Worldwide Distribution of Antagonistic-Mutualistic Relationships Between Parrots and Palms

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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

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[1]https://wcsp.science.kew.org

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.

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,

[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/

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.

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 $\sigma_{parrot}/(\sigma_{parrot} + \sigma_{palm} + \sigma_{residual})$ and $\sigma_{palm}/(\sigma_{parrot} + \sigma_{palm} + \sigma_{residual})$, 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
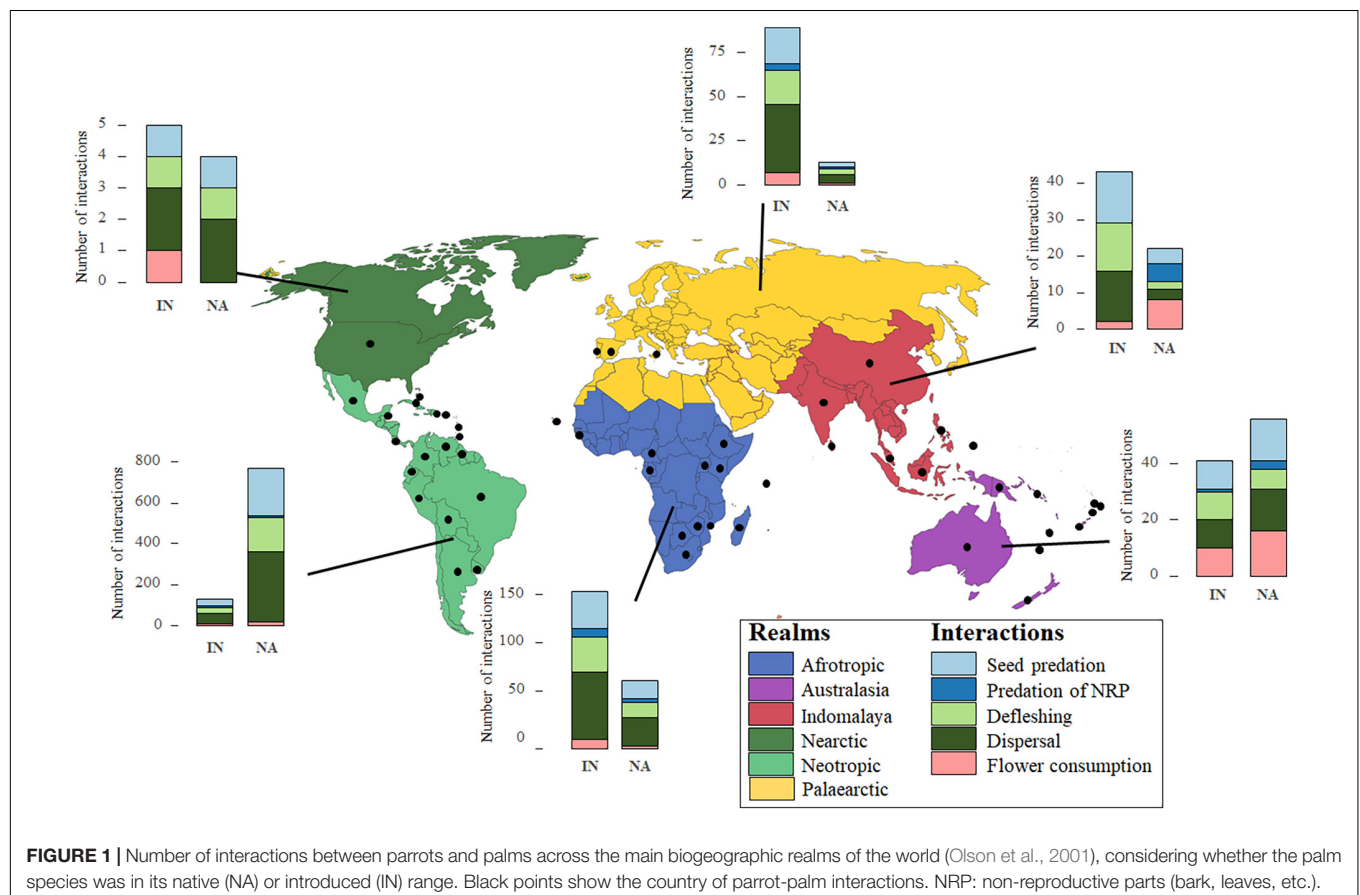
FIGURE 1 | Number of interactions between parrots and palms across the main biogeographic realms of the world (Olson et al., 2001), considering whether the palm species was in its native (NA) or introduced (IN) range. Black points show the country of parrot-palm interactions. NRP: non-reproductive parts (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**).

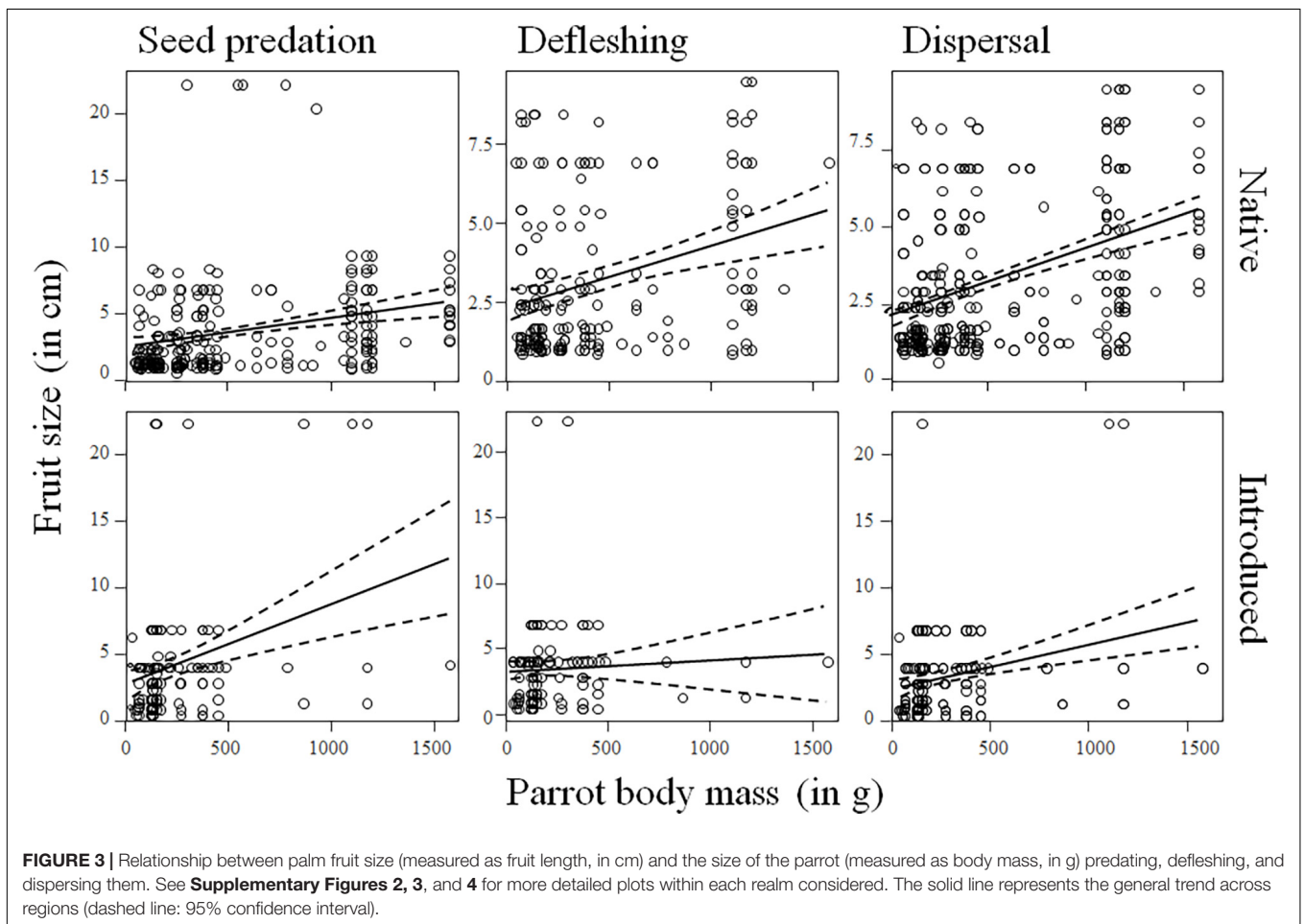## Seed Predation and Defleshing

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**).
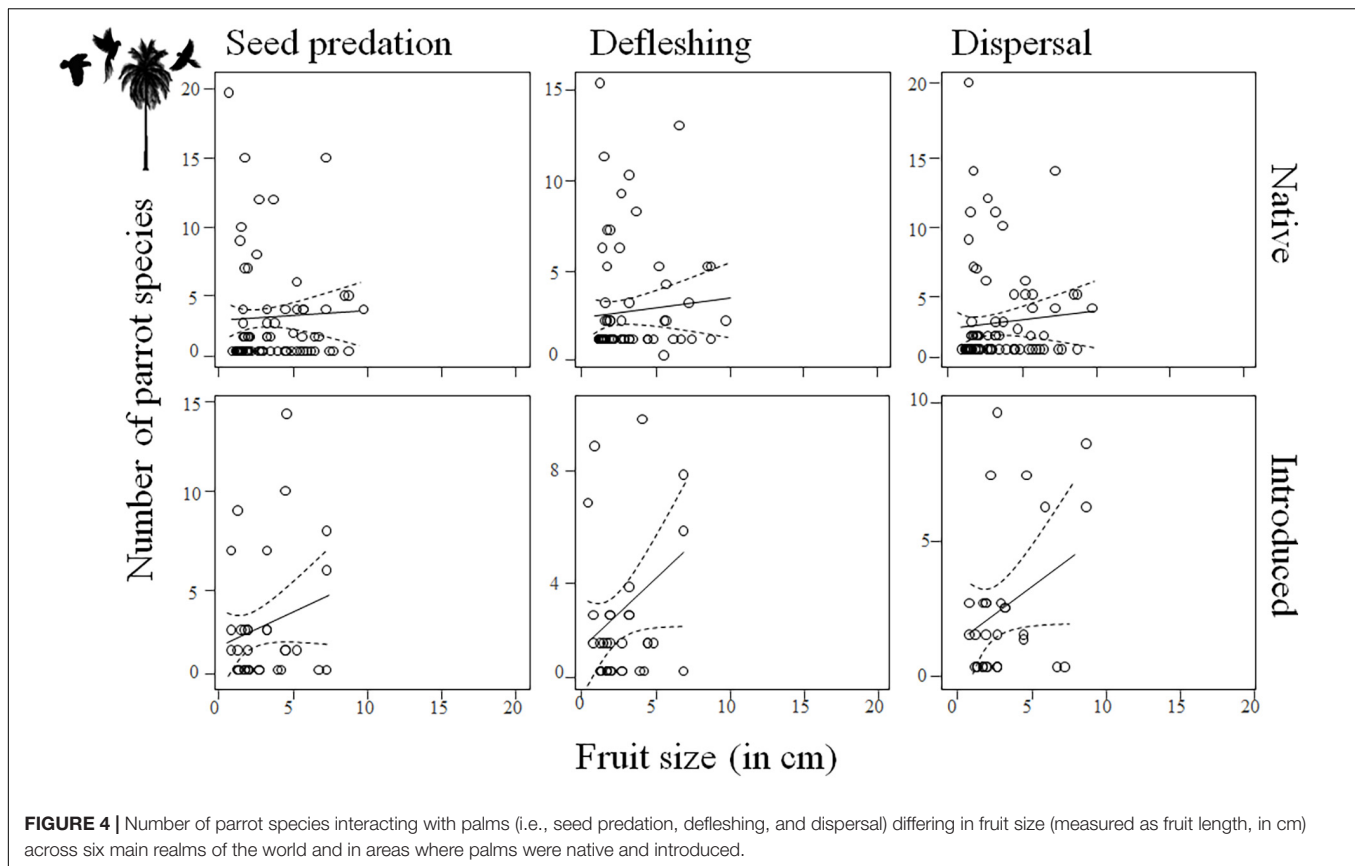
After controlling for phylogenetic relationships among species and differences among realms and for palms in their native and introduced ranges, we found a general positive relationship between palm fruit size and parrot body size (**Supplementary Tables 8, 9**), so that large-sized parrots predate and 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
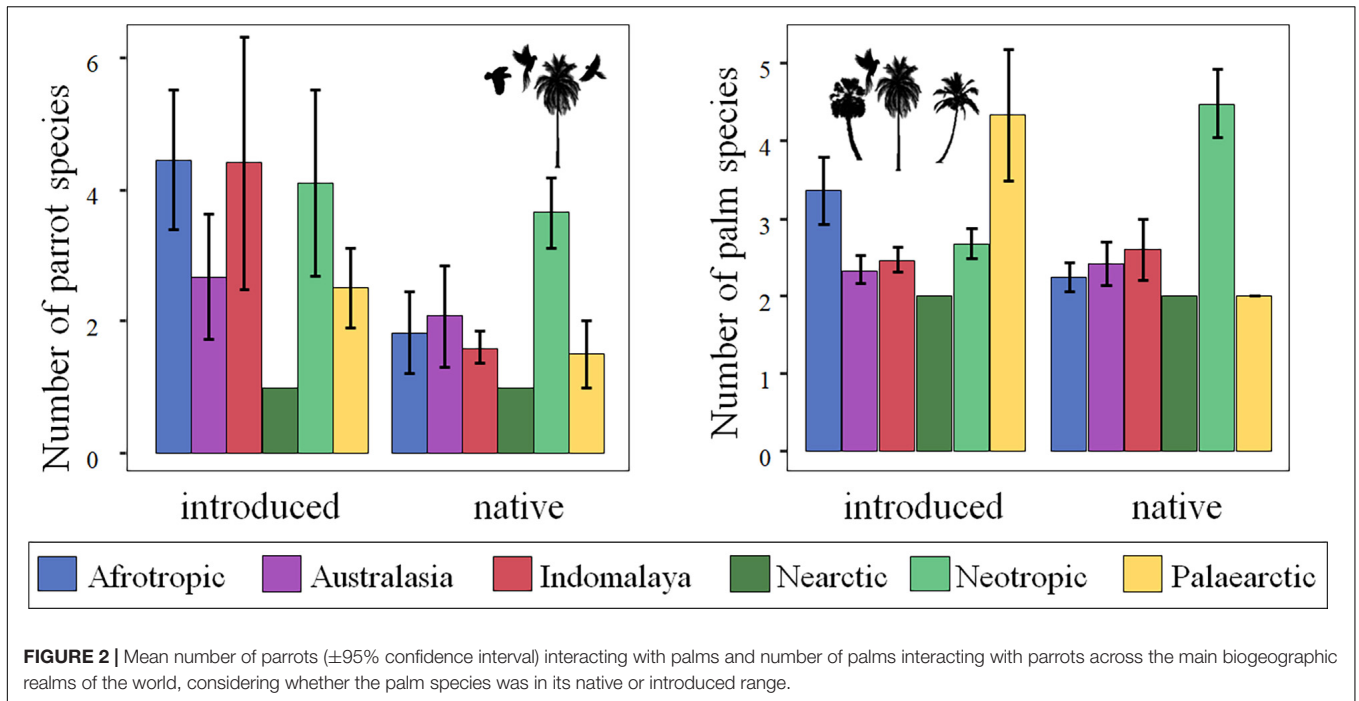
FIGURE 2 | Mean number of parrots (±95% confidence interval) interacting with palms and number of palms interacting with parrots across the main biogeographic realms of the world, considering whether the palm species was in its native or introduced range.

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**).
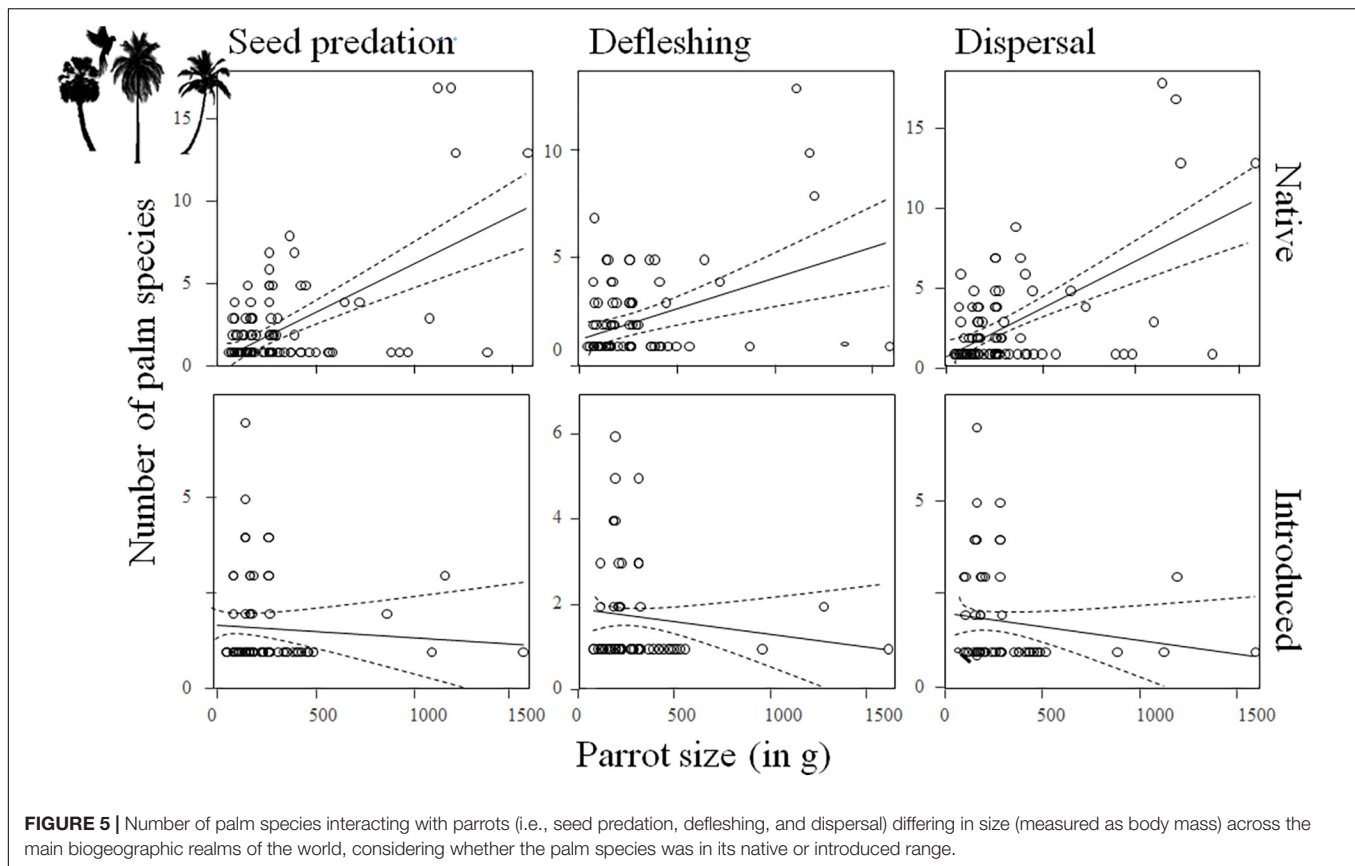
Dispersal

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),
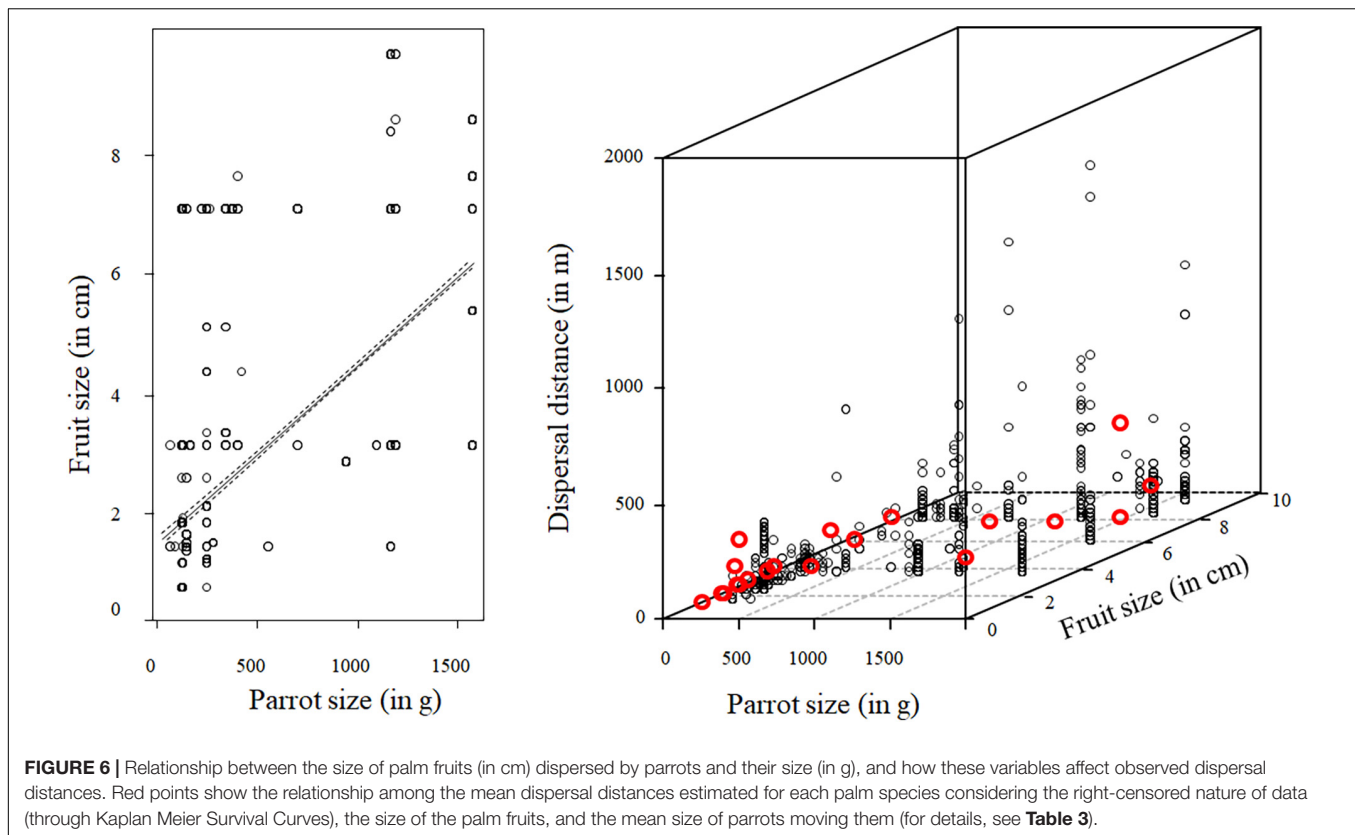
TABLE 3 | Median distances (and 95% credible intervals) at which parrots of different sizes (mean body mass ± SD of individuals dispersing each palm species; in g) can disperse different palm species varying in their fruit size (estimated as fruit length; in cm).

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*)
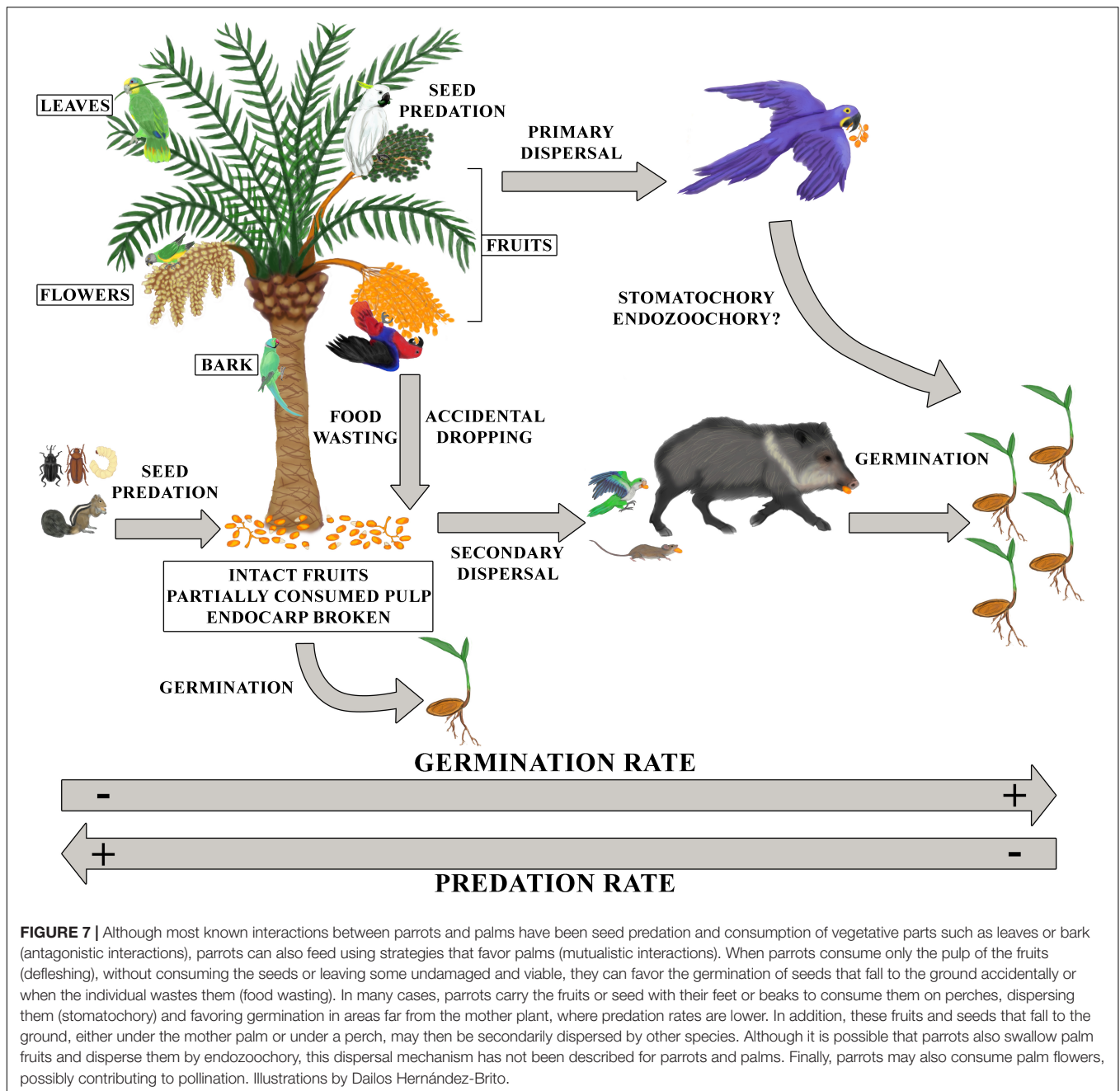
and 100% of the fruits (*Attalea barreirensis, Attalea eichleri,* and *Acrocomia aculeata*) (Tella et al., 2020; Silva et al., 2021). For smaller parrot species, these proportions are also highly variable (Sist and Puig, 1987). Moreover, parrots can accidentally or, as observed for this and other plant 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

AUTHOR CONTRIBUTIONS

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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

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