such as nutrient and moisture availability (Clark et al., 1995; Emilio et al., 2013; Cámara-Leret et al., 2017; Muscarella et al., 2019). For example, palm species distribution patterns are strongly correlated with soil phosphorus and base cations across landscape scales in lowland Amazonia (Cámara-Leret et al., 2017) and soil nitrogen availability in lower montane forests in western Panama (Andersen et al., 2010a,b). Although there have been many studies examining the relationship between soil parameters and palm species distributions, fewer studies have experimentally tested the mechanisms responsible for driving these patterns along soil gradients or examined plant functional traits.

The Panamanian Isthmus presents an ideal study system for exploring species habitat specialization because of its mosaic of environmental conditions. The complex environmental variation in this region is due to a strong rainfall gradient which ranges from 1,500 to 3,000 mm MAP from the Pacific to Caribbean sides of the 60 km Isthmus (Paton, 2020a,b), as well as a diverse geology resulting in a range of soil properties (Turner and Engelbrecht, 2011; Cusack et al., 2018). Soil nutrients and moisture are the main abiotic factors that drive a near complete floristic turnover of woody species in the lowland tropical forests across the 60 km Panama Isthmus (Pyke et al., 2001; Engelbrecht et al., 2007; Condit et al., 2013). In addition to shifts in species composition, there are large changes in fine root biomass driven by variation in soil base cation availability (Cusack et al., 2018), and changes in community-level leaf trait values, such as SLA and leaf thickness, driven by variation in both soil moisture and phosphorus (Umaña et al., 2021). This demonstrates strong species selection and trade-offs along multiple resource gradients for trees, but it is unclear whether understory plant species follow the same patterns.

One of the most extensively studied understory palm communities occurs in the Fortuna Forest Reserve (Fortuna) and surrounding lower montane forests of western Panama, a hot spot for palm species diversity and endemism (Andersen et al., 2010a; Prada et al., 2017). In Fortuna, understory palm species community composition and functional traits are related to shifts in soil nitrogen, cation, and aluminum availability (Andersen et al., 2010a, 2012), whereas tree (woody and palm) species composition is related to soil phosphorus availability and rainfall (Prada et al., 2017). Furthermore, seedling transplant experiments of understory palm species have revealed that whole-plant functional strategies of low nutrient specialist species give them a performance advantage at low soil nutrient sites (Andersen et al., 2010b, 2014; Andersen and Turner, 2013). These findings suggest that functional traits and seedling performance drive understory palm species distribution patterns across the soil nutrient gradient at Fortuna, where species show "home-site advantages" when growing in soils they are associated with compared to species absent from the site. Here, we expand on these studies by using seedling experiments to test the effects of soil nutrient and moisture availability on seedling performance of four contrasting understory palm species along soil nutrient availability and rainfall gradient in lowland tropical forests of the Panama Canal Watershed.

To specifically examine the effects of soil nutrient availability on understory palm seedling performance and functional traits, we conducted a shadehouse experiment growing seedlings of four species in soil collected from five sites varying in soil nutrient availability along the Panama Canal (**Table 1**; Turner and Engelbrecht, 2011; Cusack et al., 2018). Nutrient availability varied from "low nutrient" soil that is depleted in phosphorus and base cations to "high nutrient" soil that is rich in phosphorus. We included two site specialist species (*Chamaedorea tepejilote*), from site Pipeline Road Plot 15 (an intermediate nutrient site), and *Geonoma congesta,* from site Fort Sherman (a low nutrient site). We also included two site generalist species (*Geonoma cuneata* var. *cuneata* and *Chamaedorea pinnatifrons*) from the lower montane Fortuna sites which have soils that range in nutrient availability (**Table 2**). In this study, a species was defined as a specialist if it is found at one site, i.e., that is has a single soil nutrient ranking. A species was classified as a generalist if it is found at multiple areas which vary in soil nutrient availability. While the ratio of generalist to specialist palm species across these sites is poorly understood, in western Amazonian lowland rainforests generalist species have wide tolerances to differences in soil fertility and outnumber specialist species (Ruokolainen and Vormisto, 2000). To further understand how abiotic factors (including both soil nutrients and moisture availability) influence seedling survival of the four palm species, we also transplanted seedlings of all four species into the five field sites. We expected that, due to higher resource use efficiency and optimal biomass allocation, the specialist species (*C. tepejilote* and *G. congesta*) would show greater seedling performance in the soil and at the site that they are associated with compared to species not occurring at those sites. On that basis we tested the following four hypotheses:

> (H1) To maximize returns of investment in leaf resources, leaf traits such as SLA, LAR, photosynthesis rates (A_{sat}), and dark respiration rates (R_{dark}) will decline as soil fertility declines. Furthermore, we expected the species associated with low nutrient, phosphorus and base cation depleted soils (*G. congesta*) to have higher leaf resource-use efficiency and the species associated with intermediate nutrient soil (*C. tepejilote*) to have leaf traits to maximize carbon gains when grown in their home soil compared to species not absent from those soils.
>
> (H2) Root mass ratio (RMR) should increase as soil fertility declines to meet nutrient demands at the expense of leaf mass ratio (LMR), stem mass ratio (SMR), and growth potential. The specialist species are expected to maximize allocation to leaf biomass to increase growth potential in their home soils compared to other species absent from those soils.
>
> (H3) Due to increased resource-use efficiency (H1) and optimal biomass allocation patterns (H2), specialists growing in the soil they are associated with will achieve higher RGR compared to species not occurring in those soils.
>
> (H4) Since specialist species have higher resource-use efficiency (H1), higher nutrient/water uptake efficiency biomass allocation patterns (H2), and higher RGR (H3), they will have higher seedling survival rates when growing at the sites where they naturally occur than will species not occurring at those sites.

By simultaneously examining the above hypotheses, we aim to advance our understanding of the mechanisms that influence establishment, survival, and functional traits of seedlings of understory palm species, and thus their distribution patterns along soil nutrient and moisture gradients in lowland tropical forests.

MATERIALS AND METHODS

Study Sites and Soil Nutrient Gradient

The present study was conducted at five one-hectare sites in lowland tropical forest along the Panama Canal (Pyke et al., 2001; Engelbrecht et al., 2007; Condit et al., 2013) ForestGEO data portal[1]. These sites following nomenclature from Pyke et al. (2001) and Cusack et al. (2018), and ForestGEO data portal (see text footnote 1) include the Fort Sherman/San Lorenzo crane site (SH), La Laguna/Rio Paja (M25), Pipeline Road plot 9 (P9), Pipeline Road plot 15 (P15), and Campo Charges (CCH; **Table 1**). MAP of these sites range from 2,177 mm at site M25 to 2,848 mm at site SH, with dry seasonal precipitation deficit ranging from 570 mm at site CCH to 492 mm at site SH (Condit et al., 2013); ForestGEO data portal (see text footnote 1). In general, soil nutrient availability and dry season water deficit increase as MAP decreases among sites (Condit et al., 2013; Cusack et al., 2018; Umaña et al., 2021). The M25 site represents a low nutrient site with low MAP, however, the fine texture soil allows it to maintain high soil available water capacity for a given gravimetric soil moisture content (Kursar et al., 2005).

To quantify the soil nutrient gradient, soil samples were collected in May 2004. At each site, three subsamples were collected from the top 10 cm of the soil, representing the main rooting zone (Cavelier, 1992), and bulked at eighteen locations in each of the 1-ha plots. Each of the eighteen composite samples per site were divided into four subsamples to measure soil moisture content, nitrate and ammonium, pH, and cation (Al, Ca, Fe, K, and Mg) and phosphorous concentrations. In addition, nitrogen mineralization and nitrification rates were estimated using *in situ* PVC incubation tubes at each of the soil sampling locations. After 30 days, soil from the tubes was collected and processed for ammonium and nitrate concentrations. For nitrate and ammonium analyses, 2.0 *g* of fresh soil were extracted with 2M KCl and analyzed colormetrically on a Latchat QuikChem flow injection analyzer (Hach Company, Loveland, CO, United States). Soil pH was measured in a 1:3 fresh soil solution with distilled water. Soil cation and phosphorus analyses

---

[1] www.forestgeo.si.edu

TABLE 1 | Environmental conditions and plot locations of five sites along a soil nutrient gradient in lowland tropical forests of the Panama Canal Watershed.

Watershed	**Fort Sherman**	**La Laguna**	**Pipeline Road Plot 9**	**Pipeline Road Plot 15**	**Campo Charges**
Site code	SH	M25	P9	P15	CCH
Environmental variables					
Soil nutrient ranking	Low	Low	Intermediate	Intermediate	High
Geology[a]	Chagres sandstone	Rhyolite	Pre-tertiary basalt/Gatuncillo	Gatunocillo formation	Alhajuela formation
Soil order[a]	Oxisol	Ultisol	Inceptisol	Alfisol	Alfisol (Mollisol)
Latitude (degrees)	9.281	9.079	9.169	9.162	9.211
Longitude (degrees)	−79.975	−79.799	−79.741	−79.745	−79.600
Elevation (m)	140	110	160	70	109
Topography	Irregular	Sloping	Irregular	Level	Sloping
Succesional status	Primary	Secondary	Primary	Mature	Mature
Soil variables					
pH	4.63 ± 0.03^{c}	4.51 ± 0.03^{c}	5.90 ± 0.09^{b}	6.02 ± 0.08^{b}	6.51 ± 0.07^{a}
Al (cmol/kg dry soil)	20.78 ± 0.99^{c}	12.04 ± 0.39^{b}	7.31 ± 0.58^{a}	6.82 ± 0.44^{a}	7.86 ± 1.2^{a}
Ca (cmol/kg dry soil)	1.04 ± 0.2^{c}	0.21 ± 0.02^{c}	8.18 ± 0.46^{b}	6.19 ± 0.45^{b}	18.42 ± 1.47^{a}
Fe (cmol/kg dry soil)	1.48 ± 0.12^{a}	1.11 ± 0.11^{a}	1.13 ± 0.07^{a}	1.38 ± 0.05^{a}	1.35 ± 0.09^{a}
K (cmol/kg dry soil)	0.12 ± 0.01^{b}	0.07 ± 0.01^{b}	0.12 ± 0.01^{b}	0.27 ± 0.03^{b}	1.20 ± 0.12^{a}
Mg (cmol/kg dry soil)	1.27 ± 0.17^{c}	0.68 ± 0.07^{c}	4.77 ± 0.27^{b}	2.55 ± 0.16^{bc}	11.38 ± 1.5^{a}
P (μg g dry soil^{-1})	4.59 ± 0.42^{bc}	2.95 ± 0.15^{c}	10.74 ± 0.51^{b}	7.35 ± 0.32^{bc}	32.68 ± 4.01^{a}
CEC (%)	24.9 ± 1.1^{b}	14.4 ± 0.3^{d}	21.8 ± 0.8^{bc}	17.6 ± 0.4^{cd}	40.4 ± 3.7^{a}
NO_3 (μg g dry soil^{-1})	3.28 ± 0.50^{cd}	1.8 ± 0.15^{d}	6.43 ± 1.23^{bc}	8.34 ± 0.62^{ab}	11.65 ± 1.31^{a}
NH_4 (μg g dry soil^{-1})	30.47 ± 1.08^{c}	48.86 ± 3.16^{b}	50.08 ± 1.19^{b}	66.40 ± 3.79^{a}	27.37 ± 1.18^{c}
Nitrification (μg g dry soil day^{-1})	1.30 ± 0.16^{a}	0.96 ± 0.07^{a}	1.15 ± 0.12^{a}	1.12 ± 0.12^{a}	1.06 ± 0.21^{a}
N mineralization (μg g dry soil day^{-1})	3.24 ± 0.22^{c}	1.75 ± 0.14^{a}	2.31 ± 0.2^{a}	0.59 ± 0.2^{b}	2.35 ± 0.3^{a}
Base saturation (%)	10.29 ± 1.11^{d}	8.70 ± 0.63^{d}	61.12 ± 2.25^{b}	53.03 ± 2.72^{c}	77.31 ± 1.68^{a}
Moisture					
Annual precipitation[a] (mm)	2848.2	2176.9	2344.7	2330.1	2481.2
Dry season moisture deficit[b] (mm)	−491.7	−553.6	−545.4	−549.4	−570.8
Soil water content (dry season;% dry mass)	70.8 ± 3.0^{c}	32.2 ± 1.2^{b}	50.3 ± 1.8^{a}	35.8 ± 1.2^{b}	46.7 ± 3.9^{a}
Soil water content (wet season;% dry mass)	89.7 ± 2.3^{d}	44.1 ± 1.7^{c}	67.7 ± 2.2^{a}	51.5 ± 1.7^{b}	73.1 ± 3.3^{a}
Soil water content (% dry mass)	81.2 ± 3.3^{c}	39.1 ± 2.1^{b}	60.5 ± 3.0^{a}	45.0 ± 2.6^{b}	62.5 ± 4.5^{a}
Combined PCA axes					
PC1 environmental	-1.88 ± 0.06^{b}	-2.01 ± 0.03^{b}	0.18 ± 0.13^{c}	0.03 ± 0.11^{c}	3.68 ± 0.31^{a}
PC2 environmental	1.86 ± 0.21^{d}	-0.22 ± 0.17^{b}	-0.46 ± 0.17^{b}	-1.89 ± 0.19^{c}	0.72 ± 0.26^{a}
PC3 environmental	-0.12 ± 0.28^{d}	-0.55 ± 0.16^{b}	0.31 ± 0.21^{b}	0.60 ± 0.19^{c}	-0.23 ± 0.44^{a}

Geology, soil order, and annual precipitation is based on Cusack et al. (2018). Dry season moisture deficit is based on ForestGEO data portal (www.forestgeo.si.edu). Soil samples were collected 10 cm below the soil surface from each plot (n = 90 samples). Cation exchange capacity is abbreviated as CEC. All means are shown ± SE and different letters among sites indicate statistically significantly different means after a Bonferroni correction ($P < 0.05$).

TABLE 2 | List of species and their general morphology and associated habitats.

Genus and species	***Chamaedorea pinnatifrons***	***Chamaedorea tepejilote***	***Geonoma congesta***	***Geonoma cuneata* var. *gracilis***
Authority	(Jacq.) Oerst.	Liebm.	H. Wendl. ex Spruce	(H. Wendl. ex Spruce) Skov
Growth habit	Aerial	Aerial	Aerial	Acualescent
Life form	Treelet	Treelet	Treelet	Shrub
Leaf shape	Pinnate	Pinnate	Pinnate	Bifid
Habit	Solitary	Solitary or Clumped	Solitary or Clumped	Solitary or Clumped
Elevational range	0 to 2,700 m	0 to 1,600 m	0 to 1,000 m	0 to 1,200 m
Site associations	Fortuna Forest Reserve	P15	SH	Fortuna Forest Reserve
Seed collection location	Fortuna Forest Reserve	Pipeline Road forests	SH	Fortuna Forest Reserve

were conducted by extracting 2.5 *g* fresh soil with Mehlich III extractant (Mehlich, 1984) and the filtrate analyzed by inductively coupled plasma optical emission spectroscopy on a Perkin-Elmer Optima 2000 (Perkin Elmer Inc., Shelton, CT, United States). Soil water content was measured by weighing fresh soil and soil samples dried at 100°C for 72 h to enable the calculation of the amount of dry soil used in all measurements. We used principal components analysis (PCA, see statistical analyses for details) to rank the sites by soil nutrient availability. The sites with the lowest nutrient availability were SH and M25, with sites P9 and P15 being intermediate, and site CCH having high soil fertility, with the main soil nutrient gradient driven by soil P and cation concentration and soil pH (**Figure 1A**).

Species Selection and Seed Collection

We focused on four common understory palms species within the subfamily, Arecoideae (**Table 2**): *C. pinnatifrons* (Jacq.) Oerst*,* *C. tepejilote* Liebm., *G. congesta* H. Wendl. ex Spruce, and *G. cuneata* subsp. *cuneata* (H. Wendl. ex Spruce; Baker et al., 2011; Henderson, 2011). All species are Neotropical long-lived perennials that differ in general morphology, life history, habitat association, and spatial distribution (Henderson et al., 2019). We define soil-based habitat associations on occurrence within the Panama Canal Watershed region. Preliminary surveys suggest that two of the four species are site specialists: *C. tepejilote* occurs at intermediate soil nutrient sites and *G. congesta* occurs at a low soil nutrient sites in the lowland tropical forests of the Panama Canal Watershed (**Table 2**). The other two species are generalist species in the lower montane forests of Fortuna Forest Reserve in western Panama, including the most abundant species in the lower montane forests of Fortuna, *G. cuneata*, as well as *C. pinnatifrons* (Andersen et al., 2010a). *G. congesta*, ranges from Honduras to Panama and occurs locally at the SH site where the seeds for the experiments were collected from. *C. tepejilote*, ranges from Mexico to Colombia and occurs at the P15 site and seeds of this species were collected along the Pipeline Road forests. *G. cuneata*, ranges from Nicaragua to Ecuador and contains a complex of subspecies (Henderson, 2011) including several within Panama. *G. cuneata* subsp. *indivisa* Henderson, occurs locally at SH, P9, and P15. However, the seeds used in the experiments were collected from *G. cuneata* subsp. *cuneata* "fortuna morphotype" (Henderson, 2011), which occurs across the soil nutrient gradient at the Fortuna Forest Reserve (Andersen et al., 2010a, 2014). *C. pinnatifrons*, spans from Mexico to northern South America (Henderson et al., 2019). However, this species did not occur at any of the five sites used in our study and seeds were collected from the Fortuna Forest Reserve where it occurs across the soil nutrient gradient (Andersen et al., 2010a, 2014). We collected seeds for all four species from the field between July and September 2005.

All seeds for the experiments were germinated at the Santa Cruz Experimental Site, Panama. Soils were collected from the five sites and mixed with washed sand in a 30:70 sand: soil ratio. Seeds were sowed into germination trays containing the soil type that the seedlings would be transplanted to for the shadehouse and field experiments.

Shadehouse Experiment

To determine the effect of soil nutrient availability on seedling performance and functional traits, we conducted a completely randomized, factorial design shadehouse experiment by growing seedlings of the four species in soil from the five field sites. Once the seedlings had germinated with one fully expanded leaf, one seedling was transplanted per pot which contained freshly collected soils from the field sites that had been mixed with sand in a 30:70 sand:soil ratio. Ten seedlings per species * soil combination were planted in pots, resulting in a total of 200 plants. Pot size ranged from 0.5L for the smaller *Geonoma* species to 2L for the larger *Chamaedorea* species. Seedlings were watered during the dry season (January–April) and as needed to supplement natural rainwater during the wet season. Temperature was maintained at ambient conditions while light levels were maintained at 2% light conditions to simulate natural understory conditions within the shadehouse. Seedlings were moved around continuously during the experiment to avoid any bias in growing conditions.

Seedling survival was monitored for the experiment over 416 days, as at this time all the seedlings had produced multiple leaves and had started to reach the size limits of their pots. Light saturated photosynthetic capacity (A_{sat}) and dark respiration (R_{dark}) were measured on the youngest fully mature leaf of all individuals surviving to the end of the experiment using a Li-Cor 6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, United States). Measurements were made with the following chamber conditions: <75% relative humidity, temperature of 25–28°C, air flow rate of 500 μmol·s^{-1} and CO_2 of 400 ppm. Light saturation curves were performed to determine saturating light conditions for a subset of individuals of each species (data not shown), after which light levels were set to 400 μmol·m^{-2} s^{-1} for the A_{sat} measurements (Chazdon, 1986). For R_{dark}, leaves were left for 15 min to stabilize with the light source turned off. The mean values of five-point measurements over 60 s were recorded for gas exchange measurements. After the gas exchange measurements were complete, all surviving seedlings were destructively harvested to measure leaf area and biomass allocation patterns. Seedlings were separated into leaf, stem, and root components and dried for 72 h at 65°C. Prior to drying, fresh leaves were digitally scanned using a Cannon CanoScan LiDE 100 flatbed scanner (Cannon, Melville, NY, United States) and leaf area was estimated using ImageJ software[2]. Harvest data were used to calculate SLA (leaf area per leaf mass; mm^2·mg^{-1}), LAR (leaf area per whole plant mass; mm^2·mg^{-1}), LMR (leaf mass divided by whole plant mass; LMR), SMR (stem mass divided by whole plant mass; SMR), and RMR (root mass divided by whole plant mass; RMR), and RGR (biomass at harvest subtracted by initial biomass divided by number of days since planting; RGR; mg·g^{-1}·day^{-1}). These parameters are indicative of resource use and acquisition, carbon allocation, and overall seedling performance. All seedlings of *G. cuneata* died before traits were measured at the end of the experiment.

Field Transplant Experiment

To examine seedling survival under field conditions, we conducted a split-plot transplant experiment with ten gardens of paired exclosure and open (control) subplots randomly located at each field site. Transplant locations were chosen to represent closed canopy forest locations for all field sites. A regional study suggests that light transmittance to the understory of these forests

---

[2] https://imagej.nih.gov

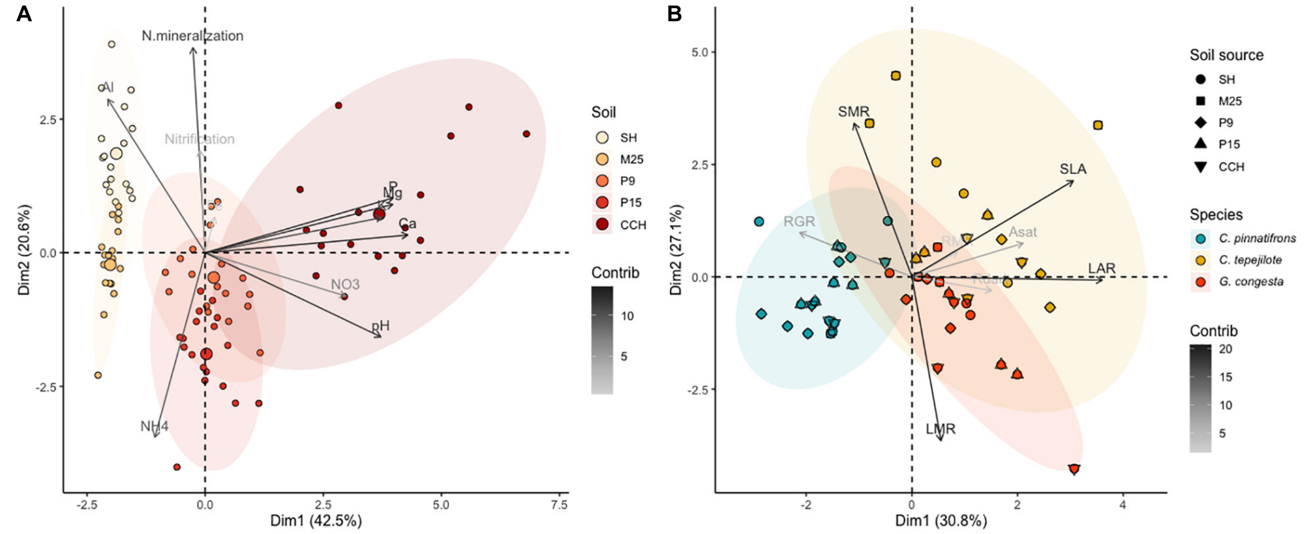


FIGURE 1 | (A) Principal component analysis of soil data for each of the five sites, SH, M25, P15, P9, and CCH. Each point represents a separate sample (*n* = 90) and shading represents increasing soil nutrient availability from SH to the CCH site. Contribution of soil properties, AL, Ca, Fe, K, Mg, P, NH_4, NO_3, N mineralization, Nitrification, and pH, are indicated by arrow shading. Concentration ellipses are displayed for each of the five soils. **(B)** Principal component analysis of seedling trait data for three species at each of the five sites, with each point representing a separate sample (*n* = 59). Contribution of seedling traits are indicated by arrow shading. Concentration ellipses are displayed for each of the three species. The primary seedling trait ordination axis (PC 1) represents a shift from high relative growth rate (RGR) to investment in high leaf quality, specific leaf area (SLA), leaf area ratio (LAR), root mass ratio (RMR), maximum photosynthetic rate (A_{sat}), and dark respiration rates (R_{dark}). The secondary seedling trait ordination axis (PC 2) represents a shift from high leaf mass ratio (LMR) to high stem mass ratio (SMR).

are generally around 1–2% annually throughout the Panamanian Isthmus (Brenes-Arguedas et al., 2011). In November 2005, twenty seedlings of each of the four species were transplanted at each of the five sites, resulting in 400 seedlings in total. Within each site we set up ten randomly located gardens and established paired 50 × 50 cm subplots, i.e., a control subplot and a treatment subplot. One seedling per species was transplanted into each paired subplot (i.e., two seedlings per garden). Paired subplots were <1 m from each other and gardens were at least 20 m from each other. Exclosure subplots were covered by 1 mm transparent mesh to exclude herbivores, while control subplots were completely open to herbivores. Soil cores were taken adjacent to the experimental subplots at every census to monitor gravimetric soil moisture. Seedlings were monitored on average every 63 days on eight occasions, or 505 days in total. Seedling performance did not differ between the paired control and exclosure subplots and data was pooled prior to analysis by calculating the mean survival rate (%) per species per garden (*n* = 10 per site).

Data Analysis

To examine how soil nutrients affect seedling leaf functional traits, biomass allocation and RGRs in the shadehouse experiment, we conducted two-way ANOVAs to test for differences in mean values among species, soil, and their interaction. We assessed whether model assumptions were met using graphical diagnostics. We used a backward elimination model simplification approach based on Akaike Information Criterion values and reported the statistics from the final (best fit) models. Tukey's *post hoc* tests were then used to identify significant differences between means at $P = 0.05$, using the R package "emmeans" (Lenth, 2021).

To examine seedling survival in the field transplant experiment, we used generalized linear mixed effect models using the glmer function in the R package "lme4" (Bates et al., 2015). Mean seedling survival rates per garden were fitted using Poisson distribution and log link families with species, site, and their interactions as fixed effects and garden as a random effect. To examine species specific survival rates at the end of the field transplant experiment, generalized linear models (glm) were performed for each species separately followed by Tukey's *post hoc* tests at $P = 0.05$ to examine differences in the mean survival among sites.

We conducted two separate PCA. The first analysis was performed on the soil nutrient data, to enable us to rank the five sites by overall soil nutrient availability. The second analysis was performed on the seedling trait and RGR data from the shadehouse experiment to examine whole-plant trade-offs among species and soil type. The PCAs were conducted using the R package FactoMineR (Lê et al., 2008). The data was centered and standardized to one unit of variance, but not transformed prior to analysis.

RESULTS

Shadehouse Experiment

Leaf Functional Traits

In the shadehouse experiment, the mean and standard error for SLA across all the seedlings was 306 ± 9.5 $mm^2 \, g^{-1}$. The best fit model for SLA showed that only species differed significantly ($F_{2,\ 86}$ = 70.91, $p < 0.0001$). Across all soil sources, *C. tepejilote* a significantly higher mean SLA (362 ± 7.9 mm^2 g^{-1}) than the other species, and *G. congesta* had a significantly higher SLA (276 ± 12.5 mm^2 g^{-1}) than *C. pinnatifrons* (187 ± 12.8 mm^2 g^{-1}; **Figure 2A**).

The mean LAR across all the seedlings was 138 ± 4.1 mm^2 g^{-1}. The best fit model for LAR retained both species ($F_{2,\ 82}$ = 38.5, $p < 0.0001$) and soil ($F_{4,\ 82}$ = 3.99, $p < 0.01$), but not their interaction. *C. pinnatifrons* had a significantly lower mean LAR (86.6 ± 6.35 mm^2 g^{-1}) than either *C. tepelijote* (154.0 ± 3.88 mm^2 g^{-1}) or *G. congesta* (143.0 ± 6.13 mm^2 g^{-1}; **Figure 2B**). In addition, LAR was higher across all species growing in soil from P15 (143 ± 10 mm^2 g^{-1}) and CCH (150 ± 9.97 mm^2 g^{-1}) than M25 (122 ± 7.62 mm^2 g^{-1}), with intermediate values for SH and P9.

The mean light-saturated photosynthesis (A_{sat}) across all seedlings was 2.29 ± 0.115 μmol·m^{-2}·s^{-1}. Photosynthetic rates significantly differed among species ($F_{2},_{46}$ = 8.03, $p < 0.001$) but were unaffected by soil or its interaction with species. Photosynthetic rate was significantly higher for *C. tepejilote* (2.90 ± 0.131 μmol·m^{-2}·s^{-1}) than *C. pinnatifrons* (1.73 ± 0.131 μmol·m^{-2}·s^{-1}), with intermediate rates for *G. congesta* (2.21 ± 0.157 μmol·m^{-2}·s^{-1}; **Figure 2C**).

The mean R_{dark} for all seedlings was 0.54 ± 0.04 μmol·m^{-2}·s^{-1}. The best fit model for R_{dark} showed a significant difference between species means ($F_{2,\ 42}$ = 7.19, $p < 0.01$) with a non-significant soil effect retained in the model ($F_{4},_{42}$ = 2.29, p = 0.08). Leaf respiration was significantly greater for *G. congesta* (0.74 ± 0.11 μmol·m^{-2}·s^{-1}) than for *C. pinnatifrons* (0.34 ± 0.035 μmol·m^{-2}·s^{-1}), with intermediate R_{dark} rates for *C. tepejilote* (0.61 ± 0.042 μmol·m^{-2}·s^{-1}; **Figure 2D**).

Biomass Allocation

In the shadehouse experiment, the mean LMR across all seedlings was 0.463 ± 0.009. LMR was significantly influenced by the interaction between species and soil ($F_{8},_{74}$ = 2.38, $p < 0.05$) and by the main effects of species ($F_{2},_{74}$ = 15.17, $p < 0.0001$) and soil ($F_{4},_{44}$ = 12.03, $p < 0.0001$; **Figure 3A**). Among species and soil combinations, LMR was highest for *G. congesta* in soil from P15 (0.58 ± 0.03) and lowest for *C. tepejilote* in soil from M25 (0.33 ± 0.02). We found that LMR for *C. tepejilote* was lower than *C. pinnatifrons* when growing in the M25 site soil (t = 5.89, $p < 0.001$). Furthermore, *C. tepejilote* LMR differed among soils, with lower LMR when growing in low nutrient site soils compared to high nutrient soils and had an intermediate LMR in the P9 soil, although LMR in P9 soil was significantly higher than in M25 soil (t = 5.26, $p < 0.001$).

The mean SMR across all seedlings was 0.330 ± 0.009. SMR was significantly influenced by the interaction between species and soil ($F_{8},_{74}$ = 2.78, $p < 0.01$), and by the main effects of species ($F_{2},_{74}$ = 14.82, $p < 0.0001$), and soil ($F_{4},_{74}$ = 11.60, $p < 0.0001$; **Figure 3B**). For all soil and species combinations, *C. tepejilote* in soil from M25 had the highest SMR (0.47 ± 0.02) while *G. congesta* in soil from CCH had the lowest SMR (0.21 ± 0.03). *C. tepejilote* had higher SMR compared to the two other species when growing in the M25 site soil. Further*more*, for *C. tepejilote*, SMR was higher when growing in the M25 site soil compared to all other soil sources.

The mean RMR across all seedlings was 0.197 ± 0.005. There was no significant interactive effect between species and soil, but root mass was significantly influenced by the main effects of species ($F_{2},_{74}$ = 13.58, $p < 0.001$) and soil ($F_{4},_{74}$ = 7.45, $p < 0.0001$). RMR of *C. tepejilote* (0.21 ± 0.01) was higher than that of the other two species (**Figure 3C**). Across all species, RMR of seedlings growing in soils from SH (0.23 ± 0.01) was higher than for the other four soils (**Figure 3C**).

Relative Growth Rate

In the shadehouse experiment, the mean RGR across all species and soils was 11.5 ± 0.25 mg·g^{-1}·day^{-1}. There was a significant interaction between soil and species ($F_{8},_{74}$ = 3.01, $p < 0.01$), and significant differences among the species ($F_{2},_{74}$ = 9.76, $p < 0.0001$) and soil ($F_{4},_{74}$ = 7.16, $p < 0.0001$) on RGR. For all soil and species combinations, *C. tepejilote* in soil from P15 had the highest RGR (14.5 ± 0.58 mg·g^{-1} day^{-1}) while *G. congesta* in soil from CCH had the lowest RGR (9.41 ± 0.92 mg·g^{-1} day^{-1}; **Figure 4**). When growing in the P15 soil, *C. tepelijote* had significantly higher RGR than *G. congesta* (t = 3.77, p = 0.05). Furthermore, *C. tepejilote* had significantly higher RGR growing in P15 soil, where it naturally occurs, than in lower nutrient soils, whereas RGR in the highest nutrient soil (CCH) was similar to all soils (**Figure 4**).

Principal Components Analysis of Traits

For the PCA of the seedling trait data for the shadehouse experiment, the primary ordination axis (PC1) explained 30.8% of the total variation and represented increasing values of LAR and SLA, and more acquisitive leaf traits (**Figure 1B**). Species aligned along PC1. The second axis (PC2) explained 27.1% of the total variation and represented a shift from high leaf investment (LMR) to high stem investment (SMR). Soils aligned along PC2. As soil fertility increased (from soils from sites SH and M25 to soils from sites P9, P15, and CCH), there was an increase in seedling LMR and a decrease in SMR.

Field Experiment

Seedling Survival

Seedling survival by the end of the field experiment was significantly influenced by the interaction between site and species (χ^2 = 214, df = 12, $p < 0.0001$), and by the main effects of site (χ^2 = 540, df = 5, $p < 0.0001$) and species (χ^2 = 986, df = 4, $p < 0.0001$). After 505 days, overall survival across all species except *C. tepejilote* was highest at SH (low-nutrient, high-rainfall site; mean ± SE = 57.5 ± 5.23%), and lowest at CCH (high-nutrient, low-rainfall site; 0.0% ± 0.0) where all seedlings of all species died after 120 days during the first dry season (**Figure 5**). Among species, survival rates across all sites were highest for *C. tepejilote* (40.2 ± 5.69%) and lowest for *C. pinnatifrons* (26.3 ± 3.71%). For the species that naturally occurs at the P15 site (*C. tepejilote*), survival rates were 80.0 ± 2.83% at that site and did not differ from survival at the P9 or SH sites, but survival at these three sites were higher than that for M25 (45 ± 2.12%;

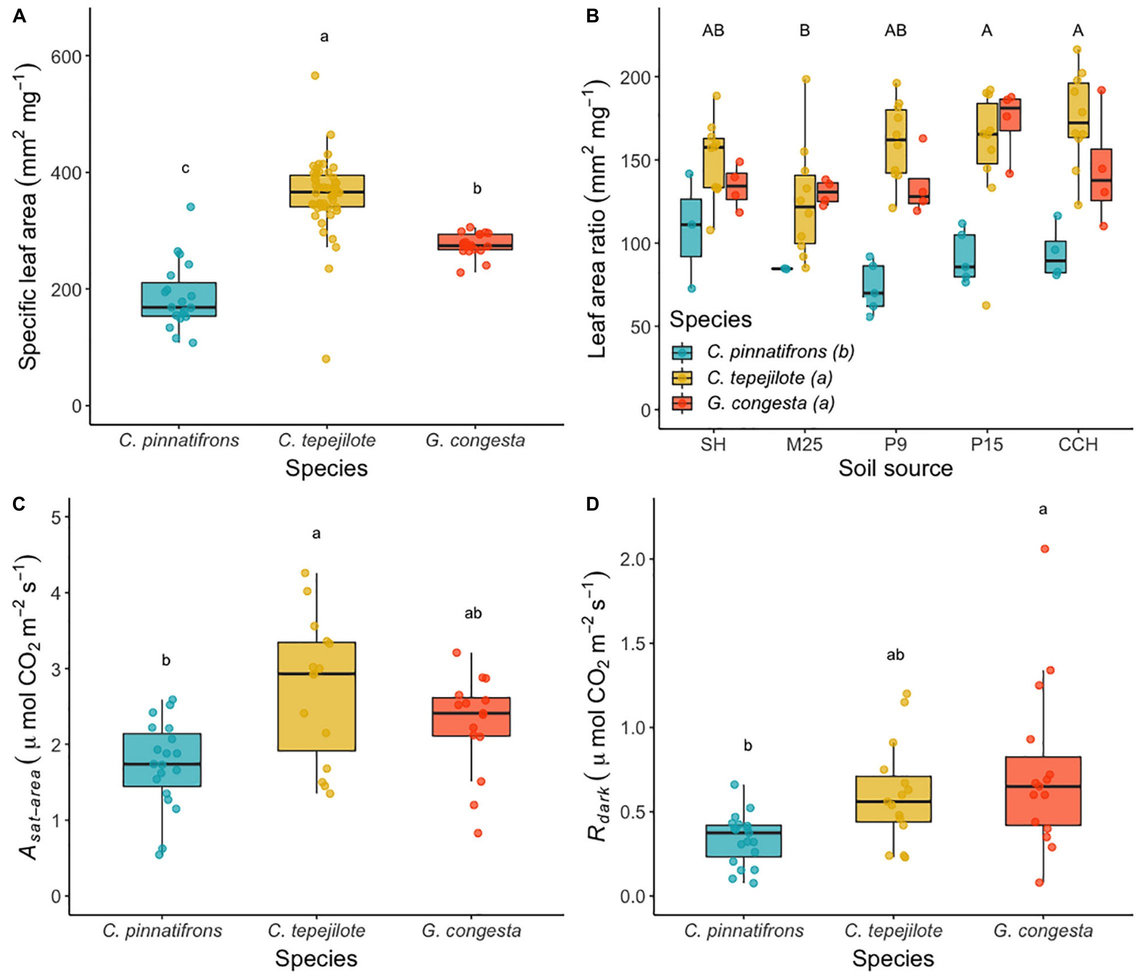


FIGURE 2 | (A) Specific leaf area (SLA), **(B)** leaf area ratio (LAR), **(C)** photosynthetic rates (A_{sat}), and **(D)** dark respiration rates (R_{dark}), in a greenhouse transplant experiment. Boxplots represent median shown by the solid black horizontal line in the middle of each box and bounds represent 25th and 75th percentiles and individual values. Soil is sourced from five sites across a soil nutrient gradient and sites are ranked and listed in order of increasing overall soil nutrient availability. Different letters above the bars and boxplots indicate statistically significant different means according to Tukey's test ($P < 0.05$), with lower case letters representing species differences and capital letters representing soil differences.

z-ratio = 9.89, $p < 0.0001$) and for CCH (with zero seedlings surviving). For the species that naturally occurs at the SH site (*G. congesta*), survival was higher at its "home-site" (65 ± 2.5%) than at the other four sites, i.e., P15 (z-ratio = 2.89, $p < 0.05$), P9 (z-ratio = 11.36, $p < 0.0001$), M25 (z-ratio = 17.68, $p < 0.0001$), and CCH (z-ratio = 25.5, $p < 0.0001$; **Figure 5C**).

DISCUSSION

We used seedling experiments to better understand how four understory palm species respond to gradients of soil nutrients and rainfall in lowland tropical forests of Panama. In the shadehouse experiment, leaf functional traits were determined by species, whereas RMR was highest at the lowest nutrient site and with generally biomass allocation and RGR shifting with species-specific responses to soil source. By contrast, in the field transplant experiment seedling mortality was largely determined by dry season water availability rather than soil nutrient availability among the sites. Together, these results suggest that seedling performance is responsive to soil fertility when there is sufficient soil moisture. Thus, by pairing controlled and field experiments, we determined that seedling survival, and hence potentially species distribution, are strongly constrained by dry season water availability, whereas soil nutrient availability shapes subsequent seedling biomass allocation and RGRs.

Species Identity Is Driving Leaf Functional Traits

In contrast to the predictions of our first hypothesis, we did not find that leaf morphological traits such as SLA and LAR, or physiological traits, such as A_{sat} and R_{dark}, responded to soil fertility, and these traits were instead mainly determined by species identity. The only trait that differed among soils was LAR which was lower for seedlings growing in one of

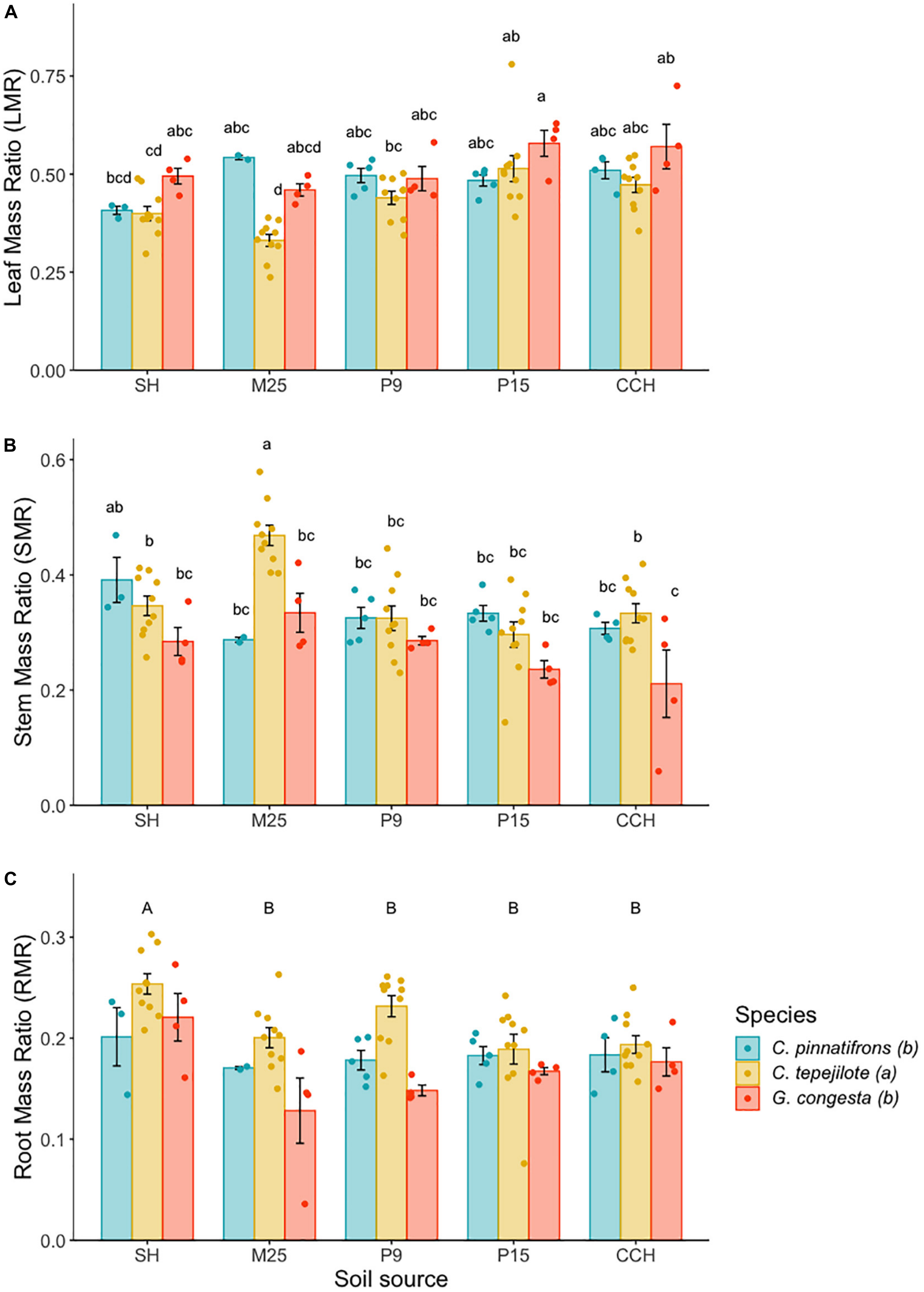


FIGURE 3 | Biomass allocation (mean ± SE) of seedlings growing in soil from five sites along a soil nutrient gradient. **(A)** Leaf mass ratio (LMR), **(B)** Stem mass ratio (SMR), and **(C)** Root mass ratio (RMR). Soil is sourced from five sites across a soil nutrient gradient and sites are ranked and listed in order of increasing overall soil nutrition. Different letters above the bars indicate statistically significant different means according to Tukey's test ($P < 0.05$), with lower case letters representing differences among species *soil source combinations and capital letters representing differences among soil sources. The legend represents species fill color for all panels and the letters represent species differences for RMR only. *Represents the interaction between species and soil.

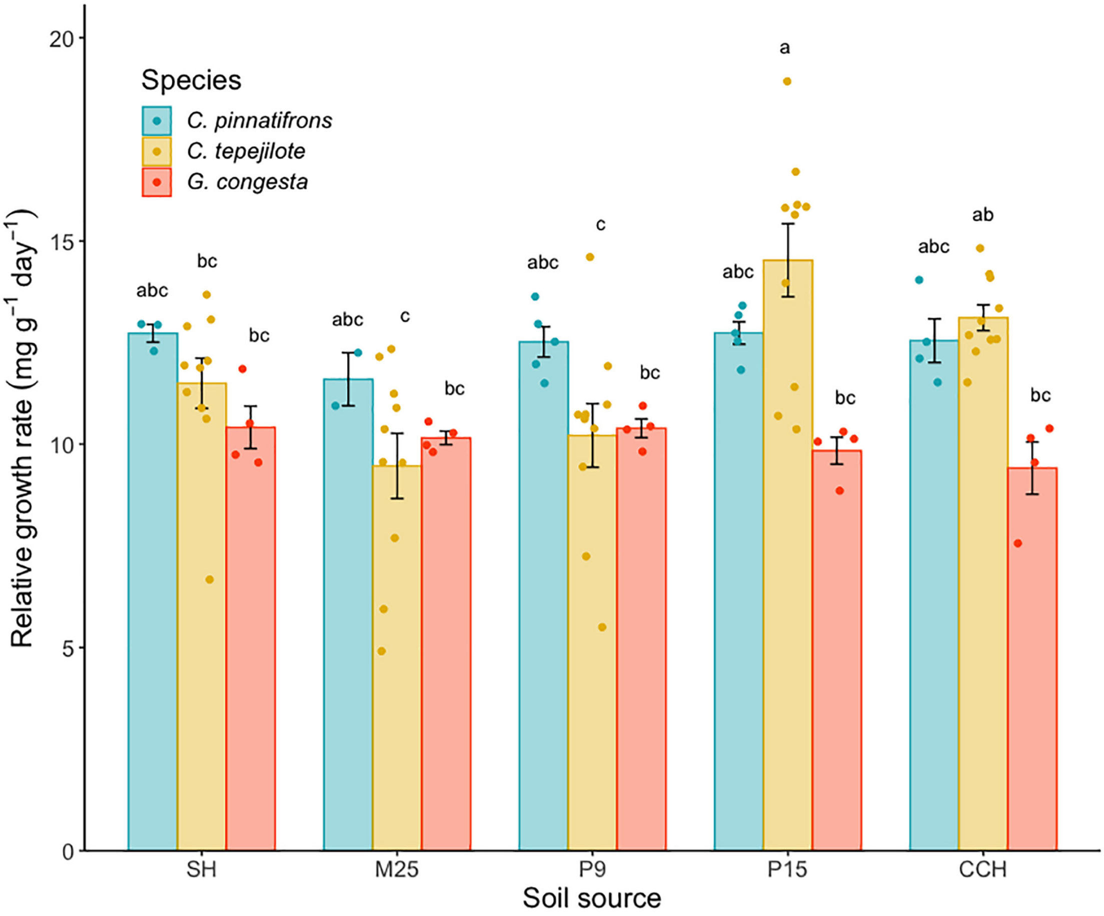


FIGURE 4 | Relative growth rate (RGR; mean ± SE) of seedlings growing in soil from five sites along a soil nutrient gradient. Soil sources are ranked and listed in order of increasing overall soil fertility. Bars are shaded by species. Different letters above the bars indicate statistically significant differences among means according to Tukey's test ($P < 0.05$).

the low nutrient soils compared to high nutrient soils. In addition, we did not find any differences between generalist and specialist species leaf trait responses to soil fertility. Among the three species, the species associated with the intermediate fertility P15 site (*C. tepejilote*) had the most acquisitive leaf trait strategy whereas the generalist species found throughout the lower montane Fortuna sites in western Panama (*C. pinnatifrons*) had the most conservative leaf trait strategy. Our findings contrast experiments where leaf traits of seedlings grown in contrasting soil types follow the leaf economic strategy with higher SLA and LAR when growing in high resource environments (Baltzer et al., 2005; Dent and Burslem, 2009). Our findings also contrast with a parallel shadehouse experiment of five *Chamaedorea* species across the Fortuna soil gradient, where seedlings of *C. pinnatifrons* had higher photosynthetic rates than *C. tepejilote* and all species showed strong soil-driven shifts in photosynthetic rates (Andersen, 2021). One possible explanation for the discrepancy between these experiments is that soil nitrogen, a key nutrient for photosynthesis, is generally high across the lowland soil gradient (**Figure 1A**, PC2), whereas soil nitrogen partly drives the lower montane soil gradient (Andersen et al., 2010b, 2014). This suggests that soil phosphorus and cations, the main drivers of the lowland soil nutrient gradient, do not strongly influence palm seedling leaf traits. However, evidence from tree species along the lowland Panama Isthmus shows changes in community-level leaf trait measures such as SLA and thickness are driven by variation in both soil phosphorus and moisture (Umaña et al., 2021). Thus, it is possible that understory palm leaf traits are more responsive to variation in soil nitrogen than phosphorus availability, while tree species are more responsive to variation to soil phosphorus among sites.

Biomass Allocation Responds to Soil Nutrient Availability

Our second hypothesis predicted that RMR for each species would increase as soil fertility declines to meet nutrient demands at the expense of LMR, SMR and overall growth potential. While palms use roots to access water and nutrients, in this shadehouse experiment, nutrient availability varied by soil source

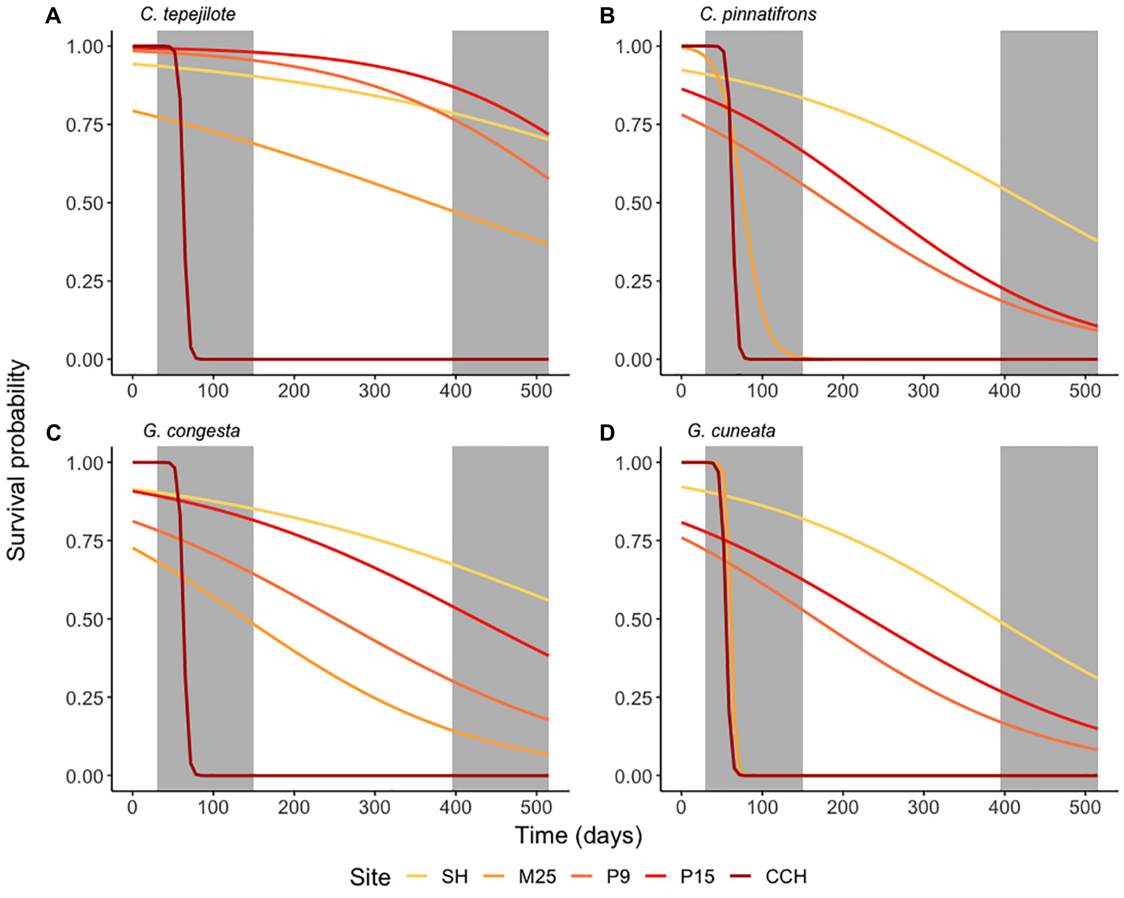


FIGURE 5 | Field transplant experiment of seedling survival of four understory palm species, **(A)** *Chamaedorea tepejilote*, **(B)** *C. pinnatifrons*, **(C)** *Geonoma congesta*, and **(D)** *G. cuneata*. Seedlings of each species were grown at each of five sites that differed in soil fertility. Percent survival is based on the species mean per garden per site. Curves for each species are the outputs from generalized linear models (Survival rates ∼ Site). Shading of the curve increases intensity with soil nutrient availability from SH to CCH. Gray shaded boxes represent dry seasons in year 1 and 2 of the field experiment.

while water availability remained constant for all soil and species combinations. This suggests that root mass seems to increase in response to nutrient availability. In line with this we found that RMR was greatest at the least fertile SH site, suggesting that seedlings increased investment in roots to acquire limiting nutrients when grown in the lowest nutrient soil at the expense of allocation to leaf biomass. Both LMR and SMR had interactions between species and soil source. However, LMR generally increased with increasing soil nutrient availability, whereas SMR tended to decrease. This is in line with optimal allocation theory which predicts that allocation to belowground and support tissue increases with decreasing soil nutrient availability (Chapin, 1980; Poorter et al., 2012). In shadehouse experiments in French Guiana and Malaysia, seedlings of tree species showed similar trade-offs between above and belowground allocation with soil nutrient availability (Baraloto et al., 2005; Dent and Burslem, 2009). In palm seedling field experiments in Fortuna, RMR did not respond to nitrogen addition (Andersen et al., 2010a) but did increase as soil nutrient availability decreased (Andersen et al., 2014), suggesting that RMR and biomass allocation trade-offs for palm seedlings are driven by rock-derived nutrients such as soil P and cations. Furthermore, in the Fortuna transplant experiment, seedlings of species associated with the lowest nutrient site showed biomass allocation patterns that would promote growth compared to species not occurring at that site. However, here we found that despite the influence of soil source on biomass allocation, there was no indication that species were able to optimize their biomass allocation to promote growth in the soils they were associated with compared to species not occurring in that soil type.

Home Site Advantage for Relative Growth Rate

Our third hypothesis predicted that specialist species growing in the soil they are associated with should have a higher RGR compared to species not occurring in those soils. We found that *C. tepejilote* had higher RGR when growing in the soil for which it is associated with compared to the low nutrient specialist species (*G. congesta*) but not the Fortuna generalist species *C. pinnatifrons*. Furthermore, *C. tepejilote* had higher RGR at higher compared to lower nutrient soils, suggesting that *C. tepejilote* may have adaptations that enhances growth and performance in higher fertility soils. Similarly, in a seedling transplant experiment in Fortuna, *C. tepejilote* was one of the species associated with the intermediate soil nutrient site Palo Seco and also had a growth advantage at home (Andersen et al., 2014), further supporting the hypothesis that this species is able to maximize its growth in soils where it occurs naturally. However, the mechanism for the enhanced growth performance of *C. tepejilote* in intermediate nutrient soils in lowland shadehouse experiment remains unclear as we did not observe greater resource use efficiency or optimal biomass allocation of this species compared to others. Our findings corroborate an Amazonian transplant study, where growth rates of habitat specialists were often but not always highest when growing in the soil they are associated with (Fortunel et al., 2016).

In contrast to *C. tepejilote*, the low-nutrient specialist, *G. congesta,* did not differ in RGR compared to other species when growing in the soil it is associated with. This contrasts with the general trends from the Fortuna transplant experiment, where species associated with low nutrient soils had strong growth advantages when grown at home (Andersen et al., 2014). Furthermore, *G. congesta* did not show significant differences in RGRs across the soil nutrient gradient, suggesting that *G. congesta* has a highly constrained and low RGR that may help it survive in low nutrient soils but may be outcompeted at higher nutrient sites as it had significantly lower RGR than *C. tepejilote* in the P15 soil. Alternatively, RGR of *G. congesta* may also be driven by other factors such as light and soil moisture, which may vary among sites in the field, but which were kept constant in the shadehouse experiment.

Soil and Rainfall Gradients Influence Seedling Survival

Our fourth hypothesis predicted that specialist species will have higher seedling survival rates at sites where they occur naturally compared to other species and compared to their survival at sites where they do not occur. In line with this, we found that the low nutrient specialist, *G. congesta*, had higher seedling survival rates growing at its home site compared to the other sites. However, *C. tepejilote* tended to have higher survival compared to other species regardless of lowland site. Nonetheless, for the site specialist *C. tepejilote*, survival rates were highest at its home site P15, and at sites P9 and SH, all of which have a lower dry season moisture deficit compared to the other sites. We also found that seedling survival for all species was high at the low nutrient site SH which has the highest annual rainfall (2,848 mm) and the highest soil water content during the wet season (89.7 ± 2.3 mm) and dry season (70.8 ± 3.0). Across all species, seedling survival rates were lowest at lowland site CCH which has the highest nutrient soil and dry season water deficit (571 mm). In the Fortuna seedling transplant experiment in lower montane forests, species showed strong home-site advantages in survival at low and high nutrient sites, but not intermediate nutrient sites (Andersen et al., 2014). However, the mechanisms driving home site survival advantages in the Fortuna lower montane experiment and this lowland experiment are expected to differ due to differences in MAP and seasonality. The lower montane soil gradient has a rainfall gradient of 4–10 m MAP with no substantial dry season compared to the 1.5–3 m MAP gradient and strong 4-month dry season at sites in this lowland experiment (Andersen et al., 2014). Furthermore, the lower montane experiment found that survival was mediated by herbivores, whereas protection from herbivores had no effect on survival in the lowland experiment. Similarly, our findings corroborate a transplant study where home-site survival advantages across lowland tropical forests in Amazonia were related to moisture and soil gradients, but not herbivory for seedlings of habitat specialist tree species (Fortunel et al., 2016).

Although the focus of this study was on belowground environmental variation, light availability can also influence seedling survival (Cintra and Horna, 1997; Record et al., 2016). Field transplant locations were chosen to represent closed canopy forest locations across all field sites. We do not have field light data, but a regional study suggests that light transmittance at the understory layer in these forests is generally around 1–2% annually throughout the Panamanian Isthmus (Brenes-Arguedas et al., 2011), and this is in line with previous measurements at two of our study sites, i.e., P9 (Gaviria et al., 2017) and SH (Brenes-Arguedas et al., 2011). Together, our results suggest that the main driver of seedling survival is dry season water availability, thus drought tolerance or avoidance may be important mechanisms, especially with more frequent droughts associated with extreme El Niño events, that determine species distributions along the Panama Canal Isthmus (Engelbrecht et al., 2007; Browne et al., 2021).

CONCLUSION

In this study, we found that although soil nutrient availability was an important driver of seedling biomass allocation and RGR in a controlled shadehouse setting, dry season water availability determines seedling survival in the field. This work demonstrates the necessity of transplant experiments to disentangle resource-based and climatic factors in understanding species pre-adaptions and response to environmental change. If lowland tropical forests in Panama are driven by soil nutrient and rainfall gradients, then changes in soil fertility due to nitrogen deposition (Hietz et al., 2011) and soil moisture availability caused by climate change have the potential to alter species distributions and forest dynamics (Engelbrecht et al., 2007). Conservation and restoration efforts of forests across the isthmus of Panama will need to consider the responses of individual species to such changes. Here, we observed the effects of limiting resources on four palm species. These understory species act as filters that affect seedling growth and survival in forest (Farris-Lopez et al., 2004; Wang and Augspurger, 2004). Therefore, factors that affect the growth and distribution of these palm species will indirectly impact tree seedling recruitment and forest regeneration. Further research on additional species is needed to obtain a more comprehensive view of forest dynamics in relation to spatial variation in the landscape of soil nutrient availability and rainfall patterns.

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

CC helped in statistical analysis and drafted the manuscript. DW helped to draft the manuscript. KA designed and carried out the study, helped in statistical analysis, and drafted the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

ACKNOWLEDGMENTS

We would like to thank the Smithsonian Tropical Research Institute for logistical support. This research was supported by funding from an NSF Dissertation Completion Grant, a Smithsonian Institution Predoctoral Fellowship, and funding from the Program in Ecology and Evolutionary Biology of the University of Illinois-Champaign/Urbana (KMA). Permits were provided by the Smithsonian Tropical Research Institute and the Panamanian Autoridad Nacional del Ambiente (ANAM).

REFERENCES

Aerts, R., and Chapin, F. S. (2000). The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv. Ecol. Res.* 30, 1–67. doi: 10.1016/S0065-2504(08)60016-1

Ali, A., and Yan, E. R. (2017). Functional identity of overstorey tree height and understorey conservative traits drive aboveground biomass in a subtropical forest. *Ecolog. Ind.* 83, 158–168. doi: 10.1016/j.ecolind.2017.07.054

Alvarez-Clare, S., Mack, M. C., and Brooks, M. (2013). A direct test of nitrogen and phosphorus limitation to net primary productivity in a lowland tropical wet forest. *Ecology* 94, 1540–1551. doi: 10.1890/12-2128.1

Andersen, K. M. (2021). "Palm flora and drivers of distribution in Fortuna Forest Reserve," in *Fortuna Forest Reserve, Panama: Interacting Effects of Climate and Soils on the Biota of a Wet Premontane Tropical Forest*, eds J. W. Dalling and B. L. Turner (Washington, D.C: The Smithsonian Institution, USA), 271–287. doi: 10.5479/si.14315990.v1

Andersen, K. M., and Turner, B. L. (2013). Preferences or plasticity in nitrogen acquisition by understorey palms in a tropical montane forest. *J. Ecol.* 101, 819–825.

Andersen, K. M., Turner, B. L., and Dalling, J. W. (2010a). Soil-based habitat partitioning in understory palms in lower montane tropical forests. *J. Biogeogr.* 37, 278–292. doi: 10.1111/j.1365-2699.2009.02192.x

Andersen, K. M., Corre, M. D., Turner, B. L., and Dalling, J. W. (2010b). Plant–soil associations in a lower montane tropical forest: physiological acclimation and herbivore-mediated responses to nitrogen addition. *Funct. Ecol.* 24, 1171–1180. doi: 10.1111/j.1365-2435.2010.01731.x

Andersen, K. M., Endara, M.-J., Turner, B. L., and Dalling, J. W. (2012). Trait-based community assembly of understory palms along a soil nutrient gradient in a lower montane tropical forest. *Oecologia* 168:519531. doi: 10.1007/s00442-011-2112-z

Andersen, K. M., Turner, B. L., and Dalling, J. W. (2014). Seedling performance trade-offs influencing habitat filtering along a soil nutrient gradient in a tropical forest. *Ecology* 95, 3399–3413. doi: 10.1890/13-1688.1

Baker, W. J., Norup, M. V., Clarkson, J. J., Couvreur, T. L., Dowe, J. L., Lewis, C. E., et al. (2011). Phylogenetic relationships among arecoid palms (Arecaceae: Arecoideae). *Ann. Bot.* 108, 1417–1432. doi: 10.1093/aob/mcr020

Baltzer, J. L., Thomas, S. C., Nilus, R., and Burslem, D. F. R. (2005). Edaphic specialization in tropical trees: physiological correlates and responses to reciprocal transplantation. *Ecology* 86, 3063–3077. doi: 10.1890/04-0598

Baraloto, C., Goldberg, D. E., and Bonal, D. (2005). Performance trade-offs among tropical tree seedlings in contrasting microhabitats. *Ecology* 86, 2461–2472. doi: 10.1890/04-1956

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 67, 1–48. doi: 10.18637/jss.v067.i01 doi: 10.18637/jss.v067.i01

Brenes-Arguedas, T., Roddy, A. B., Coley, P. D., and Kursar, T. A. (2011). Do differences in understory light contribute to species distributions along a tropical rainfall gradient? *Oecologia* 166, 443–456. doi: 10.1007/s00442-010-1832-9

Browne, L., Markesteijn, L., Engelbrecht, B. M., Jones, F. A., Lewis, O. T., Manzané-Pinzon, E., et al. (2021). Increased mortality of tropical tree seedlings during the extreme 2015–16 El Niño. *Glob. Chang. Biol.* 27, 5043–5053. doi: 10.1111/gcb.15809

Cámara-Leret, R., Tuomisto, H., Ruokolainen, K., Balslev, H., and Munch Kristiansen, S. (2017). Modelling responses of western Amazonian palms to soil nutrients. *J. Ecol.* 105, 367–381. doi: 10.1111/1365-2745.12708

Cavelier, J. (1992). Fine-root biomass and soil properties in a semideciduous and a lower montane rain forest in Panama. *Plant Soil* 142, 187–201. doi: 10.1007/BF00010965

Chapin, F. S. (1980). The mineral-nutrition of wild plants. *Annu. Rev. Ecol. Syst.* 11, 233–260. doi: 10.1146/annurev.es.11.110180.001313

Chazdon, R. L. (1986). Light variation and carbon gain in rain forest understorey palms. *J. Ecol.* 1986, 995–1012. doi: 10.2307/2260229

Cintra, R., and Horna, V. (1997). Seed and seedling survival of the palm Astrocaryum murumuru and the legume tree Dipteryx micrantha in gaps in Amazonian forest. *J. Trop. Ecol.* 13, 257–277. doi: 10.1017/S0266467400010440

Clark, D. A., Clark, D. B., Sandoval, R. M., and Castro, M. V. C. (1995). Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. *Ecology* 76, 2581–2594. doi: 10.2307/2265829

Condit, R., Engelbrecht, B. M., Pino, D., Pérez, R., and Turner, B. L. (2013). Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proc. Natl. Acad. Sci.* 110, 5064–5068. doi: 10.1073/pnas.1218042110

Cusack, D. F., Markesteijn, L., Condit, R., Lewis, O. T., and Turner, B. L. (2018). Soil carbon stocks across tropical forests of Panama regulated by base cation effects on fine roots. *Biogeochemistry* 137, 253–266. doi: 10.1007/s10533-017-0416-8

Dent, D. H., and Burslem, D. F. (2009). Performance trade-offs driven by morphological plasticity contribute to habitat specialization of Bornean tree species. *Biotropica* 41, 424–434. doi: 10.1111/j.1744-7429.2009.00505.x

Diaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H., Jalili, A., et al. (2004). The plant traits that drive ecosystems: evidence from three continents. *J. Veg. Sci.* 15, 295–304. doi: 10.1111/j.1654-1103.2004.tb02266.x

Díaz, S., Kattge, J., Cornelissen, J. H., Wright, I. J., Lavorel, S., Dray, S., et al. (2016). The global spectrum of plant form and function. *Nature* 529, 167–171. doi: 10.1038/nature16489

Dominy, N. J., Grubb, P. J., Jackson, R. V., Lucas, P. W., Metcalfe, D. J., Svenning, J. C., et al. (2008). In tropical lowland rain forests monocots have tougher leaves than dicots, and include a new kind of tough leaf. *Ann. Bot.* 101, 1363–1377. doi: 10.1093/aob/mcn046

Emilio, T., Quesada, C. A., Costa, F. R., Magnusson, W. E., Schietti, J., Feldpausch, T. R., et al. (2013). Soil physical conditions limit palm and tree basal area in Amazonian forests. *Plant Ecol. Div.* 7, 215–229. doi: 10.1080/17550874.2013.772257

Engelbrecht, B. M., Comita, L. S., Condit, R., Kursar, T. A., Tyree, M. T., Turner, B. L., et al. (2007). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447, 80–82. doi: 10.1038/nature05747

Farris-Lopez, K., Denslow, J. S., Moser, B., and Passmore, H. (2004). Influence of a common palm, Oenocarpus mapora, on seedling establishment in a tropical moist forest in Panama. *J. Trop. Ecol.* 2004, 429–438. doi: 10.1017/S0266467404001531

Fortunel, C., Paine, C. E. T., Fine, P. V. A., Mesones, I., Goret, J.-Y., Burban, B., et al. (2016). There's no place like home: seedling mortality contributes to the habitat specialisation of tree species across Amazonia. *Ecol. Lett.* 19:12561266. doi: 10.1111/ele.12661

Gaviria, J., Turner, B. L., and Engelbrecht, B. M. (2017). Drivers of tree species distribution across a tropical rainfall gradient. *Ecosphere* 8:e01712.

Grime, J. P. (2006). *Plant strategies, vegetation processes, and ecosystem properties*. Hoboken, NJ: John Wiley and Sons.

Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52, 107–145. doi: 10.1111/j.1469-185X.1977.tb01347.x

Henderson, A. (2011). A revision of Geonoma (Arecaceae). *Phytotaxa* 17, 1–271. doi: 10.11646/phytotaxa.17.1.1

Henderson, A., Galeano, G., and Bernal, R. (2019). *Field guide to the palms of the Americas*. Princeton, NJ: Princeton University Press. doi: 10.1515/9780691197708

Hietz, P., Turner, B. L., Wanek, W., Richter, A., Nock, C. A., and Wright, S. J. (2011). Long-term change in the nitrogen cycle of tropical forests. *Science* 334, 664–666. doi: 10.1126/science.1211979

Kumordzi, B. B., de Bello, F., Freschet, G. T., Le Bagousse-Pinguet, Y., Leps, J., and Wardle, D. A. (2015). Linkage of plant trait space to successional age and species richness in boreal forest understorey vegetation. *J. Ecol.* 103, 1610–1620. doi: 10.1111/1365-2745.12458

Kursar, T. A., Engelbrecht, B. M. J., and Tyree, M. T. (2005). A comparison of methods for determining soil water availability in two sites in Panama with similar rainfall but distinct tree communities. *J. Trop. Ecol.* 21, 297–305. doi: 10.1017/s0266467405002324

Laughlin, D. C., and Laughlin, D. E. (2013). Advances in modeling trait-based plant community assembly. *Trends Plant Sci.* 18, 584–593. doi: 10.1016/j.tplants.2013.04.012

Lê, S., Josse, J., and Husson, F. (2008). FactoMineR: an R Package for Multivariate Analysis. *J. Stat. Softw.* 25, 1–18. doi: 10.18637/jss.v025.i01

Lenth, R. V. (2021). *emmeans: Estimated MarginalMeans, aka Least-Squares Means. Rpackage version 1.5.5-1*.

Maharjan, S. K., Poorter, L., Holmgren, M., Bongers, F., Wieringa, J. J., and Hawthorne, W. D. (2011). Plant functional traits and the distribution of West African rain forest trees along the rainfall gradient. *Biotropica* 43, 552–561. doi: 10.1111/j.1744-7429.2010.00747.x

McLean, E. H., Prober, S. M., Stock, W. D., Steane, D. A., Potts, B. M., Vaillancourt, R. E., et al. (2014). Plasticity of functional traits varies clinally along a rainfall gradient in Eucalyptus tricarpa. *Plant Cell Env.* 37, 1440–1451. doi: 10.1111/pce.12251

Mehlich, A. (1984). Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. *Comm. Soil Sci. Plant Anal.* 15, 1409–1416. doi: 10.1080/00103628409367568

Muscarella, R., Bacon, C. D., Faurby, S., Antonelli, A., Kristiansen, S. M., Svenning, J. C., et al. (2019). Soil fertility and flood regime are correlated with phylogenetic structure of Amazonian palm communities. *Ann. Bot.* 123, 641–655. doi: 10.1093/aob/mcy196

Palmiotto, P. A., Davies, S. J., Vogt, K. A., Ashton, M. S., Vogt, D. J., and Ashton, P. S. (2004). Soil-related habitat specialization in dipterocarp rain forest tree species in Borneo. *J. Ecol.* 92, 609–623. doi: 10.1111/j.0022-0477.2004.00894.x

Paton, S. (2020a). Yearly Reports_Parque Natural Metropolitano Crane. The Smithsonian Institution. *Dataset* 2020:11799348. doi: 10.25573/data.11799348.v3

Paton, S. (2020b). Yearly Reports_San Lorenzo Crane. The Smithsonian Institution. *Dataset* 2020:11799309. doi: 10.25573/data.11799309.v2

Peltzer, D. A., Wardle, D. A., Allison, V. J., Baisden, W. T., Bardgett, R. D., Chadwick, O. A., et al. (2010). Understanding ecosystem retrogression. *Ecolog. Monogr.* 80, 509–529. doi: 10.1890/09-1552.1

Pollock, L. J., Morris, W. K., and Vesk, P. A. (2012). The role of functional traits in species distributions revealed through a hierarchical model. *Ecography* 35, 716–725. doi: 10.1111/j.1600-0587.2011.07085.x

Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P., and Mommer, L. (2012). Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.* 193, 30–50. doi: 10.1111/j.1469-8137.2011.03952.x

Prada, C. M., Morris, A., Andersen, K. M., Turner, B. L., Caballero, P., and Dalling, J. W. (2017). Soils and rainfall drive landscape-scale changes in the diversity and functional composition of tree communities in premontane tropical forest. *J. Veget. Sci.* 28, 859–870. doi: 10.1111/jvs.12540

Pyke, C. R., Condit, R., Aguilar, S., and Lao, S. (2001). Floristic composition across a climatic gradient in a neotropical lowland forest. *J. Veg. Sci.* 12, 553–566. doi: 10.2307/3237007

Record, S., Kobe, R. K., Vriesendorp, C. F., and Finley, A. O. (2016). Seedling survival responses to conspecific density, soil nutrients, and irradiance vary with age in a tropical forest. *Ecology* 97, 2406–2415. doi: 10.1002/ecy.1458

Richardson, S. J., Peltzer, D. A., Allen, R. B., McGlone, M. S., and Parfitt, R. L. (2004). Rapid development of phosphorus limitation in temperate rainforest along the Franz Josef soil chronosequence. *Oecologia* 139, 267–276. doi: 10.1007/s00442-004-1501-y

Ruokolainen, K., and Vormisto, J. (2000). The most widespread Amazonian palms tend to be tall and habitat generalists. *Basic Appl. Ecol.* 1, 97–108.

Santiago, L. S. (2007). Extending the leaf economics spectrum to decomposition: evidence from a tropical forest. *Ecology* 88, 1126–1131. doi: 10.1890/06-1841

Sollins, P. (1998). Factors influencing species composition in tropical lowland rain forest: does soil matter? *Ecology* 79, 23–30. doi: 10.1890/0012-9658(1998)079[0023:FISCIT]2.0.CO;2

Tilman, D., and Wedin, D. (1991). Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology* 72, 685–700. doi: 10.2307/2937208

Turner, B. L., and Engelbrecht, B. M. J. (2011). Soil organic phosphorus in lowland tropical rainforests. *Biogeochemistry* 103, 297–231. doi: 10.1007/s10533-010-9466-x

Umaña, M. N., Condit, R., Pérez, R., Turner, B. L., Wright, S. J., and Comita, L. S. (2021). Shifts in taxonomic and functional composition of trees along rainfall and phosphorus gradients in central Panama. *J. Ecol.* 109, 51–61. doi: 10.1111/1365-2745.13442

Vitousek, P. M., and Sanford, R. L. Jr. (1986). Nutrient cycling in moist tropical forest. *Annu. Rev. Ecol. Syst.* 17, 137–167. doi: 10.1146/annurev.es.17.110186.001033

Wang, Y. H., and Augspurger, C. (2004). Dwarf palms and cyclanths strongly reduce Neotropical seedling recruitment. *Oikos* 107, 619–633. doi: 10.1111/j.0030-1299.2004.13328.x

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

Yavitt, J. B., and Wright, S. J. (2008). Seedling growth responses to water and nutrient augmentation in the understorey of a lowland moist forest, Panama. *J. Trop. Ecol.* 24, 19–26. doi: 10.1017/S0266467407004713

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

frontiers | Frontiers in Forests and Global Change

ORIGINAL RESEARCH
published: 12 July 2022
doi: 10.3389/ffgc.2022.867912

Allometric Models to Estimate Carbon Content in Arecaceae Based on Seven Species of Neotropical Palms

Gerardo Avalos[1,2]*, Milena Cambronero[2] and Carolina Alvarez-Vergnani[1]

[1] Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica, [2] The School for Field Studies, Center for Sustainable Development Studies, Beverly, MA, United States

We present allometric models for estimating total carbon content and above ground carbon (AGC) for the Arecaceae family, and for seven abundant neotropical palm species: the canopy species *Socratea exorrhiza* (*n* = 10) and *Iriartea deltoidea* (*n* = 10), the sub-canopy palm *Euterpe precatoria* (*n* = 10), and the understory species *Asterogyne martiana* (*n* = 15), *Prestoea decurrens* (*n* = 10), *Geonoma interrupta* (*n* = 10), and *Chamaedorea tepejilote* (*n* = 22). Understanding the allometry of functional groups such as palms is critical for improving carbon stocks estimates in tropical forests and determining how allometric differences affect species functional diversity. The research was carried out in the tropical rainforests of the Caribbean slope of Costa Rica. We harvested 87 palms of a wide range of sizes, and separated them into roots, stems, and leaves, measured their fresh and dry biomass, and calculated their carbon content, tissue density, and dry mass fraction (dmf). Our general palm model estimating total carbon content based on these seven species and 87 samples accounted for 92% of the variation across species. We generated a similar model to estimate AGC and explained 91% of the variation. We compared our AGC model with two models used to estimate palm carbon content: Goodman et al. (2013)'s and Chave et al. (2014)'s models and found that all three converged on the estimation of AGC although our model was the most parsimonious because it achieved the same efficiency with only two variables, stem diameter and stem height. To improve the accuracy of allometric models we need to incorporate more species, a greater diversity of growth forms, a wider range of sizes, a larger sample size, and more diversity of habitats dominated by palms. Estimating carbon content using allometric approaches could benefit from more consistency in data collection across plant groups.

Keywords: allometric models, allometry, carbon stocks, carbon sequestration, tropical rain forest, carbon content

OPEN ACCESS

Edited by:
Alexander Shenkin,
University of Oxford, United Kingdom

Reviewed by:
Florian Hofhansl,
International Institute for Applied Systems Analysis, Austria
Robert Muscarella,
Uppsala University, Sweden
Paschalis Chatzopoulos,
Uppsala University, Sweden,
contributed to the review of RM

***Correspondence:**
Gerardo Avalos
gerardo.avalos@ucr.ac.cr

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

Received: *01 February 2022*
Accepted: *21 June 2022*
Published: *12 July 2022*

Citation:
Avalos G, Cambronero M and Alvarez-Vergnani C (2022) Allometric Models to Estimate Carbon Content in Arecaceae Based on Seven Species of Neotropical Palms. Front. For. Glob. Change 5:867912. doi: 10.3389/ffgc.2022.867912

INTRODUCTION

Tropical forests are important carbon sinks, influencing the atmospheric concentration of CO_2 and thus playing a significant role in mitigating the consequences of climate change (Houghton, 2007; Saatchi et al., 2011; Goers et al., 2012). However, as logging, land-use changes, droughts, and forest fires reduce their ability to absorb and store carbon, these ecosystems can become net carbon sources (Brando et al., 2019; Friedlingstein et al., 2020). To better understand how different species, ontogenetic stages, and life forms contribute to carbon sequestration in terrestrial ecosystems, we must refine methodologies for quantifying carbon inventories in tropical forests, as well as expand the information on plant groups other than trees (Dewar, 1991; Dewar and Cannell, 1992; Brown, 1997; Achard et al., 2004).

There are several methods for estimating carbon stocks in tropical forests (Zhang et al., 2012). Remote sensing techniques enable low-cost monitoring of large areas (Jucker et al., 2017; Rodríguez-Veiga et al., 2019), but are limited by field validation using ground-based techniques. Traditional allometric methods, on the other hand, are time-consuming and often expensive. These methods are based on regression models that relate morphological measurements to biomass or stored carbon (Hairiah et al., 2001; Chave et al., 2005, 2014; Montero and Montagnini, 2005; Zhang et al., 2012), and can use morphological traits available in extensive databases (Chave et al., 2005; Curtis, 2008; Lal, 2008; Lorenz and Lal, 2010; Kissling et al., 2019). However, most allometric studies were developed for woody dicotyledonous trees, particularly the most common and commercially important species (Brown, 1997; Hairiah et al., 2001; Chave et al., 2005, 2014; Zhang et al., 2012), and typically include only a handful of individuals of a limited size range per species and restricted geographic range, and have excluded life forms such as lianas, hemiepiphytes, ferns, and palms (Clark et al., 2001; Chave et al., 2005, 2014; Jucker et al., 2017). Our understanding of the biomass contribution of different life forms is thus very limited because few studies have considered them in their biomass inventories (Saldarriaga et al., 1988; Hughes et al., 1999; Nascimento and Laurance, 2002; Lima et al., 2012).

With over 2,600 species and 181 genera, palms (Arecaceae) are one of the most diverse and extensively distributed plant families in tropical and subtropical environments (Baker and Dransfield, 2016). They dominate many tropical ecosystems (Mejia and Kahn, 1990; Myers, 2013). Seasonally or permanently inundated wetlands, such as the "aguajales" of the Peruvian Amazon (dominated by *Mauritia flexuosa*, Sampaio et al., 2008), the "yolillales" of Costa Rica (dominated by *Raphia taedigera*, Serrano-Sandí et al., 2013; Yaap et al., 2015), and peatlands in tropical swamp forests of the Congo basin (some dominated by *R. laurentii* and *R. hookeri*), are important soil carbon reservoirs (Lähteenoja et al., 2009; Dargie et al., 2017). Due to their abundance in the Amazon lowlands, palms have been considered "hyperdominant" elements (ter Steege et al., 2013), with seven out of the 20 most abundant species being palms. In the tropical rainforest of La Selva Biological Station in Costa Rica, palms account for 5.4% of AGB, but make up 25% of stems $\geq$ 10 cm DBH (Clark and Clark, 2000). Although palms contribute a small percentage of above ground biomass (AGB) in neotropical rainforests (ranging from 0.44% in Manaus, Brazil, DeWalt and Chave, 2004, to 10.9% at the Luquillo tropical rainforest in Puerto Rico, which is dominated by the palm *Prestoea montana*, Frangi and Lugo, 1985) their high abundance ensures a significant role in forest structure and function (ter Steege et al., 2013; Boukili and Chazdon, 2017). Palms, for example, play an important role in food webs by providing habitat and food for a variety of animal species (Zona and Henderson, 1989; Howard et al., 2001; Onstein et al., 2017). Thus, they provide key resources for seed dispersers, which in turn secure the dispersal of old growth canopy species that store most of the carbon in mature forests (Bello et al., 2015). This is an example of how functional diversity (i.e., the variety and number of species that fulfill different functional roles that influence ecosystem functioning, Petchey and Gaston, 2006) affect carbon sequestration. Palms are also valuable to many human groups who use them as raw materials for construction, food, drink, clothing, fuel, medicine, and fibers (Jones, 1995; Henderson, 2002; Dransfield et al., 2008; Sylvester et al., 2012). To understand the link between carbon stocks and functional diversity it is essential to comprehend how the allometry and carbon sequestration of groups like palms differ from that of dicotyledonous woody plants.

Despite their critical functional roles, palms have been excluded from most tropical forest carbon stock inventories (DeWalt and Chave, 2004; Chave et al., 2005; Lorenz and Lal, 2010), as well as from comprehensive allometric analyses of diameter vs. height relationships (Feldpausch et al., 2011). The few studies that have generated allometric equations to estimate carbon sequestration in tropical forest palms are limited to the nine wetland and *terra firme* species of Goodman et al. (2013), *Euterpe precatoria* (Da Silva et al., 2015) and *Astrocaryum mexicanum* (Hughes et al., 1999), as well as commercially important species, such as peach palm, *Bactris gasipaes* (Ares et al., 2002), oil palm, *Elaeis guineensis* (Thenkabail et al., 2004; Syahrinudin., 2005; Leblanc et al., 2006; Ekadinata et al., 2010; Khasanah et al., 2012; Pulhin et al., 2014), the betel nut palm, *Areca catechu* (i.e., Das et al., 2021), and coconut, *Cocos nucifera* (Zahabu et al., 2018). These latter studies have been conducted mostly in monocrop plantations. Palms, as monocots, have a different structure, allometry, and strategy of resource use than trees (Tomlinson, 2006, 2011). With a few exceptions, palms are monopodial and lack aerial branching, have only one shoot meristem, and lack dormancy and secondary growth. In palm species where stem diameter and stem height show a significant relationship, diameter increases through sustained primary growth (i.e., through the division, lignification, and expansion of parenchyma cells, which also differentiate into fibers, Tomlinson, 2011). Furthermore, palms show higher leaf longevity and leaf construction costs than dicotyledonous trees (Renninger and Phillips, 2016), which have smaller leaves than palms and may drop leaflets rather than the entire frond to acclimate to new light conditions.

The goals of this research are: (a) to generate allometric models to estimate carbon content in seven species of neotropical palms from different forest strata, (b) to produce general models to estimate above-ground carbon and total carbon for the family Arecaceae based on these species using measurements commonly taken in forest inventories, and (c) to compare our models with two of the most widely used models to estimate the contribution of palms to carbon storage: the Goodman et al. (2013)'s model, developed for a subset of nine species of neotropical palms, and the pantropical model of Chave et al. (2014), developed for dicotyledonous trees.

We expected that the diameter and stem height would be the best predictors of carbon content, because they are related to biomass accumulation (Goodman et al., 2013), are functionally linked to carbon sequestration, determine mechanical support (Avalos et al., 2019), and reflect palm size. We do not expect wood density (or the density of the sclerotized tissue in palms) to be a good predictor of carbon content because palms do not develop wood; instead, they have a sclerotized tissue that is often unevenly distributed along the stem, and which increases in density and mechanical strength from the base and the stem periphery toward the crown (Rich, 1986; Henderson, 2002). We also expected that using the Chave et al. (2014)'s model, which was developed for trees, would lead to an erroneous estimation of carbon storage in palms, due to the significant structural and allometric differences between dicotyledonous trees and palms, and the importance that this model places on wood density.

It is essential to increase the knowledge on the allometry of functional groups like palms, not only for developing more accurate estimates of carbon stocks in tropical forests, but also for understanding the ecological basis of species differences in morphological structure and determining how allometry drives resource allocation and plant responses to environmental gradients, influencing species diversity (Weiner, 2004; Vasseur et al., 2012).

MATERIALS AND METHODS

Study Site

Palms were harvested in three tropical rain forest sites in the Caribbean lowlands of Costa Rica (**Figure 1**). The first two were La Selva Biological Station (10°26'N – 83°59'W, 30–150 masl, annual precipitation 4,162 mm) and Tirimbina Biological Reserve (10°24'N – 84°06W, 180–220 masl, annual precipitation 3,833 mm), both situated in Sarapiquí, Heredia. The third site was the lowland forest of the agroecological farm El Progreso (10°30'35" N – 83°44'39" W, 45 masl, annual precipitation of 4,000 to 5,000 mm), located in Pococí, Limón. The three sites present an average daily temperature of 25°C and have a weak climatic seasonality, with November, December and February being the rainiest months (McDade et al., 1994).

Study Species

We selected four understory and three canopy palm species representing a wide range of growth forms and regeneration strategies. Understory species included *Prestoea decurrens* (*n* = 10), *Chamaedorea tepejilote* (*n* = 22), *Geonoma interrupta* (*n* = 10), and *Asterogyne martiana* (*n* = 15). *Prestoea decurrens* (Nicaragua to Ecuador, 0–900 masl), is a clonal species reaching 10 m in height in the tallest individuals (Grayum, 2003). *Chamaedorea tepejilote* (S Mexico to Colombia, 0–1,600 masl) is a dioecious species which can grow up to 5 m (Castillo-Mont et al., 1994; Grayum, 2003). *Geonoma interrupta* (S Mexico to Peru, 0–850 masl) has a solitary stem and may reach 6 m in height (or over 10 m in exceptional cases), being considered as one of the tallest species in the genus (Grayum, 2003). Finally, *Asterogyne martiana* (Belize to Ecuador, 0–1,000 masl) is shade-tolerant species with a decumbent stem often reaching 2 m in height, and with simple, bifid leaves. The canopy species *Socratea exorrhiza* (*n* = 10, S Nicaragua to Brazil, 0–750 masl) and *Iriartea deltoidea* (*n* = 10, SE Nicaragua to Brazil, 0–800 masl) can reach 25 and 30 m of stem height, respectively, and are characteristic canopy components of mature forests (Grayum, 2003). Both species have a cone of stilt roots, although roots in *I. deltoidea* are clustered at the base of the stem and grow up to 1.5 m above ground, and in *S. exorrhiza* roots are well-separated, covered by spines, and can grow up to 4 m above the ground (Henderson et al., 1995). Both species show plasticity in the diameter vs. height allometry associated with geographic location and terrain slope (Avalos et al., 2019). *Euterpe precatoria* (*n* = 10, Belize to Bolivia, 0–1,150 masl) var *longevaginata* (Henderson, 1995) is often classified as a subcanopy species (Zuidema and Boot, 2000). It is a single-stemmed palm that can reach 26 m in height, developing a stilt root cone that in extreme cases may reach over 2 m above the ground (Avalos and Schneider, 2011). It is a cryptic pioneer since it regenerates under disturbed conditions like canopy gaps but can also withstand shade and regenerates along with the forest as the gap closes (Avalos, 2019).

Palm Harvesting, Morphological Measurements, and Biomass Estimation

From September 2013 to May 2015, we harvested 87 palms, taking care to represent the full range of size classes representative of the population structure of each species (**Appendix Table 1**). We selected individual palms to obtain a sufficient spread of the data and reflect the size classes characteristic of the population of each species. We measured stem diameter at 1.3 m above the ground (DBH), at half the stem length in palms less than 1.3 m in height, or immediately above the stilt roots in palms with a stilt root cone higher than 1.3 m. We termed this measurement in all cases as *diameter* (abbreviated as *diam*), since strictly DBH was not measured in all cases. Harvested palms were separated into modules (stems, roots, and leaves) and we measured the total fresh biomass of each module using a Pesola® Macro-Line Spring Scale (30 ± 0.25 kg). We carefully dug out the roots, collected all the root material to the extent that was possible, including fine roots (2–5 mm in diameter). In instances in which it was difficult to extract all the roots, due to their size or depth, a representative section was extracted, and from this, we estimated the total root biomass. We washed out the roots in the field and sun-dried them before weighing them in the laboratory. To determine the dry biomass (and carbon content) we collected 300 mg samples from each module. For leaves, this sample included one young, one intermediate, and one mature frond, determined according to their position from the tip of the apical meristem. In stems, the biomass sample was collected from the base, middle, and upper parts of the stem until reaching the base of the leaf crown. The total stem height of the palm (H_{bc}) was measured from stem base above the stilt roots (if present) to the base of the crown We also measured the height of the stilt root cone in stilt-rooted palms (*S. exorrhiza*, *I. deltoidea*, *E. precatoria*, and *P. decurrens*) from the ground to the base of the stem (H_{sr}). In

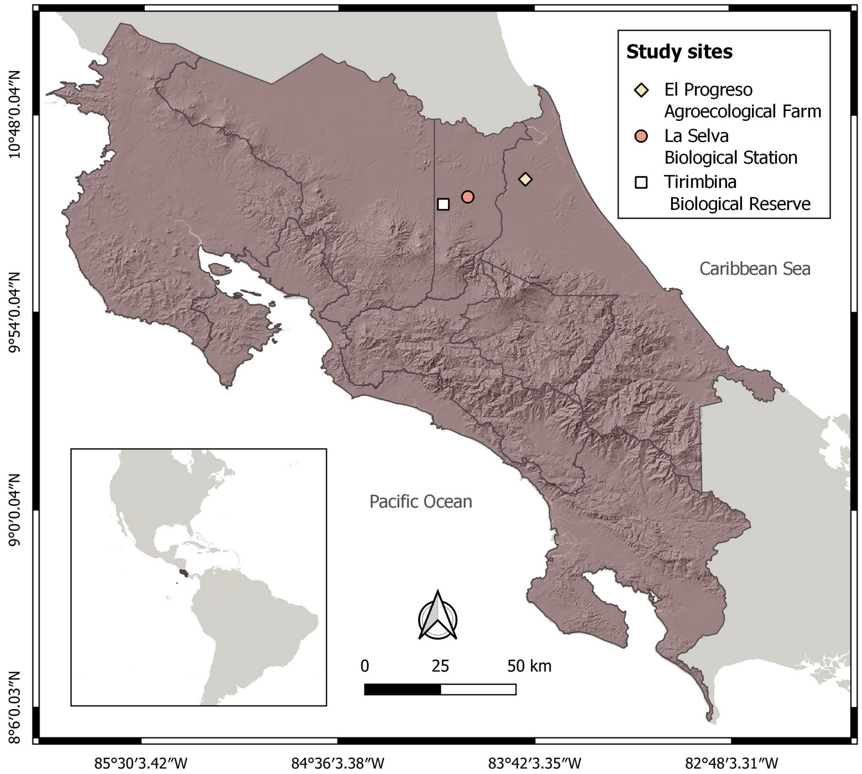


FIGURE 1 | Location of study sites in the lowland rainforests of the NE Caribbean slope of Costa Rica.

palms without stilt roots, H_{bc} corresponded to the total length of the stem, from the connection with the first root to the base of the crown. In *A. martiana* H_{bc} also included the section of the subterranean stem from the first root to the insertion of the oldest frond. Finally, to estimate the tissue density of the stem (specific gravity, ρ), we used a Haglof 2-Thread Increment Borer, to collect a tissue sample from the stem, following the methods of Chave et al. (2005). Accordingly, we selected a point of entry for the increment borer near the base of the stem, in the middle, and near the base of the palm crown to place the borer at the center of the internode and carry out the perforation. Once the sclerotized tissue was extracted, the sample was placed in a test tube, sealed, and transferred back to the laboratory for the estimation of tissue density.

Estimation of Carbon Content and Stem Tissue Density

We dried the samples in an oven at 65°C for 48 h or until constant weight. Once dried, we ground the samples and determined their carbon content using an automatic analyzer TruSpec CN, LECO Corporation, at the Department of Systematic Botany at the University of Ulm, Germany, and an automatic elemental carbon and nitrogen analyzer, VarioMacrocube, at the University of Costa Rica. The magnitude of the carbon content in g was calculated by multiplying the total dry weight of each module by the percentage of carbon obtained in the laboratory and adding up all the dry biomass per individual palm. The average carbon fraction for the palms analyzed here was 43.9% ± 1.28 (Cambronero et al., 2018), but for our models we used the average carbon fraction obtained for each species. Stem tissue density (specific gravity, ρ) was calculated as the ratio of dry biomass (g) over volume (cm^3). Volume was measured by water displacement. A summary table of all measured morphological characters is shown in (**Appendix Table 1**).

Calculation of Species-Specific Allometric Models for Estimating Carbon Content

Palms were selected to represent a broad range of sizes characteristic of the species in the field. Thus, our sampling in these regards was not random and corresponded to an ordinary least squares regression (model I) since the magnitude of the predictor variable was selected by the experimenter. As a result, a model II regression with a random predictor variable was not practical.

We developed models including a combination of variables commonly measured under field conditions, such as diameter and stem height, aiming for simplicity. Therefore, only linear (or log-transformed) models were tested, and we did not consider non-linear models even though they could have provided better fits because we consider that linear (and logarithmic) models better represented the mechanistic relationship between the allometric variables.

We included stem tissue density to investigate the significance of this parameter in palms, even though measuring it requires access to instrumentation that may not be readily available in the field. To predict carbon content, we calculated linear and logarithmic backward stepwise regressions between the natural logarithm of the total amount of carbon content in kg per palm (LnC, response variable), and a set of explanatory variables including diameter in cm (diam), total stem height from the base of the stem to the base of the leaf crown (H_{bc}, m, excluding stilt roots if present), the height of the stilt root cone above the ground (H_{sr}) if present, the dry mass fraction or tissue moisture (dry mass over fresh mass, dmf), and stem tissue density (g cm^{-3}). This latter parameter was calculated so that we could compare our family-level models to those of Goodman et al. (2013), who include this variable. The predictor variables were included in the models with their Ln-transformed values as well as in their linear scales. We performed backward stepwise regression analysis for each species, and then chose the most parsimonious general regression models for all seven species based on the magnitudes of the R^2 value, the mean square of error (MSE), and the Akaike Information Criterion (AIC). The chosen models were listed in decreasing order of R^2, and the lowest MSE and AIC values. We chose models with at least one size-related variable (i.e., diameter and height). We discarded models that were not statistically significant or had R^2 values < 0.8 and included models with a single variable only if the model was statistically significant. Because the response variable required a logarithmic transformation, a correction factor was calculated following Sprugel (1983). The correction factor was used to remove the systematic bias introduced by the logarithmic transformation. The predicted value coming from the regression was multiplied by this correction factor, which is calculated as:

$$CF = e^{\frac{\left(\left(SEE\right)^2\right)}{2}} \tag{1}$$

Where SEE = standard error of estimate of the regression (the absolute value of $\ln y_i$ in boldface):

$$SEE = \sqrt{\sum \left(lnyi - \boldsymbol{lnyi}\right)^2 / (N-2)}$$

Allometric Models for Estimating Total Carbon Content and Above Ground Carbon at the Family Level

We combined all the data from the seven species to generate a series of family-level models to estimate total carbon per palm. The response variable was the natural logarithm of the total amount of carbon content in kg per palm (LnC), and the predictor variables were the set of morphological variables described above (except for Hsr, which was not present in all palms). We applied the same backward stepwise regression protocol to find the most parsimonious models based on the magnitudes of the R^2 value, MSE, the AIC, and in this case, the Mean Absolute Error (MAE), which is the average absolute difference between predicted and observed values. We compared the saturated model including all the predictor variables, with simpler, more parsimonious models coming from the stepwise regression, using a k-fold cross-validation protocol (James et al., 2013) where $k = 8$. We randomly divided the data into eight-folds of approximately equal size, one of which served as the test set and the rest as the training set. The resampling process was carried out in R using the library "caret," which allowed us to estimate the value of MAE, in addition to the R^2, MSE and AIC values, and obtained the most parsimonious models by considering the number of predictor variables and the magnitude of the selection parameters (R^2, MSE, AIC). We used a similar cross-validation procedure to generate the AGC models.

Comparison Between Models Estimating Above Ground Carbon for Arecaceae

To compare our Arecaceae AGC family model with those of Goodman et al. (2013) and Chave et al. (2014), we estimated the aboveground carbon content (AGC in kg) by adding the carbon content fractions of stems and leaves without considering the carbon content of roots (AGB). Goodman et al. (2013)'s model estimates AGB for nine species of neotropical palms, including *E. precatoria*, *I. deltoidea* and *S. exorrhiza*, examined here, using $AGB^{0.25} = 0.56^{*}(dmfD^2H_{stem})^{0.25}$, where dmf is the dry mass fraction defined above, D is DBH, and H_{stem} is the height of the palm from the ground to the highest leaf. To determine AGC, we applied the conversion factor of 50% of the dry biomass, which has traditionally been used to determine the carbon accumulated in trees (Chave et al., 2005; Houghton, 2007; Lorenz and Lal, 2010). This model is only valid for individuals with a stem height $\geq$ 1 m. The pantropical model of Chave et al. (2014) estimates AGB using $0.0673\ (\rho D^2 H)^{0.976}$, where ρ corresponds to wood stem density (g cm^{-3} or tissue density for palms), D is the DBH (cm), and H is the total height (m); this model is based on data from 4,004 trees $\geq$ 5 cm DBH. AGC was then calculated by applying the carbon fraction of 50% to AGB as in the case of Goodman et al. (2013)'s model. We did not include other models developed for palms such as the one by Frangi and Lugo (1985), or by Brown (1997) since these had lower performance and lower R^2 values when applied to our data (0.78 and 0.79, respectively).

We used the actual carbon fraction per palm species measured directly here (Cambronero et al., 2018) for the comparison with Goodman et al. (2013) and Chave et al. (2014) models. In both cases, the accuracy of all models was contrasted against the observed values of AGC using the R^2 value and the magnitude of their residuals. We used natural logarithmic models for the comparisons. For all regression analyses we used R software (R Core Team, 2022), and the library MASS with the function stepAIC().

RESULTS

Species-Level Allometric Models to Estimate Total Carbon Content

Canopy and Subcanopy Species

In *S. exorrhiza* the most parsimonious model for predicting total carbon content had the linear form of diameter. Entering other variables in the model (total height and stem height from the base, in linear and logarithmic forms), in addition to Ln(diam), produced similar R^2 values but not a lower AIC (**Table 1**). In *I. deltoidea*, the most parsimonious model had logarithmic forms of diameter and total height. For the subcanopy palm, *E. precatoria*, the most parsimonious models had the logarithmic form of total height and diameter. As expected, height and diameter were the most frequent variables in the models to predict carbon content, while tissue density explained the variation in carbon content only in the understory species *P. decurrens* and *A. martiana*.

Understory Species

In *C. tepejilote*, we did not find differences in morphological parameters among male and female plants, and thus, the analyses were done for the overall species. In this species, the best-fit model included the logarithmic form of total height and diameter. In *P. decurrens*, the best-fit model had the logarithmic forms of stem length and tissue density (R^2 value = 0.95). For *A. martiana*, the model with the highest R^2 had the logarithmic forms of the four predictor variables diameter, total height, dmf and tissue density. Finally, *G. interrupta* showed the highest fit for models including stem height (logarithmic and linear, with a R^2 of 0.98 and 0.91, respectively).

Family-Level Model to Estimate Total Carbon and Above-Ground Carbon Content (AGC)

To predict total carbon content the saturated model (model 1, **Table 2**) included all predictor variables and served as a baseline against which the other models were compared. This model had the highest R^2, and the lowest MSE, AIC and MAE values, but its practical value was low. Models 2 and 3, which included logarithmic values of tissue density, diameter, stem length, and dmf, explained a similar proportion of the variation with fewer variables. From this point of view, model 4 is the most parsimonious since it reached an R^2 value comparable to that of the previous models with only two variables (diameter and stem height). MAE values for models 2, 3, and 4 were very similar showing that these models were not overfit. Model 5 reached the R^2 threshold value of 0.8 but its AIC and MAE values were the highest.

We followed a similar procedure to estimate AGC at the family level (**Table 3**). As in the previous case, the saturated model (model 1, **Table 3**) included all the predictor variables, serving as a baseline against which the other models could be compared. Model 2 explained a portion of the variation in Ln (AGC) similar to that of models 1 and 3, with lower MSE, AIC, and MAE values, but with an additional variable [Ln(dmf)] in comparison to model 3. Model 3 was the most parsimonious, since with two variables (Lndiam and $\mathrm{LnH_{bc}}$) maintained a high R^2 (0.91) and low AIC and MAE. Model 4 met the threshold value of $R^2 \geq 0.80$, but its efficiency in predicting Ln(AGC) was low.

We then compared model 3 to the pantropical model proposed by Chave et al. (2014) and the palm model of Goodman et al. (2013) using Ln (AGC). All three models predicted the observed Ln (AGC) with high R^2 values ranging from 0.89 to 0.913 (**Figure 2**). Our model had the highest R^2 value (0.913) followed by Goodman et al. (2013)'s with 0.875 and Chave et al. (2014) with 0.890. We consider all three models have similar ability to predict the AGC of the palm species analyzed here although ours is the most parsimonious because it uses two variables (diameter and stem height) vs. the three variables of Goodman et al. (2013), diameter, stem height and dmf, and the three variables of the Chave et al. (2014) model (diameter, height, and tissue density). Contrary to our prediction, the Chave et al. (2014)'s model satisfactorily predicted the stored AGC of palms despite of being a model generated for dicotyledonous trees.

DISCUSSION

Developing allometric models specific for palms will improve the accuracy of the estimates of tropical forest carbon stocks, as existing models need to be refined to include this and other life forms (e.g., lianas, epiphytes, tree ferns), that, while not as massive as trees, play essential ecological roles and vary in abundance depending on forest type, elevation, and edaphic factors (Chazdon, 1996). Palms have a major role as keystone plant resources providing food, nesting sites, and habitat for a wide range of vertebrate species (van der Hoek et al., 2019), many of which are seed dispersers and seed predators that regulate plant species diversity and carbon storage (Bello et al., 2015) and contribute to the maintenance of healthy food webs. Palms may account for a higher proportion of AGB in wetlands where they are the dominant group and are established on soils that store large amounts of carbon (Lähteenoja et al., 2009). Therefore, while palms account for a small proportion of neotropical rainforest carbon stocks, they are functionally important by affecting forest succession (Boukili and Chazdon, 2017), food webs (Zona and Henderson, 1989), and varying their abundance according to topography and edaphic conditions, being dominant elements in wetlands (Myers, 2013). Allometric analyses incorporating palm biomass in studies of carbon stocks in tropical forests are still rare (but see Nascimento and Laurance, 2002; Lima et al., 2012); their inclusion would not only improve the accuracy of such models, but would also broaden our understanding of the mechanistic basis of key functional traits, such as the limits of the allometry of the stem diameter versus stem height in palms, and the allocation strategies of plants lacking a vascular cambium in response to wide environmental gradients (Avalos et al., 2019).

Currently, family-level models proposed for Arecaceae are based on a small number of species, a small number of tribes represented, and a limited range of sizes of harvested individuals (i.e., Goodman et al., 2013; and this study). Many canopy palms frequently show heights that exceed the ranges included in these studies. Large individuals are difficult to harvest, and many field sites do not allow it. In addition to sample size bias, allometric relationships may change geographically due to environmental conditions (Avalos et al., 2019), such topography, edaphic factors, successional stage, climate, and nutrient availability

TABLE 1 | Models to estimate carbon content (C; Ln kg), in seven species of neotropical palms.

Species		**Model**	**CF**	**R^2**	**F**	**P**	**MSE**	**AIC**
Socratea exorrhiza	Ln(C)	$-1.79 + 2.21\text{ Ln(diam)} + 0.68\text{ Ln}(H_{bc}) + 1.46\text{ Ln(dmf)}$	1.01	0.99	426.86	<0.0001	0.02	−32.96
	Ln(C)	$-2.6 + 0.34\text{ diam}$	1.06	0.97	280.74	<0.0001	0.12	−19.28
	Ln(C)	$-1.64 + 2.16\text{ Ln}(H_{bc})$	1.16	0.94	126.52	<0.0001	2.09	−11.64
	Ln(C)	$-5.25 + 2.91\text{ Ln(diam)}$	1.01	0.92	101.8	<0.0001	2.56	−9.61
	Ln(C)	$-1.1 + 0.44\ H_{sr}$	1.3	0.88	57.76	<0.0001	0.53	−4.49
Iriartea deltoidea	Ln(C)	$0.03 + 1.01\text{ Ln(diam)} + 0.81\text{ Ln}(H_{bc}) + 1.1\text{ Ln(dmf)} + 0.68\text{ Ln}(H_{sr})$	1.0	0.99	333	<0.0001	0.01	−38.21
	Ln(C)	$-1.14 + 0.33\ H_{bc} + 0.58\ H_{sr}$	1.06	0.96	76.15	<0.0001	0.14	−17.57
	Ln(C)	$-4.43 + 2.48\text{ Ln(diam)}$	1.07	0.94	150.18	<0.0001	0.13	−18.16
	Ln(C)	$-1.14 + 0.2\text{ diam}$	1.12	0.92	86.86	<0.0001	0.22	−13.06
Euterpe precatoria	Ln(C)	$4.7 + 1.35\text{ Ln}(H_{bc}) + 3.13\text{ Ln(dmf)} + 0.79\text{ Ln}(H_{sr})$	1.03	0.96	43.93	<0.0001	0.1	−20.06
	Ln(C)	$-1.49 + 0.37\text{ Ln(diam)}$	1.04	0.94	134.3	<0.0001	0.09	−21.5
	Ln(C)	$-1.5 + 0.38\text{ diam}$	1.06	0.93	114.86	<0.0001	0.11	−20.04
	Ln(C)	$-0.77 + 0.38\ H_{bc}$	1.06	0.93	109.96	<0.0001	0.94	−19.62
Chamaedorea tepejilote	Ln(C)	$-3.94 + 1.75\text{ Ln(diam)} + 0.89\text{ Ln}(H_{bc})$	1.02	0.81	43.18	<0.0001	0.23	−29.43
Prestoea decurrens	Ln(C)	$1.44 + 1.04\text{ Ln}(H_{bc}) + 0.68\text{ Ln}(\rho)$	1.04	0.95	70.18	0.0001	0.09	−21.13
	Ln(C)	$-0.08 + 1.53\text{ Ln}(H_{bc})$	1.05	0.87	55.06	0.0001	0.22	−13.31
Asterogyne martiana	Ln(C)	$-1.42 + 1.48\text{ Ln(diam)} + 0.88\text{ Ln}(H_{bc}) + 0.66\text{ Ln(dmf)} + 0.31\text{ Ln}(\rho)$	1.22	0.93	276.29	<0.0001	0.22	−124.32
	Ln(C)	$-2.48 + 1.2\text{ Ln(diam)} + 0.88\text{ Ln}(H_{bc})$	1.1	0.88	322.17	<0.0001	0.36	−83.72
	Ln(C)	$-3.78 + 2.84\text{ Ln(diam)} + 1.04\text{ Ln}(\rho)$	1.06	0.85	34.94	<0.0001	0.14	−26.66
	Ln(C)	$-6.42 + 1.24\text{ diam} + 2.7\ \rho$	1.10	0.80	35.85	<0.0001	0.18	−22.42
Geonoma interrupta	Ln(C)	$-3.23 + 1.34\text{ Ln(diam)} + 1.42\text{ Ln}(H_{bc})$	1.02	0.98	206.98	<0.0001	0.05	−26.93
	Ln(C)	$-1.2 + 0.41\ H_{bc}$	1.13	0.91	83.58	<0.0001	0.24	−12.34

Diam, stem diameter (cm); dmf, dry mass fraction; H_{sr}, Height of stilt roots if present (m); H_{bc}, Height at the base of the crown (m); ρ, density of the sclerotized tissue (g/cm^3); CF, Correction factor recommended by Sprugel (1983); MSE, Mean square of error; AIC, Akaike's information criterion; Ln, Natural logarithm. Models are listed by decreasing R^2 and increasing AIC values.

TABLE 2 | General allometric models to estimate total carbon content (C; kg) based on seven species of neotropical palms.

Model number			**CF**	**R^2**	**F**	**P**	**MSE**	**AIC**	**MAE**
1	Ln(C)	$-3.57 - 0.1\text{ diam} + 0.02\ H_{bc} + 3.69\ \rho - 4.38\text{ dmf} + 2.97\text{ Ln(diam)} - 0.6\text{ Ln}(\rho) + 0.6\text{ Ln}(H_{bc}) + 1.26\text{ Ln(dmf)}$	1.14	0.93	143.7	<0.0001	0.30	−97.16	0.43
2	Ln(C)	$-3.32 + 0.54\text{ Ln}(\rho) + 2.19\text{ Ln(diam)} + 0.68\text{ Ln}(H_{bc})$	1.19	0.92	308.09	<0.0001	0.36	−84.54	0.49
3	Ln(C)	$-1.4 + 1.4\text{ Ln(diam)} + 0.94\text{ Ln}(H_{bc}) + 0.97\text{ Ln(dmf)}$	1.2	0.91	294.19	<0.0001	0.38	−80.87	0.48
4	Ln(C)	$-3.64 + 1.84\text{ Ln(diam)} + 0.88\text{ Ln}(H_{bc})$	1.22	0.90	403.56	<0.0001	0.40	−74.84	0.50
5	Ln(C)	$-2.14 + 0.098\text{ diam} + 0.32\ H_{bc} + 1.9\text{ dmf}$	1.54	0.80	108.53	<0.0001	0.89	−6.05	0.74

Diam, stem diameter (cm); H_{bc}, stem height from the base of the stem to the base of the crown (m); dmf, dry mass fraction; ρ, density of the sclerotized tissue (g/cm^3). CF, Correction factor recommended by Sprugel (1983); MSE, Mean square of error; AIC, Akaike's information criteria; MAE, mean absolute error (average absolute difference between predicted and observed values); Ln, Natural logarithm. Models are listed by decreasing R^2 and increasing AIC values. Model 1 is the saturated model, against which the rest were compared.

(Eiserhardt et al., 2011). The species composition of the palms also affects the accuracy of a family-level allometric model.

The accuracy of allometric models is also limited by an incomplete inventory of functional traits for tropical plants, particularly palms. Tissue density (Rich, 1986, 1987), dmf, slenderness ratio, leaf toughness, and specific leaf area (SLA), as well as stem height and gas exchange parameters, are rarely inventoried for palms as a group or are limited to specific species (i.e., Araus and Hogan, 1994; Da Silva et al., 2015; Renninger and Phillips, 2016). Much less is known about how these traits change depending on environmental and geographic factors, ontogenetic stage, and palm size (but see Chazdon, 1986a,b). Although Kissling et al. (2019) provide a highly comprehensive compilation, functional trait databases still lack data for palms and tropical plants in general. These databases are built using a few individuals per species[1], and frequently lack metadata. It is necessary to incorporate more species, a larger sample size per species, a wider range of sizes, and phylogenetic bias corrections. Finally, many tropical habitats where palms are very abundant and dominant (Myers, 2013) are not regularly inventoried for carbon stocks.

---

[1] http://db.worldagroforestry.org

TABLE 3 | General allometric models to estimate above-ground carbon content (AGC; kg) based on seven species of neotropical palms.

Model number			CF	R^2	F	P	MSE	AIC	MAE
1	Ln(AGC)	$-7.46 - 005$ diam $- 0.004$ Hbc $+ 3.18\ \rho + 2.32$ dmf $+ 2.65$ Ln(diam) $- 0.31$ Ln(ρ) $+ 0.56$ Ln(H_{bc}) $- 0.58$ Ln(dmf)	1.15	0.92	135.5	<0.0001	0.31	−91.63	0.47
2	Ln(AGC)	$-3.8 + 2.32$ Ln(diam) $+ 0.61$ Ln(H_{bc}) $+ 0.53$ Ln(dmf)	1.18	0.92	342.09	<0.0001	0.33	−92.16	0.46
3	Ln(AGC)	$-4.11 + 1.96$ Ln(diam) $+ 0.8$ Ln(H_{bc})	1.2	0.91	443.31	<0.0001	0.38	−81.51	0.48
4	Ln(AGC)	$-4.77 + 2.82$ Ln(diam)	1.4	0.84	464.8	<0.0001	0.66	−33.03	0.66

Diam, stem diameter (cm); H_{bc}, stem height from the base of the stem to the base of the crown (m); CF, Correction factor recommended by Sprugel (1983); MSE, Mean square of error; AIC, Akaike's information criteria; Ln, Natural logarithm; MAE, mean absolute error (average absolute difference between predicted and observed values); Ln, Natural logarithm. Models are listed by decreasing R^2 and increasing AIC values. The first line shows the complete model, against which the rest were compared.

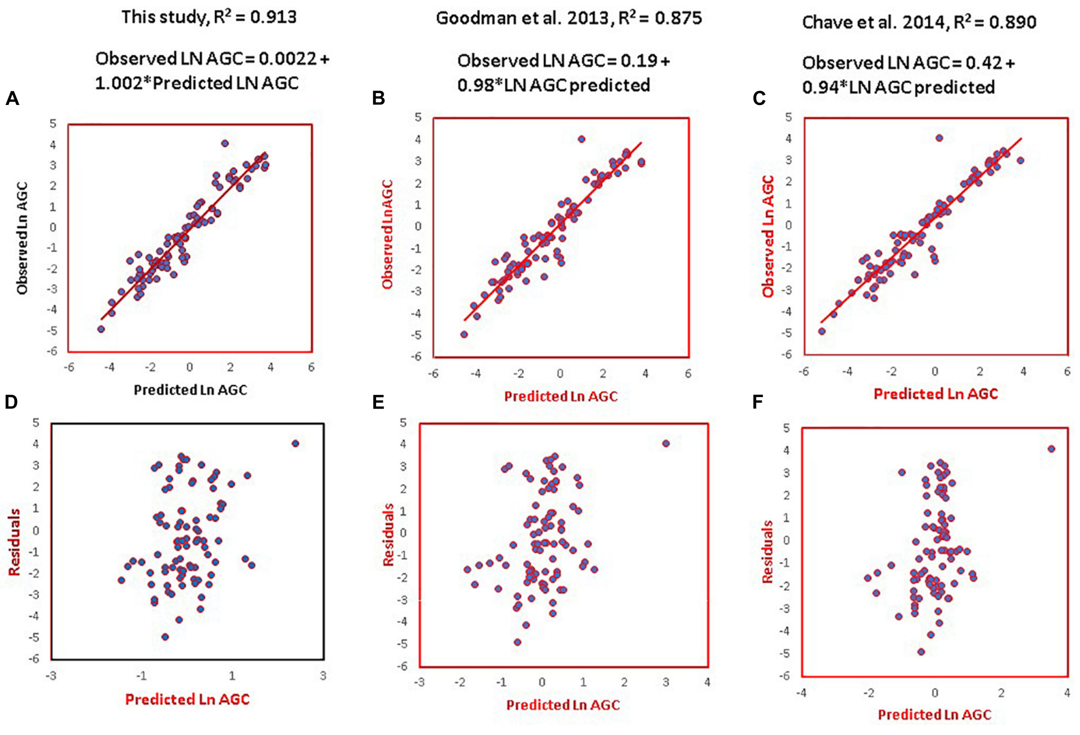


FIGURE 2 | Predicted vs. observed values **(A–C)** and residuals **(D–F)** of the Ln of AGC in kg following the general palm model proposed in this study, Goodman et al. (2013)'s model, and the pantropical model of Chave et al. (2014).

Developing species-specific models has intrinsic value because it increases the level of information at the geographic level and enriches databases, improving the accuracy of carbon inventories in tropical forests, particularly by adding information on a group of plants as abundant as palms. Our first hypothesis was correct because diameter and height were the most common variables in the models and had a significant role in predicting total carbon content as well as AGC. Because these variables reflect the size of the organism it was logical that they would be good predictors of carbon sequestration. Other functional characteristics, such as dmf and tissue density, had a lower predictive value and were more associated with biomass partitioning rather than organismal size. In general, their influence on carbon sequestration was limited across the species studied here. Dmf and tissue density were correlated in Goodman et al. (2013)'s palm assemblage, and ultimately improved their mixed species model estimates of AGB, although they did not measure tissue density directly and instead used data from online databases. Chave et al. (2014)'s model incorporated wood density, and once applied to our subset of palm species, the results were very similar to the general palm family model generated here. The magnitude of the regression slope and degree of residual dispersion for all three models were very similar, but we consider that our model has greater utility value for its application in carbon inventories because it uses diameter and height of the stem, which are commonly measured variables that do not require additional laboratory work, as it is required by the Goodman et al. (2013) and Chave et al. (2014) models that incorporate tissue density and dmf, respectively.

Standardizing data collection to construct family-specific allometric models is difficult due to the variety of palm growth forms (arborescent, acaulescent, and climbing). We measured total stem height from the base of the stem to the base of the leaf crown (H_{bc}), whereas other studies (e.g., Goodman et al., 2013; Chave et al., 2014) measured total stem height from the ground to the highest point of the plant, which may include the last leaf, with or without stilt roots, if present. We measured AGB from the base of the stem to the apex of the meristem, excluding the cone of stilt roots; this cone is produced above the ground but we considered it part of the below-ground biomass. Similarly, in *A. martiana* a portion of the stem grows underground, but we considered it as part of AGB. Dioecious palms, such as *C. tepejilote*, may differ in biomass allocation between sexes, as demonstrated by Oyama and Dirzo (1988), although they harvested 15 individuals, including male and female plants, as well as juveniles. We found no differences in allometric patterns between male and female plants and juveniles. The study by Oyama and Dirzo (1988) was based on the follow-up of 810 individuals in a more comprehensive demographic study. In other cases, stem height is inferred from species descriptions rather than measured directly (de Castilho et al., 2006). Despite efforts to standardize functional trait measurements (e.g., Perez-Harguindeguy et al., 2013), the emphasis remains on woody plants, with little regard for the structural and morphological diversity of other plant groups such as palms.

Estimation of Root Biomass and Carbon Content

Estimating root biomass and carbon content remains a significant challenge in palm allometric analyses. Because the data is still fragmentary and often limited to a few individual species (e.g., Goodman et al., 2013; Da Silva et al., 2015), much of the information focuses on aerial biomass. In general, the functional ecology of roots is still poorly understood, particularly in terms of the integration of above- and below-ground characters. When resources are scarce, for example, leaf life span does not correlate with fine root longevity (Weemstra et al., 2016). Under these conditions, long-lived leaves are preferred, but fine roots, which are responsible for increasing surface area and absorption capacity, have a high turnover rate. Future research should examine the degree of integration between above-ground and below-ground functional traits (Laliberté, 2017). In our case, as in other studies attempting to estimate root biomass (e.g., Da Silva et al., 2015), obtaining all roots, particularly fine roots, was difficult. Many palm species have shallow roots, which may explain their dominance in flooded environments and very wet forests, which are rich in palm species or are dominated by one or two species, because shallow roots perform better in wet environments (Eiserhardt et al., 2011). There have been few studies estimating root biomass for palms in the tropics (Frangi and Lugo, 1985), so comparative data is scarce (but see Da Silva et al., 2015).

Conclusion

This is the only recent study, following Goodman et al. (2013), to propose a family-level model to estimate not only AGC but also total carbon content per individual for Arecaceae. We also provided individual models for seven of the most common and abundant palm species in tropical rainforests, as well as estimates of their below-ground biomass (**Appendix Table 1**). Allometric models can be very complex because they include a multitude of variables often related non-linearly. The goal of this study was to simplify the selection of allometric models by considering variables of practical importance and easy to measure in forest inventories, as well as to investigate the role of morphological variables on carbon storage without proposing complex variable combinations. The models proposed here had a logarithmic form, which is consistent with the functional relationship between diameter, stem height, and other palm size traits.

To improve the accuracy of allometric models in general, and specifically for palms, more species, a greater diversity of growth forms, a wider range of sizes, and a larger sample size are required. Palm species that dominate wetlands are still lacking in this regard; despite dominating carbon-rich environments, there are few studies that include them, possibly due to the logistical difficulties of conducting research in flooded environments. Finally, progress in estimating carbon content using allometric approaches, which remains a viable and efficient option for estimating carbon stocks, necessitates greater consistency in data collection across plant groups.

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

GA conceived and designed the experiments and wrote the manuscript. MC and CA-V conducted the fieldwork with assistance from GA. GA, MC, and CA-V analyzed the data and edited the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

This work was supported by a research grant from the International Palm Society to MC, and scholarships from the Organization for Tropical Studies (MC and CA-V), the University of Costa Rica (MC), and Tirimbina Biological Reserve (CA-V). The School for Field Studies provided logistic support.

ACKNOWLEDGMENTS

Orlando Vargas facilitated fieldwork at La Selva. Juan Manuel Ley facilitated fieldwork at Tirimbina. Nutrient analyses were facilitated by Floria Bertsch at the Centro de Investigaciones Agronómicas, University of Costa Rica, and by Steven Jansen at the Department of Systematic Botany and Ecology, University of Ulm. The Alpízar Chaves family of El Progreso facilitated work in their property.

REFERENCES

Achard, F., Eva, H. D., Mayaux, P., Stibig, H. J., and Belward, A. (2004). Improved estimates of net carbon emissions from land cover change in the tropics for the 1990's. *Global Biogeochem. Cycles* 18, 1–11. doi: 10.1029/2003GB002142

Araus, J. L., and Hogan, K. P. (1994). Leaf structure and patterns of photoinhibition in two neotropical palms in clearings and forest understory during the dry season. *Am. J. Bot.* 81, 726–738. doi: 10.1002/j.1537-2197.1994.tb15507.x

Ares, A., Boniche, J., Quesada, J. P., Yost, R., Molina, E., and Smyth, T. J. (2002). Estimación de biomasa por métodos alométricos, nutrimentos y carbón en plantaciones de palmito en Costa Rica. *Agronomía Costarricense* 26, 19–30.

Avalos, G., and Schneider, R. (2011). Quantification of ramet production in the neotropical palm Euterpe precatoria (Arecaceae) in Costa Rica. *Ecotropica* 17, 95–102.

Avalos, G. (2019). Shade tolerance within the context of the successional process in tropical rain forests. *Rev. Biol. Trop.* 67, 53–77. doi: 10.15517/rbt.v67i2supl.37206

Avalos, G., Gei, M., Ríos, L. D., Otárola, M. F., Cambronero, M., Alvarez-Vergnani, C., et al. (2019). Scaling of stem diameter and height allometry in 14 neotropical palm species of different forest strata. *Oecologia* 190, 757–767. doi: 10.1007/s00442-019-04452-7

Baker, W. J., and Dransfield, J. (2016). Beyond *Genera Palmarum*: progress and prospects in palm systematics. *Bot. J. Linn. Soc.* 182, 207–233. doi: 10.1111/boj.12401

Bello, C., Galetti, M., Pizo, M. A., Magnago, L. F. S., Rocha, M. F., Lima, R. A., et al. (2015). Defaunation affects carbon storage in tropical forests. *Sci. Adv.* 1:e1501105. doi: 10.1126/sciadv.1501105

Boukili, V. K., and Chazdon, R. L. (2017). Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. *Perspect. Plant Ecol. Evol. Syst.* 24, 37–47. doi: 10.1016/j.ppees.2016.11.003

Brando, P. M., Paolucci, L., Ummenhofer, C. C., Ordway, E. M., Hartmann, H., Cattau, M. E., et al. (2019). Droughts, wildfires, and forest carbon cycling: a pantropical synthesis. *Annu. Rev. Earth Planet Sci.* 47, 555–581. doi: 10.1146/annurev-earth-082517-010235

Brown, S. (1997). *Estimating Biomass and Biomass change of Tropical Forests: a primer. FAO Forestry Paper –134*. Rome: FAO.

Cambronero, M., Avalos, G., and Alvarez-Vergnani, C. (2018). Variation in the carbon fraction of seven neotropical palm species of different forest strata. *Palms* 62, 25–34.

Castillo-Mont, J. J., Gallardo, N. R., and Johnson, D. V. (1994). The pacaya palm (*Chamaedorea tepejilote*. Arecaceae) and its food use in Guatemala. *Econ. Bot.* 48, 68–75. doi: 10.1007/BF02901383

Chave, J., Andalo, C., Brown, S., Cairns, M. A., Chambers, J. Q., and Yamakura, T. (2005). Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145, 87–99. doi: 10.1007/s00442-005-0100-x

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M., Delitti, W., et al. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Change Biol.* 20, 3177–3190. doi: 10.1111/gcb.12629

Chazdon, R. L. (1986a). Light variation and carbon gain in rain forest understorey palms. *J. Ecol.* 74, 995–1012. doi: 10.2307/2260229

Chazdon, R. L. (1986b). Physiological and morphological basis of shade tolerance in rain forest understory palms. *Principes* 30, 92–99.

Chazdon, R. L. (1996). Spatial heterogeneity in tropical forest structure: canopy palms as landscape mosaics. *Trends Ecol. Evol.* 11, 8–9. doi: 10.1016/0169-5347(96)81057-3

Clark, D. B., and Clark, D. A. (2000). Landscape-scale variation in forest structure and biomass in a tropical rain forest. *For. Ecol. Manage.* 137, 185–198. doi: 10.1016/S0378-1127(99)00327-8

Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., and Ni, J. (2001). Measuring net primary production in forests: concepts and field methods. *Ecol. Appl.* 11, 356–370. doi: 10.1890/1051-07612001011

Curtis, P. S. (2008). "Estimating aboveground carbon in live and standing dead trees," in *Field measurements for Forest Carbon Monitoring, a Landscape-Scale Approach*, ed. C. M. Hoover (New York, NY: Springer). 39–44. doi: 10.1007/978-1-4020-8506-2_4

Da Silva, F., Suwa, R., Kajimoto, T., Ishizuka, M., Higuchi, N., and Kunert, N. (2015). Allometric equations for estimating biomass of *Euterpe precatoria*, the most abundant palm species in the Amazon. *Forests* 6, 450–463. doi: 10.3390/f6020450

Dargie, G. C., Lewis, S. L., Lawson, I. T., Mitchard, E. T., Page, S. E., Bocko, Y. E., et al. (2017). Age, extent and carbon storage of the central Congo Basin peatland complex. *Nature* 542, 86–90. doi: 10.1038/nature21048

Das, M., Nath, P. C., Sileshi, G. W., Pandey, R., Nath, A. J., and Das, A. K. (2021). Biomass models for estimating carbon storage in Areca palm plantations. *Environ. Sust. Indic.* 10:100115. doi: 10.1016/j.indic.2021.100115

de Castilho, C. V., Magnusson, W. E., de Araújo, R. N. O., Luizao, R. C., Luizao, F. J., Lima, A. P., et al. (2006). Variation in aboveground tree live biomass in a central Amazonian Forest: effects of soil and topography. *For. Ecol. Manage.* 234, 85–96. doi: 10.1016/j.foreco.2006.06.024

DeWalt, S. J., and Chave, J. (2004). Structure and biomass of four lowland Neotropical forests. *Biotropica* 36, 7–19. doi: 10.1111/j.1744-7429.2004.tb00291.x

Dewar, R. C. (1991). Analytical model of carbon storage in the trees, soils and wood products of managed forests. *Tree Physiol.* 8, 239–258. doi: 10.1111/j.1744-7429.2004.tb00291.x

Dewar, R. C., and Cannell, M. G. R. (1992). Carbon sequestration in the trees, products and soils of forest plantations using UK samples. *Tree Physioll.* 11, 49–71. doi: 10.1093/treephys/11.1.49

Dransfield, J., Uhl, N. W., Amussen, C. B., Baker, W. J., Harley, M. M., and Lewis, C. E. (2008). *Genera Palmarum: The Evolution and Classification of Palms*. Kew: Kew Publishing. 732.

Eiserhardt, W. L., Svenning, J. C., Kissling, W. D., and Balslev, H. (2011). Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Ann. Bot.* 108, 1391–1416. doi: 10.1093/aob/mcr146

Ekadinata, A. E., Khasanah, N., Rahayu, S., Budidarsono, S., and van Noordwijk, M. (2010). *Carbon Footprint of Indonesian Palm Oil Production: Sample Design and Methodology*. Nairobi: World Agroforestry Centre.

Feldpausch, T. R., Banin, L., Phillips, O. L., Baker, T. R., Lewis, S. L., Quesada, C. A., et al. (2011). Height-diameter allometry of tropical forest trees. *Biogeosciences* 8, 1081–1106. doi: 10.5194/bg-8-1081-2011

Frangi, J. L., and Lugo, A. E. (1985). Ecosystem dynamics of a subtropical floodplain forest. *Ecol. Monogr.* 55, 351–369. doi: 10.2307/1942582

Friedlingstein, P., O'Sullivan, M., Jones, M. W., Andrew, R. M., Hauck, J., Olsen, A., et al. (2020). Global carbon budget 2020. *Earth Syst. Sci. Data* 12, 3269–3340. doi: 10.5194/essd-12-3269-2020

James, G., Hastie, T., Tibshirani, R., and Witten, D. (2013). *An Introduction to Statistical Learning: With Applications in R*. Berlin: Springer. 431. doi: 10.1007/978-1-4614-7138-7

Goers, L., Ashton, M. S., and Tyrrell, M. L. (2012). "Introduction," in *Managing Forest Carbon in a Changing Climate*, eds M. S. Ashton, M. L. Tyrrell, D. Spalding, and B. Gentry (New York, NY: Springer) 1–4. doi: 10.1007/978-94-007-2232-3_1

Goodman, R., Phillips, O. L., Torres, D., Freitas, L., Tapia-Cortese, S., Monteagudo, A., et al. (2013). Amazon palm biomass and allometry. *For. Ecol. Manage.* 310, 994–1004. doi: 10.1016/j.foreco.2013.09.045

Grayum, M. H. (2003). "Arecaceae," in *Manual de Plantas de Costa Rica, Vol. III*, eds B. E. Hammel, M. H. Grayum, C. Herrera, and N. Zamora (St. Louis: Missouri Botanical Garden). 201–293.

Hairiah, K., Sitompul, S. M., van Noordwijk, M., and Palm, C. (2001). *Methods for Sampling Carbon Stocks Above and Below Ground*. Nairobi: International Centre for Research in Agroforestry.

Henderson, A. (1995). *The Palms of the Amazon*. New York: Oxford University Press. 374.

Henderson, A., Galeano, G., and Bernal, R. (1995). *Field Guide to the Palms of the Americas*. New York: Princeton University Press. 352.

Henderson, A. (2002). *Evolution and Ecology of Palms*. New York, NY: New York Botanical Garden. 259.

Houghton, R. A. (2007). Balancing the global carbon budget. *Ann. Rev. Earth Planet. Sci.* 35, 313–347. doi: 10.1146/annurev.earth.35.031306.140057

Howard, F. W., Moore, D., Giblin-Davis, R. M., and Abad, R. G. (2001). *Insects on Palms*. Wallingford: CABI Publishing. 131. doi: 10.1079/9780851993263.0000

Hughes, R. F., Kauffman, J. B., and Jaramillo, V. J. (1999). Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology* 80, 1892–1907. doi: 10.1890/0012-96581999080[1892:BCANDO]2.0.CO;2

Jones, D. L. (1995). *Palms throughout the World*. Washington DC: Smithsonian Institution Press. 410.

Jucker, T., Caspersen, J., Chave, J., Antin, C., Barbier, N., Bongers, F., et al. (2017). Allometric equations for integrating remote sensing imagery into forest monitoring programmes. *Glob. Change Biol.* 23, 177–190. doi: 10.1111/gcb.13388

Khasanah, N., van Noordwijk, M., Ekadinata, A., Dewi, S., Rahayu, S., Ningsih, H., et al. (2012). *The Carbon Footprint of Indonesian Palm Oil Production. (Technical Brief No 25: Palm oil series)*. Nairobi: World Agroforestry Centre - ICRAF.

Kissling, W. D., Balslev, H., Bake, R. W. J., Dransfield, J., Göldel, B., Lim, J. Y., et al. (2019). PalmTraits 1.0, a species-level functional trait database of palms worldwide. *Sci. Data* 6, 1–13. doi: 10.1038/s41597-019-0189-0

Lähteenoja, O., Ruokolainen, K., Schulman, L., and Oinonen, M. (2009). Amazonian peatlands: an ignored C sink and potential source. *Glob. Change Biol.* 15, 2311–2320. doi: 10.1111/j.1365-2486.2009.01920.x

Lal, R. (2008). Carbon sequestration. *Philos. Trans. R. Soc. B Biol. Sci.* 363, 815–830. doi: 10.1098/rstb.2007.2185

Laliberté, E. (2017). Below-ground frontiers in trait-based plant ecology. *New Phytol.* 213, 1597–1603. doi: 10.1111/nph.14247

Leblanc, H., Russo, R., Cueva, J. J., and Subía, E. (2006). Fijación de carbono en palma aceitera en la región tropical húmeda de Costa Rica. *Tierra Tropical* 2, 197–202.

Lima, A. J. N., Suwa, R., de Mello Ribeiro, G. H. P., Kajimoto, T., dos Santos, J., da Silva, R. P., et al. (2012). Allometric models for estimating above-and below-ground biomass in Amazonian forests at São Gabriel da Cachoeira in the upper Rio Negro, Brazil. *For. Ecol. Manage.* 277, 163–172. doi: 10.1016/j.foreco.2012.04.028

Lorenz, K., and Lal, R. (2010). *Carbon Sequestration in Forest Ecosystems*. Berlin: Springer. 279. doi: 10.1007/978-90-481-3266-9

McDade, L. A., Bawa, K. S., Hespenheide, H. A., and Hartshorn, G. S. (1994). *La Selva: Ecology and Natural History of a Neotropical Rainforest*. Chicago: University of Chicago Press. 493.

Mejia, K., and Kahn, F. (1990). Palm communities in wetland forest ecosystems of Peruvian Amazonia. *For. Ecol. Manage.* 3, 169–179. doi: 10.1016/0378-1127(90)90191-D

Montero, M., and Montagnini, F. (2005). Modelos alométricos para la estimación de biomasa de diez especies nativas en plantaciones en la región Atlántica de Costa Rica. *Recursos Naturales Ambiente* 45, 112–119.

Myers, R. L. (2013). Humedales dominados por palmas (Arecaceae) en el Neotrópico: Una introducción. *Rev. Biol. Trop.* 61, 5–24.

Nascimento, H. E., and Laurance, W. F. (2002). Total aboveground biomass in central Amazonian rainforests: a landscape-scale study. *For. Ecol. Manage.* 168, 311–321. doi: 10.1016/S0378-1127(01)00749-6

Onstein, R. E., Baker, W. J., Couvreur, T. L., Faurby, S., Svenning, J. C., and Kissling, W. D. (2017). Frugivory-related traits promote speciation of tropical palms. *Nat. Ecol. Evol.* 1, 1903–1911. doi: 10.1038/s41559-017-0348-7

Oyama, K., and Dirzo, R. (1988). Biomass allocation in the dioecious tropical palm *Chamaedorea tepejilote* and its life history consequences. *Plant Species Biol.* 3, 27–33. doi: 10.1111/j.1442-1984.1988.tb00168.x

Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., et al. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* 61, 167–234. doi: 10.1071/BT12225

Petchey, O. L., and Gaston, K. J. (2006). Functional diversity: back to basics and looking forward. *Ecol. Lett.* 9, 741–758. doi: 10.1111/j.1461-0248.2006.00924.x

Pulhin, F. B., Lasco, R. D., and Urquiola, J. P. (2014). Carbon sequestration potential of oil palm in Bohol. Philippines. *Ecosyst. Dev. J.* 4, 14–19.

R Core Team (2022). *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing*. Vienna: R Core Team.

Renninger, H. J., and Phillips, N. G. (2016). "Palm physiology and distribution in response to global environmental change," in *Tropical Tree Physiology*, eds G. Goldstein and L. S. Santiago (New York, NY: Springer). 67–101. doi: 10.1007/978-3-319-27422-5_4

Rich, P. M. (1986). Mechanical architecture of arborescent rain forest palms. *Principes* 30, 117–131.

Rich, P. M. (1987). Mechanical structure of the stem of arborescent palms. *Bot. Gazzette* 148, 42–50. doi: 10.1098/rsif.2012.0341

Rodríguez-Veiga, P., Quegan, S., Carreiras, J., Persson, H. J., Fransson, J. E., and Hoscilo, A. (2019). Forest biomass retrieval approaches from earth observation in different biomes. *Int. J. Appl. Earth Obs. Geoinf.* 77, 53–68. doi: 10.1016/j.jag.2018.12.008

Saatchi, S. S., Harris, N. L., Brown, S., Lefsky, M., Mitchard, E. T., Salas, W., et al. (2011). Benchmark map of forest carbon stocks in tropical regions across three continents. *Proc. Natl. Acad. Sci.U.S.A* 108, 9899–9904. doi: 10.1073/pnas.1019576108

Saldarriaga, J. G., West, D. C., Tharp, M. L., and Uhl, C. (1988). Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. *J. Ecol.* 76, 938–958. doi: 10.2307/2260625

Sampaio, M. B., Schmidt, I. B., and Figueiredo, I. B. (2008). Harvesting effects and population ecology of the buriti palm (*Mauritia flexuosa* L. f., Arecaceae) in the Jalapão Region, Central Brazil. *Econ. Bot.* 62, 171–181. doi: 10.1007/s12231-008-9017-8

Serrano-Sandí, J., Bonilla-Murillo, F., and Sasa, M. (2013). Distribución, superficie y área protegida de humedales dominados por pantanos de palmas (Arecaceae) en Costa Rica y Nicaragua. *Rev. Biol. Trop.* 61, 25–33.

Sprugel, D. G. (1983). Correcting for bias log-transformed allometric equations. *Ecology* 64, 209–210. doi: 10.2307/1937343

Syahrinudin. (2005). The potential of oil palm and forest plantations for carbon sequestration on degraded land in Indonesia. *Ecol. Dev. Series* 28, 1–9.

Sylvester, O., Avalos, G., and Chávez-Fernández, N. (2012). Notes on the ethnobotany of Costa Rica's palms. *Palms* 56, 190–201.

ter Steege, H., Pitman, N. C. A., Sabatier, D., Baraloto, C., Salomão, R. P., Guevara, J. E., et al. (2013). Hyperdominance in the Amazonian tree flora. *Science* 342, 325–342. doi: 10.1126/science.1243092

Thenkabail, P. S., Stucky, N., Griscom, B. W., Ashton, M. S., Diels, J., Van Der Meer, B., et al. (2004). Biomass estimations and carbon stock calculations in the oil palm plantations of African derived savannas using IKONOS data. *Int. J. Remote Sens.* 25, 5447–5472. doi: 10.1080/01431160412331291279

Tomlinson, P. B. (2006). The uniqueness of palms. *Bot. J. Linn Soc.* 151, 5–14. doi: 10.1111/j.1095-8339.2006.00520.x

Tomlinson, P. B. (2011). *The anatomy of palms*. New York, NY: Oxford University Press, 251. doi: 10.1093/acprof:osobl/9780199558926.001.0001

van der Hoek, Y., Álvarez Solas, S., and Peñuela, M. C. (2019). The palm *Mauritia flexuosa*, a keystone plant resource on multiple fronts. *Biodivers. Conserv.* 28, 539–551. doi: 10.1007/s10531-018-01686-4

Vasseur, F., Violle, C., Enquist, B. J., Granier, C., and Vile, D. (2012). A common genetic basis to the origin of the leaf economics spectrum and metabolic scaling allometry. *Ecol. Lett.* 15, 1149–1157. doi: 10.1111/j.1461-0248.2012.01839.x

Weemstra, M., Mommer, L., Visser, E. J., van Ruijven, J., Kuyper, T. W., Mohren, G. M., et al. (2016). Towards a multidimensional root trait framework: a tree root review. *New Phytol.* 211, 1159–1169. doi: 10.1111/nph.14003

Weiner, J. (2004). Allocation, plasticity and allometry in plants. *Perspect. Plant Ecol. Evol. Syst.* 6, 207–215. doi: 10.1078/1433-8319-00083

Yaap, B., Watson, H., and Laurance, W. F. (2015). Mammal use of *Raphia taedigera* palm stands in Costa Rica's Osa Peninsula. *Mammalia* 79, 357–362. doi: 10.1515/mammalia-2014-0033

Zahabu, E., Mugasha, W. A., Malimbwi, R. E., and Katani, J. Z. (2018). *Allometric Biomass and Volume Models for Coconut Trees*. Dar es Salaam: E&D Vision Publishing Ltd.

Zhang, X., Zhao, Y., Ashton, M. S., and Lee, X. (2012). "Measuring carbon in forests," in *Managing Forest Carbon in a Changing Climate*, eds M. S. Ashton,

M. L. Tyrrell, D. Spalding, and B. Gentry (Netherlands: Springer). 139–164. doi: 10.1007/978-94-007-2232-3_7

Zona, S., and Henderson, A. (1989). A review of animal-mediated seed dispersal of palms. *Selbyana* 11, 6–21.

Zuidema, P. A., and Boot, R. G. (2000). "Demographic constraints to sustainable palm heart extraction from a sub-canopy palm in Bolivia," in *Demography of Exploited Tree Species in the Bolivian Amazon*, ed. P. Zuidema (Riberalta: Utrecht Univ). 54–79.

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

APPENDIX

TABLE A1 | Summary of morphological variables of seven palm species harvested in the Caribbean lowlands of Costa Rica to obtain allometric models to estimate carbon content and above ground biomass.

Species (Abbreviation)	Stratum	Tribe[1]	N	DBH (cm)	H (m)	Tissue density (g/cm)	Total dry biomass (kg)	AGB (kg)	Number of leaves	Leaf area (m^2)	Dry weight leaves (kg)	Dry weight stem (kg)	Dry weight roots (kg)	Carbon in leaves (kg)	Carbon in stems (kg)	Carbon in roots (kg)	Total carbon per palm (kg)	Root:shoot (carbon)	Root:shoot (biomass)
Asterogyne martiana (AM)	Understory	Geonomateae	15	2.5 (1.53–3.88)	0.78 (0.28–1.66)	0.35 (0.26–0.51)	0.3 (0.02–0.63)	0.05 (0.005–0.12)	9 to 26	1.17 (0.13–3.04)	0.10 (0.0003–0.29)	0.16 (0.005–0.4)	0.03 (0.002–0.08)	0.04 (0.005–0.13)	0.07 (0.002–0.18)	0.01 (0.001–0.03)	0.3 (0.02–0.63)	0.16 (0.032–0.36)	0.6 (0.11–2.54)
Chamaedorea tepejilote (CT)	Understory	Chamaedorea	22	3.04 (1.27–5.09)	2.82 (0.55–6.72)	0.31 (0.14–0.6)	0.9 (0.05–2.93)	0.32 (0.01–1.2)	3 to 6	2.34 (0.22–4.65)	0.14 (0.02–0.34)	0.48 (0.01–2)	0.28 (0.006–1.14)	0.06 (0.02–0.15)	0.2 (0.006–0.89)	0.12 (0.003–0.51)	0.9 (0.04–2.93)	0.51 (0.10–2.54)	0.2 (0.03–0.76)
Prestoea decurrens (PD)	Understory	Euterpeae	10	6.74 (5.0–8.6)	6.31 (1.1–11.5)	0.34 (0.1–0.6)	9.16 (0.85–21.1)	2.88 (0.34–7.76)	5 to 12	8.8 (1.67–18.01)	3.8 (0.76–5.8)	11.34 (0.37–28.41)	5.57 (0.63–17.23)	1.64 (0.31–2.46)	4.92 (0.14–12.34)	2.6 (0.28–7.89)	9.15 (0.85–21.1)	0.40 (0.17–0.84)	0.38 (0.16–0.78)
Geonoma interrupta (GI)	Understory	Geonomateae	10	6.74 (5–8.6)	4.48 (0.69–11.62)	0.34 (0.16–0.48)	12.7 (0.4–54.51)	3.68 (0.2–14.53)	6 to 20	7.9 (1.58–25.04)	1.18 (0.14–5.16)	7.4 (0.23–32.68)	4.12 (0.02–19.64)	0.5 (0.06–2.21)	3.28 (0.08–14.66)	1.66 (0.01–6.66)	12.7 (0.4–54.51)	0.36 (0.07–0.56)	0.36 (0.07–0.56)
Euterpe precatoria (EP)	Subcanopy	Euterpeae	10	7.03 (3.5–12.8)	7.01 (2.2–12.6)	0.2 (0.15–0.26)	5.55 (0.36–27.14)	4.38 (0.33–14.75)	5 to 9	10.5 (2.6–28.66)	2.26 (0.57–10.1)	8.14 (0.08–42.97)	2.06 (0.08–7.89)	1.06 (0.26–4.78)	3.54 (0.03–18.75)	0.94 (0.03–3.59)	5.55 (0.36–27.14)	0.26 (0.02–1.28)	0.25 (0.02–1.24)
Iriartea deltoidea (ID)	Canopy	Iriarteeae	10	12.03 (4.4–23.6)	5.93 (1.0–11.5)	0.14 (0.08–0.2)	8.26 (0.22–28.46)	11.78 (0.24–39.17)	5 to 9	25.86 (2.63–79.66)	6.16 (0.34–20.92)	11.01 (0.07–41.94)	2.19 (0.07–8.82)	2.6 (0.14–9.0)	4.68 (0.02–17.84)	0.97 (0.03–3.84)	8.25 (0.22–28.46)	0.15 (0.02–0.36)	0.14 (0.01–0.31)
Socratea exorrhiza (SE)	Canopy	Iriarteeae	10	12.86 (2.4–20)	8.0 (1.4–14.8)	0.17 (0.09–0.38)	16.22 (0.09–58.06)	14.24 (0.11–34.64)	3 to 11	21.4 (1.28–53.31)	5.62 (0.08–15.96)	17.64 (0.02–63.19)	12.64 (0.11–49.16)	2.54 (0.04–7.25)	7.83 (0.008–28.62)	5.85 (0.05–22.92)	16.22 (0.09–58.06)	0.83 (0.31–1.9)	0.78 (0.31–1.7)

Values correspond to means (minimum-maximum values). [1] *Follows Dransfield et al. (2008).*

Advantages of publishing in Frontiers

OPEN ACCESS
Articles are free to read
for greatest visibility
and readership

FAST PUBLICATION
Around 90 days
from submission
to decision

HIGH QUALITY PEER-REVIEW
Rigorous, collaborative,
and constructive
peer-review

TRANSPARENT PEER-REVIEW
Editors and reviewers
acknowledged by name
on published articles

Frontiers
Avenue du Tribunal-Fédéral 34
1005 Lausanne | Switzerland

Visit us: www.frontiersin.org
Contact us: frontiersin.org/about/contact

REPRODUCIBILITY OF RESEARCH
Support open data
and methods to enhance
research reproducibility

DIGITAL PUBLISHING
Articles designed
for optimal readership
across devices

FOLLOW US
@frontiersin

IMPACT METRICS
Advanced article metrics
track visibility across
digital media

EXTENSIVE PROMOTION
Marketing
and promotion
of impactful research

LOOP RESEARCH NETWORK
Our network
increases your
article's readership