ORIGINAL ARTICLE

Geographic patterns in the diet of the Old World fruit bats: a review

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ABSTRACT

Fruit bats of the family Pteropodidae are distributed in Africa, Asia, and Oceania, including many Pacific islands. Although known as good seed dispersers, there is no broader assessment of the diversity of the diet of the genera (44 to 46 recognized genera) across different localities. We analyzed the frugivorous diet of the family Pteropodidae through an extensive bibliographical review, using consumption records to document bat-fruit relations across the Old World and variation among the biogeographic realms proposed by Holt et al. (2013). Our review resulted in 239 studies and 2.597 records of 33 bat genera consuming 642 species of 320 genera from 104 angiosperms families. The most consumed fruit genus was *Ficus*, in almost all zoogeographic realms. However, bat-fruit relationships vary among realms with numerous links to regionally endemic plant species, suggesting a relation between the bats' distribution and diversification of the associated flora. The genus *Pteropus* in particular, shows a strong geographic pattern in diet composition. Data of this nature help to visualize patterns in resource use among different regions of the globe and across diverse bat species assemblages and can direct further research on the evolution of pteropodid bats, their critical food resources, and their role in seed dispersal and ecosystem processes.

INTRODUCTION

Old World fruit bats are members of the family Pteropodidae, distributed throughout the tropical regions of Africa, Asia, and Oceania, including many Pacific islands, including some non-tropical localities of these continents (Simmons 2005, IUCN 2021). There are currently 197 recognized species in 44 to 46 recognized genera, six of which are considered extinct (Simmons 2005, Fenton & Simmons 2014, American Society of Mammalogists 2021). They are characterized by their often large size, but the family has species with forearm lengths ranging from 42 to 200 mm. The largest species are found in the genera commonly referred to as flying foxes: *Pteropus* Brisson, 1762 and *Acerodon* Jourdan, 1837 (Nowak 1999, Simmons 2005, Almeida et al. 2011). Many species of pteropodids are at some risk of extinction (*Pteropus* has 35 species considered threatened and six already extinct – see IUCN 2021) primarily related to loss of habitat, extermination to protect plantations, control of diseases, and hunting (Mickleburgh et al. 2002, Vincenot et al. 2017).

Based upon molecular-based phylogenies, the Pteropodidae, along with the other groups within Yinpterochiroptera, first appeared in Asia (broadly defined by Teeling et al. 2005), though other analyses (Almeida et al. 2011) suggest New Guinea and Melanesia and the Sunda shelf for the origin and diversification of modern families. Despite the scarce fossil evidence (Gunnell & Simmons 2005), phylogenetic analyses point to an explosive diversification of Chiroptera in the Eocene, separating Pteropodidae from other families approximately 52 to 50 million years ago (Teeling et al. 2005, Almeida et al. 2011, Nesi et al. 2021), following the great diversification of their angiosperm food resources (Davies et al. 2004). Nevertheless, radiation of the pteropodid crown-group began between 31 and 20 million years ago (Almeida et al. 2011), after the Eocene-Oligocene global cooling, as fruit resources became patchily distributed in space (Eriksson 2016). According to Eriksson (2016), this climate shift created a "flying frugivore niche" that favoured animals with great movement capacities such as passerines and bats, which could utilize an existing - but scattered - variety of zoochoric fruit, previously exploited by extinct arboreal mammals. Therefore, the ecological opportunities

(*sensu* Simpson 1953) involved in this radiation may be related to the extinction of competitive groups, demographic changes, or key innovations such as the diversification of body size and the emergence of phytophagous foraging habits, including frugivory and nectarivory (Yoder et al. 2010, Eriksson 2016, Nesi et al. 2021).

These plant-visiting bats are considered generalists, consuming fruits, nectar, pollen, and even leaves. They interact with many species of plants of importance to people (Marshall 1983, Fujita & Tuttle 1991). Their role in seed dispersal and pollination has both positive economic and ecological impacts, especially in promoting forest recovery through the increase of seed rain and seed banks or the dispersal of plants to recent oceanic islands, as was the case on Krakatau in Indonesia (Docters van Leeuwen 1935, Whittaker & Jones 1994, Muscarella & Fleming 2007).

The frugivorous diet of pteropodids is documented mainly by direct observations, seed collection, and ejecta pellets under the feeding roost (Voigt et al. 2009). In general, pteropodid diet studies are limited to consumption records of a particular species or some species at a given location (e.g. Banack 1998, Picot et al. 2007, Mahmood-Ul-Hassan et al. 2010, Andrianaivoarivelo et al. 2011, Sudhakaran & Doss 2012). A few articles present a more comprehensive assessment, assessing the diversity within the group and its broad geographic distribution (e.g. Fujita & Tuttle 1991). There is no broader assessment of the number of plant species or genera in the diet of the pteropodid bat genera across different localities or continental regions to elucidate possible preferred resources or seek patterns in bat-plant interactions.

We documented bat-plant consumption patterns across the various major biomes where pteropodids occur. We used Holt et al. (2013) as our geographic template, which includes an update of the six zoogeographic regions of Wallace, dividing the planet into 11 realms and 20 different zoogeographic regions. These maps were generated from distribution data and phylogenetic relationships of the world's amphibians, non-pelagic birds, and non-marine mammals (Holt et al. 2013).

We had three primary objectives in this study: 1) We examined the frugivorous diet of the Pteropodidae family through an extensive bibliographical review, creating a database to document the diversity of fruit consumption and geographic patterns in these bat-fruit interactions in the Old World, 2) We analyzed patterns of diet composition to elucidate changes in species composition throughout the range of the family Pteropodidae, and 3) We conducted a similar but focused analysis for the widely distributed and speciose genus *Pteropus* to determine if similar shifts in composition occurred within a single broadly distributed genus.

MATERIAL AND METHODS

The study consisted of a literature review and data compilation of fruit consumption by representatives of the family Pteropodidae throughout the geographic distribution of the family. We performed an exhaustive search through the 20th of January 2020 in Web of Science (http://apps.webofknowledge.com) with the following keywords and combinations: "bat", "Chiroptera", "diet", "flying fox", fruit", "frugivory", "frugivorous", "dispersal", "megabat", "Megachiroptera", "Old World fruit bat", "plant", "Pteropodidae", "preference", "seed" and "Yinpterochiroptera" (Supplementary Material 1). After this first round, all the listed references were analyzed to extract any data on pteropodid diets.

Records without any reference to the locality for the dietary record or to bat genus or species, captivity experiments, and duplicate information derived from compilations of primary data sources (i.e. review articles, or studies referring to data collected and published in other sources), were excluded. Secondary data were only used in a few cases if the cited study could not be located.

The spreadsheet was organized with the following metadata entries: bat (species and/or genus), fruit consumed (species, genus, and/or family), location and source. For the distribution of points by zoogeographic realms (Holt et al. 2013), the information of longitude and latitude of the consumption points were taken from the data source (when available) or Google Earth, based on information provided by the authors. Each entry of a plant species (genus or family when unknown species) accounted for one record, including direct observations, the analysis of stomach contents, analysis of faecal samples, and ejecta pellets. These methods may have some limitations due to the identification of different plant parts or solely liquids from fruit presence on the diet, for example. The large number of records in the database should minimize this bias.

The records were initially organized on the spreadsheet as cited in the sources, and the taxonomy was subsequently standardized according to Simmons (2005) for bats, except the genus *Desmalopex* Miller, 1907, which was maintained as published by the authors (Esselstyn et al. 2008). Given the varying age of the citations, we had to make several edits at the species level, but our records for *Melonycteris* were all *M. melanops* which was not subsequently assigned to *Nesonycteris*, and our citations on *Pteralopex* were all at the generic level. Plant species names were standardized based upon The Plant List (The Plant List 2013) for the plant species included in the spreadsheet. To add information on fruit distribution, all genera and species of plant were searched at Plants of the World Online (POWO 2019) and classified as "native", " introduced", and "unknown", depending on location. Some unclear points, such as a role continent or region, were classified as "introduced (probably)" or "native (probably)", depending on the case.

To analyze the data using the update published by Holt et al. (2013), we used the shapefiles provided by the authors (http://macroecology.ku.dk/resources/wallace) to assign the diet records to realms and to build the maps. Only data on the level of realms were included in maps and analysis.

We used two procedures to compare the composition of dietary fruit species/genera (records at the level of plant family were not included in this analysis) across zoogeographic realms: a standardized Principal Components

Analysis ordination (PCA) and a Flexible Beta cluster on the Sørensen (Bray-Curtis) distance measures. Based upon records, we included eight zoogeographic realms in the initial analysis: Saharo-Arabian, Afrotropical, Madagascan, Palearctic, Sino-Japanese, Oriental, Australian, and Oceanian. Upon inspection, all 14 Palearctic records were in Turkey, near the border with Syria, so these were classified as Saharo-Arabian for the Pteropodidae level analysis. In addition, the localities for Sino-Japanese were for islands between Japan and Taiwan and were pooled with the Oriental realm localities, resulting in six final realms (Afrotropical, Australian, Madagascan, Oceanian, Oriental, and Saharo-Arabian). For the analysis of only the genus *Pteropus*, there were no Palearctic localities. The only Afrotropical sites were for Pemba Island off the coast of Tanzania, and these few observations were grouped with Madagascar, which includes several other oceanic islands. As with the family Pteropodidae, Sino-Japanese sites were merged with the Oriental realm, as were a few localities assigned to Saharo-Arabian, but which were all in Pakistan near the border with India. This resulted in only four realms (Australian, Afro-Madagascan, Oceanian and Oriental) for the genus-level analysis.

The analysis was based upon a matrix of plant genera by realm; these data were input using Sørensen (Bray-Curtis) distance measures. An ordination was conducted using a standardized PCA. Standardization was used so that the results emphasized generic composition and not abundance since the genus *Ficus* often dominated abundance across all realms and, in a centred PCA, it tended to be biased toward more heavily studied sites. The output therefore provided information on the plant genera most commonly associated with the six or four realms, depending upon the comparison, both through inspection of the strength of association of genera with each realm on the graphical output and with the associated PCA scores of each plant genus. A randomization test was run on both PCA procedures to evaluate the statistical significance of the PCA solutions.

We also ran a Flexible Beta cluster analysis on the Sørensen (Bray-Curtis) distance measures (Faith et al. 1987) with Beta set to -0.025 to gain additional insights on the relationships among zoogeographic realms. Flexible Beta gives similar results to Ward's analysis but is compatible with Sørensen (Bray-Curtis) distance measures. The combined analysis of the PCA and the Cluster procedure generate insights on geographic patterns of diet. All analyses were run in PC-ORD Version 7 (Peck 2016). The program Quantum GIS was used to build the maps (QGIS Development Team 2015), using Holt et al. (2013) for the zoogeographic realms and IUCN (2014) for the distribution of bat species.

RESULTS

The literature review resulted in 239 studies and 2.597 records of fruit consumption by 33 bat genera, with the oldest record from Richardson (1839) and the most recent from Amponsah-Mensah et al. (2019). Altogether, we recorded 642 plant species of 320 genera from 104 botanical families. Of these records, 2.094 were identified to the species level, 491 only to genus, and the remainder (n=12) to family. A total of 93 bat species were documented with some record of fruit consumption, with 2.551 records identified to bat species and 46 only to genus. A listing of the bats, localities, realms, the number of records for each is presented in Supplementary Material 2 (Supplementary Material 3 is a list of the complete references of all the studies used).

The bat genera with the most records were *Pteropus* (n=1.419) with 35 species, *Cynopterus* (n=355) with four species, and *Rousettus* (n=261) with five species, with the genus *Pteropus* responsible for over half of all records (54,6%). The genera of fruit consumed by bats varied by genus of bat and by zoogeographic realm (Table 1). The plant genera most consumed by bats were *Ficus* (n=561 records of 95 fig species), followed by *Syzygium* (n=117 records of 35 species) and *Psidium* (n=105 records of two species). Analyzing the data by bat genera, the pattern repeats, with *Ficus* being the fruit with the largest number of records (Table 1). Only the genera *Macroglossus*, *Syconycteris* (both in the nectar-feeding subfamily Macroglossinae), *Dobsonia*, *Harpyionycteris* (Harpyionycterinae), *Eonycteris* (Rousettinae), *Lissonycteris* (Myonycterini), *Megaerops* (Cynopterinae), and *Nanonycteris* (Epomophorinae) did not show this pattern. However, all of these genera had a very small number of records. In general, the genus *Ficus* was also the most recorded in almost all the realms, representing 18,11% of all records from Afrotropical (n=79), 21,13% from Australian (n=71), 18,35% from Madagascan (n=47), 14,25% from Oceanian (n=68), 27,04% from Oriental (n=245), 27,69% from Saharo-Arabian (n=36), 28,26% from Sino-Japanese (n=13). The only exception was the Palearctic realm, with most of the records (21,42%) for *Prunus* (n=3) and only two for *Ficus*. However, there were only 14 records for this realm across 11 genera and only one species of bat (*Rousettus aegyptiacus*). We compiled records by zoogeographic realm and the number of consumed fruit genera and species consumed according to Holt et al. (2013) (Table 2).

When we observe the data on the origin of these plants, it is clear that the majority of all records are from native plants, with realms like Australian (n=244), Madagascan (n=181), Oriental (n=703), Palearctic (n=10), and Sino-Japanese (n=40) with more than 70% of the total records for native genera (Table 2). The same scenario appears for the species consumed: only 13,46% from the species consumed on the Afrotropical realm are introduced (n=14), 8,8% of Australian (n=11), 12,59% of Madagascan (n=17), 15,9% of Oceanian (n=21), 18,93% of Oriental (n=46), 20% of Saharo-Arabian (n=10) and 14,28% of Sino-Japanese (n=4). Palearctic had two introduced species (22,2%), but this realm had only nine species consumed (Table 2). The "unknown" status varied among realms, so the real number of native and introduced plants could change. In the case of the Oceanian and Oriental realms, most unknown records relate to the lack of information on the distribution of plants in many small Pacific islands (Table 2).

We mapped the distribution of the bat family and the consumption records used in the study (Fig. 1). By using a standardized PCA approach, we isolated differences in species composition of the diet without weighting these by abundance; however, we presented that information in
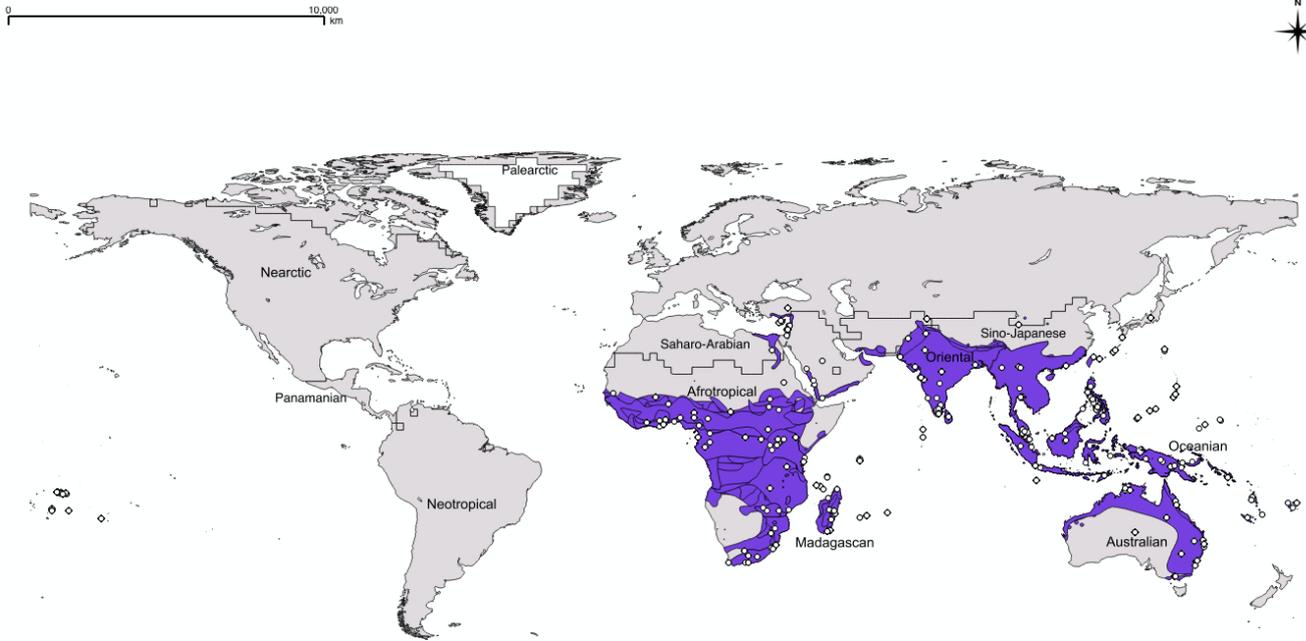
Fig. 1 - Old World fruit bat distribution (purple) and the localities with diet records found in this study (white circles). Zoogeographic realms, according to Holt et al. (2013).
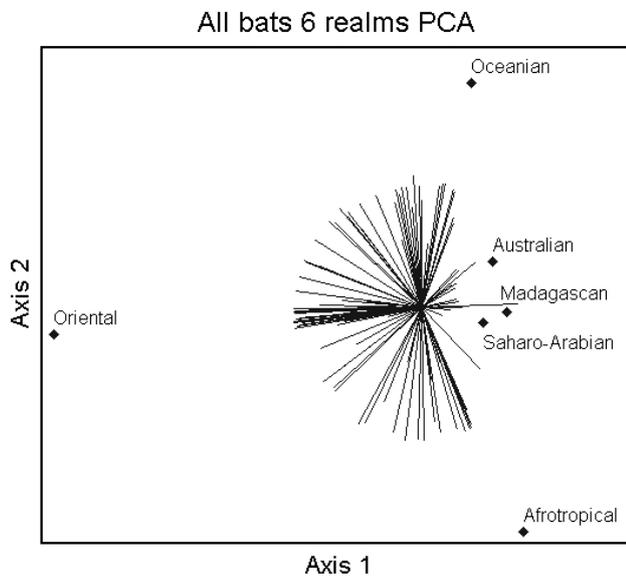

Fig. 2 - Ordination analysis using a standardized PCA of the realms by fruits present within the diet of Pteropodidae. Lines represent the scores of species and the strength of their association with the four quadrants of the PCA.

a separate table (Table 1). The PCA for all members of the Pteropodidae across six realms and the randomization test suggested interpretation beyond the first two axes was not necessary (Table 3). The results of the PCA for all bats across six realms reveal broad dispersion of zoogeographic realms based upon fruit consumption records, albeit with some realms showing many strongly associated plant genera (Fig. 2). Examination of the loadings of the genera on the PCA axes reveals associations among certain fruit genera and the zoogeographic realms (Supplementary Material 4). The Afrotropical realm is dominated by species typical of the Central African rainforests and shrublands (e.g. *Adansonia*, *Musanga*, *Sclerocarya*, *Sterculia*, *Trichilia*). Mediterranean species like *Arbutus* and *Ceratonia* are typical of the Saharo-Arabian realm. The Madagascan is also highly distinctive and dominated by regional and Malagasy endemics (e.g. *Anthocleista*, *Brexia*, *Bakerella*, *Canephora*, *Fenerivia*, and *Sarcolaena*). The Oriental and Oceanian realms are along an almost horseshoe gradient dominated by a very high richness of a more tropical selection of fruit genera with a strong separation along Axis 1 (Fig. 2). These two realms are in close geographic proximity in the middle of the gradient, suggesting a clinal variation in dominant species in the diet composition across the two regions.

The cluster analysis (Fig. 3) shows a strong similarity between the Oceanian and the Australian realms, suggesting a more similar diet composition across these two realms with many shared species of bats and genera of plants. The other branch of this cluster of tropical regions includes the Afrotropical realm, though less strongly clustered than Oceanian and Australian realms. The Madagascar, Oriental, and Saharo-Arabian realms are outliers and weakly related to the other realms.

Table 1 - The most consumed fruit genera per pteropodid and zoogeographic realms. Up to three fruit genera with the major number of records are represented, followed by its record number (n). Ngen= number of fruit genera; Nrec= total number of records.

Bat genera	Ngen	Nrec	Most common fruit genera	Realms
Acerodon Jourdan, 1837	2	10	*Ficus* (n=9); *Nauclea* (n=1)	Oriental
Aproteles Menzies, 1977	1	2	*Ficus* (n=2)	Oceanian
Balionycteris Matschie, 1899	15	24	*Ficus* (n=6); *Fragraea* (n=2); *Nauclea* (n=2)	Oriental
Chironax K. Andersen, 1912	5	9	*Ficus* (n=5); *Adinandra* (n=1); *Diospyros* (n=1)	Oriental
Cynopterus F. Cuvier, 1824	90	355	*Ficus* (n=83); *Psidium* (n=17); *Syzygium* (n=14)	Oriental
Desmalopex Miller, 1907	3	3	*Ficus* (n=1); Melastomataceae (n=1); *Musa* (n=1)	Oriental
Dobsonia Palmer, 1898	14	23	*Ficus* (n=6); *Carica* (n=3); *Musa* (n=3)	Australian (*Ficus*, n=1); Oceanian (*Ficus*, n=4; *Carica*, n=3; *Musa*, n=3); Oriental (*Areca*, n=1; *Borassus*, n=1; *Ficus*, n=1)
Dyacopterus K. Andersen, 1912	3	6	*Ficus* (n=4); *Elaeocarpus* (n=1); *Prunus* (n=1)	Oriental
Eidolon Rafinesque, 1815	54	142	*Ficus* (n=24); *Psidium* (n=10); *Mangifera* (n=8)	Afrotropical (*Ficus*, n=15; *Mangifera*, n=8; *Musa*, n=7); Madagascan (*Ficus*, n=8; *Solanum*, n=2); Saharo-Arabian (*Ficus*, n=1; *Phoenix*, n=1)
Eonycteris Dobson, 1873	1	1	*Palaquium* (n=1)	Oriental
Epomophorus Bennett, 1835	50	150	*Ficus* (n=29); *Mangifera* (n=10); *Musa* (n=7)	Afrotropical (*Ficus*, n=28; *Mangifera*, n=10; *Musa*, n=7); Saharo-Arabian (*Ficus*, n=1)
Epomops Gray, 1870	19	37	*Ficus* (n=7); *Solanum* (n=5); *Musa* (n=4)	Afrotropical
Haplonycteris Lawrence, 1939	1	2	*Ficus* (n=2)	Oriental
Harpyionycteris Thomas, 1896	2	2	*Ficus* (n=1); *Freycinetia* (n=1)	Oriental
Hypsignathus H. Allen, 1861	10	24	*Ficus* (n=5); *Anthocleista* (n=3); *Mangifera* (n=3)	Afrotropical
Latidens Thonglongya, 1972	4	11	*Ficus* (n=6); *Elaeocarpus* (n=2); *Prunus* (n=2)	Oriental
Lissonycteris K. Andersen, 1912	8	12	*Ficus* (n=3); *Solanum* (n=3); *Adenia* (n=1)	Afrotropical
Macroglossus F. Cuvier, 1824	1	1	*Eugenia* (n=1)	Oceanian
Megaerops Peters, 1865	5	7	*Ficus* (n=2); *Palaquium* (n=2); *Elaeocarpus* (n=1)	Oriental
Melonycteris Dobson, 1877	1	2	*Ficus* (n=2)	Oceanian
Micropteropus Matschie, 1899	10	21	*Ficus* (n=6); *Annona* (n=3); *Psidium* (n=3)	Afrotropical
Myonycteris Matschie, 1899	4	7	*Solanum* (n=3); *Adenia* (n=2); *Ficus* (n=1)	Afrotropical
Nanonycteris Matschie, 1899	4	4	*Carica* (n=1); *Ficus* (n=1); *Milicia* (n=1)	Afrotropical
Nyctimene Borkhausen, 1797	5	14	*Ficus* (n=7); *Atractocarpus* (n=2); *Psidium* (n=2)	Australian (*Ficus*, n=4; *Atractocarpus*, n=2; *Psidium*, n=2); Oceanian (*Ficus*, n=3; *Gymnostoma*, n=1)

Table 1 - continuation: The most consumed fruit genera per pteropodid and zoogeographic realms. Up to three fruit genera with the major number of records are represented, followed by its record number (n). Ngen= number of fruit genera; Nrec= total number of records.

Bat genera	Ngen	Nrec	Most common fruit genera	Realms
Otopteropus Kock, 1969	1	1	*Ficus* (n=1)	Oriental
Paranyctimene Tate, 1942	2	2	*Ficus* (n=1); *Piper* (n=1)	Oceanian
Ptenochirus Peters, 1861	9	19	*Ficus* (n=11); *Bischofia* (n=1); *Ceiba* (n=1)	Oriental
Pteralopex Thomas, 1888	13	16	*Ficus* (n=3); *Canarium* (n=2); *Annona* (n=1)	Oceanian
Pteropus Brisson, 1762	234	1419	*Ficus* (n=264); *Syzygium* (n=81); *Terminalia* (n=54)	Afrotropical (*Ficus*, n=6; *Artocarpus*, n=3; *Syzygium*, n=2); Australian (*Ficus*, n=64; *Syzygium*, n=24; *Citrus*, n=11); Madagascan (*Ficus*, n=28; *Psidium*, n=12; *Mangifera*, n=11); Oceanian (*Ficus*, n=52; *Artocarpus*, n=30; *Syzygium*, n=25); Oriental (*Ficus*, n=88; *Syzygium*, n=19; *Psidium*, n=16); Saharo-Arabian (*Ficus*, n=13; *Diospyros*, n=5; *Psidium*, n=3); Sino-Japanese (*Ficus*, n=13; *Morus*, n=3; *Musa*, n=3)
Rousettus Gray, 1821	65	261	*Ficus* (n=65); *Phoenix* (n=11); *Eriobotrya* (n=10)	Afrotropical (*Ficus*, n=6; *Eriobotrya*, n=4; *Diospyros*, n=3); Madagascan (*Ficus*, n=11; *Carica*, n=1; *Musa*, n=1); Oceanian (*Ficus*, n=1); Oriental (*Ficus*, n=24; *Psidium*, n=8; *Syzygium*, n=7); Palearctic (*Prunus*, n=3; *Ficus*, n=2; *Diospyros*, n=1); Saharo-Arabian (*Ficus*, n=21; *Ceratonia*, n=8; *Melia*, n=7)
Scotonycteris Matschie, 1894	2	3	*Solanum* (n=2); *Ficus* (n=1)	Afrotropical
Syconycteris Matschie, 1899	3	6	*Ficus* (n=2); *Piper* (n=1); Solanaceae (n=1)	Australian (*Ficus*, n=2; *Piper*, n=1); Oceanian (Moraceae, n=1; Piperaceae, n=1; Solanaceae, n=1)
Thoopterus Matschie, 1899	1	1	*Ficus* (n=1)	Oriental

Table 2 - Number of recorded feeding events, different fruit genera and species consumed by pteropodids in each zoogeographic realm (Holt et al. 2013), and its distribution status (native, introduced or unknown - POWO 2019). N= native; I= introduced; U= unknown.

| Zoogeographic Realm	Rec	Gen	Spe	Genera distribution	Genera distribution (records)	Species distribution	Species distribution (records)
Afrotropical	436	83	104	I=12; N=63; U=16	I=62; N=293; U=81	I=14; N=70; U=26	I=57; N=173; U=75
Australian	332	85	125	I=10; N=60; U=21	I=31; N=244; U=57	I=11; N=87; U=30	I=18; N=173; U=49
Madagascan	256	87	135	I=14; N=67; U=15	I=37; N=181; U=36	I=15; N=117; U=9	I=34; N=158; U=26
Oceanian	477	92	132	I=18; N=58; U=57	I=70; N=234; U=168	I=21; N=83; U=70	I=67; N=185; U=142
Oriental	906	139	243	I=23; N=107; U=42	I=104; N=703; U=99	I=46; N=158; U=77	I=161; N=392; U=217
Palearctic	14	11	9	I=1; N=7; U=3	I=1; N=10; U=3	I=2; N=3; U=4	I=2; N=3; U=4
Saharo-Arabian	130	37	50	I=8; N=15; U=20	I=24; N=68; U=38	I=10; N=12; U=34	I=21; N=37; U=59
Sino-Japanese	46	22	28	I=1; N=17; U=4	I=1; N=40; U=5	I=4; N=16; U=8	I=6; N=24; U=11
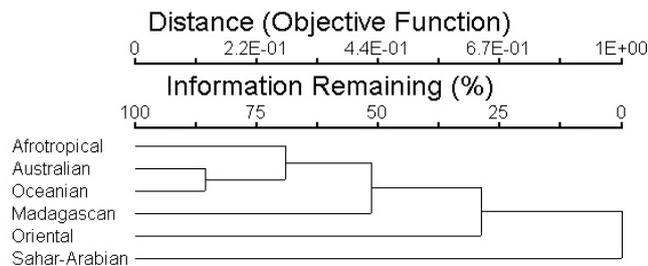
Fig. 3 - Cluster analysis for the family Pteropodidae based upon the Sørenson distance measure.
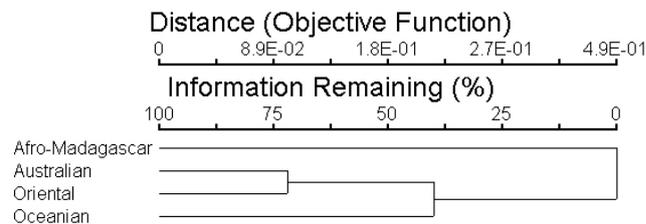

Fig. 5 - Cluster analysis for the genus *Pteropus* based upon the Sørenson distance measure.
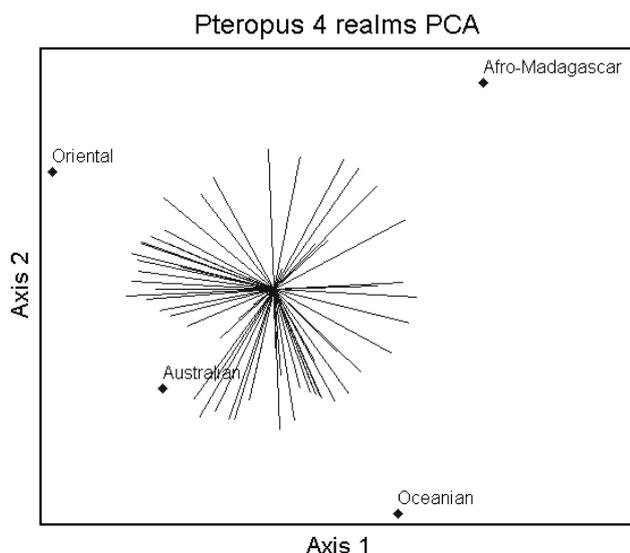

Fig. 4 - Ordination analysis using standardized PCA of realms by fruit present in the diet of the genus *Pteropus*. Lines represent the scores of species and the strength of their association with the four quadrants of the PCA.

Table 3 - Results of the standardized Principal Components Analysis for the family Pteropodidae and the genus *Pteropus*. Broken stick projections for useful axes for Pteropodidae were five, or only two for observed eigenvalue compared to the average randomized eigenvalue. For *Pteropus* the broken stick projection was three axes, but zero for observed eigenvalue compared to the average randomized eigenvalue. Projection on two axes shows patterns very clearly.

Pteropodidae and Six Realms			
Axis	Eigenvalue	% Variance	Cum. % Variance
1	107.50	33.70	33.70
2	69.02	21.64	55.34
3	58.07	18.20	73.54
4	45.62	17.44	90.98
Pteropus and Four Realms			
1	81.91	34.71	34.71
2	80.61	34.16	68.86
3	73.47	31.13	100.00

There are similar results for the genus *Pteropus* (Figs. 4 & 5), with marked differences in diet composition among realms. The resultant PCA and randomization tests support the interpretation of from zero to three axes (Table 3), but the results are plotted in two dimensions for ease of interpretation. Differences among realms are less distinctive in PCA space, and the first three axes all account for approximately the same amount of variance explained. The Oriental and Oceanian realms show some clustering of species more strongly associated with these realms, but on opposite poles of Axis 2 in diet composition across the geographical distance of the two realms. A cluster of Australian endemics is associated with Australia (Supplementary Material 5), with species with high negative scores on both Axis 1 and 2. The cluster analysis (Fig. 5) shows a strong association between Australian and the Oriental, with Oceanian more distantly associated with that cluster. Afro-Madagascan is highly distinctive in fruits consumed by *Pteropus*, similar to the results for all Pteropodidae.

DISCUSSION

Our analysis of the frugivorous diet of bats of the family Pteropodidae throughout their distribution revealed a large number of fruit taxa in the diet, but also a consistent consumption of *Ficus* fruits by the majority of bat species across all zoogeographic realms. Nevertheless, there are clear differences among the realms in bat-fruit relationships, evidencing associations with vegetation ecoregions and bat's distribution.

The literature review resulted in data on the frugivorous diet for 33 of more than 40 genera of Pteropodidae (Simmons 2005, Almeida et al. 2011). The genus with the highest number of consumption records was *Pteropus*, corresponding to more than 50% of all records. This genus has the largest number of species – approximately 63 – which are widely distributed across the Oceanian realm and the Pacific islands (Simmons 2005, American Society of Mammalogists 2021). *Cynopterus* and *Rousettus* are the genera with the next most records, with the former restricted to the Oriental realm and the latter with records in all the Old World realms except for the Australian and Sino-Japanese. The genera *Eonycteris*, *Macroglossus*, *Melonycteris*, and *Syconycteris* are morphologically adapted to nectarivory (Fleming et al. 2009), but although nectar is their main food resource, they can also feed on fruits, such as *Ficus*, *Piper*, and *Eugenia* (e.g. Law 2001, Shanahan et al. 2001, Bumrungsri et al. 2013). Several of the genera have few records of consumption, with

few published studies on the frugivorous fraction of their diet, for example, *Thoopterus*, endemic to Sulawesi (Oriental realm), for which only one record of fruit consumption was found (Mickleburgh et al. 1992).

We found consumption records of 320 genera of plants within 104 botanical families. Pteropodids are recognized as generalists, consuming a diversity of fruits, nectar, and pollen (Marshall 1985), attributed to lower predictability in resource availability and sparse distribution of these resources in the Old World (Dumont 2003). Marshall (1983) treats pteropodids as "sequential specialists" since they select a range of fruits among those available. Our data shows that the majority of fruit consumption is of native fruits, approximately 75% (excluding the "unknown" records) which corroborates with Andrianaivoarivelo et al. (2012), who states that fruit bats prefer native fruits when available.

Even though there are also records of consumption of cultivated species (e.g. *Anacardium*, *Carica*, *Mangifera*, *Morus*, *Musa*, *Psidium*, and *Solanum*) - which could reinforce their notoriety as a crop pest (Srinivasulu & Srinivasulu 2002, Vincenot et al. 2017 but see Korine et al. 1999) - the number of observations of identifiably introduced fruits in the diet was small overall (approximately 16% of the records). *Mangifera*, for example, had only 48 records of consumption that were likely from introduced localities, besides being native in some of the realms. The numbers for *Psidium* (n=44) and *Carica* (n=28) were also small. This data shows that even though frugivorous pteropodids are generalists, they consume more native than introduced fruits.

Our data show many fruit genera with few records in the diet and only a few highly utilized genera, both by a genus of bat and a zoogeographic realm, especially highlighting the genus *Ficus*. Figs have a big-bang fruiting strategy and also are intraspecifically asynchronous (fruit production is short and abundant within an individual tree but not within a species; Gentry 1974), serving as a food resource of great importance for several groups of vertebrates, particularly mammals and birds (Shanahan et al. 2001) both in the New and Old World. Our data found 78 pteropodid species in 31 genera feeding on figs. This consistent diet pattern is even more pronounced than that observed for the somewhat more generalist Neotropical bat species, where the so-called "preferential" fruit varies among bat genera (Parolin et al. 2016). However, Kalko et al. (1996) predicted that Old World fruit bats might include different fig sizes in their diets, regardless of their size (bat or fig), because of their foraging behaviour, which could be the case, as we recorded almost 100 fig species of their diet. This is certainly a fruitful area for further research. Patterns of use of space by pteropodids may be determined by the availability of *Ficus* fruits, driving ecological interactions based upon this important food supply and the high quantity of fruits available during fruiting (Dumont 2003). This heavy dependence on *Ficus* possibly contributed to the colonization of oceanic islands by *Ficus* many miles from the continent through the dispersal of seeds carried by bat vectors (Whittaker & Jones 1994, Bush et al. 1995, Thornton et al. 1996, 2001, Dumont 2003). These pioneer figs acted as "evolutionary catalysts", facilitating the

establishment of later successional plants (Fleming & Kress 2013) and, with that, new animal-plant relations.

This result of fig dominance in bat diets could be taken as a bias due to the small seed size and the ease in swallowing and subsequently passing these seeds in faeces, increasing the likelihood of identification in the diet mainly on faecal analysis. However, Pteropodids have small guts and rapid seed passage times (e.g. Utzurrum & Heideman 1991, Hodgkison et al. 2003), so if the amount of consumption of *Ficus* was low, faecal samples would not reveal this accentuated importance of figs for these bats.

Updated zoogeographic realms vs bat diet

We created an extensive database of the diet of pteropodid bats across their entire distribution to make available to the research community for future studies on these bats. In addition, we generated preliminary analyses to see if diet composition varied in accordance with zoogeographic realms (Holt et al. 2013) for the family Pteropodidae as a whole, as well as for the diverse and abundant genus *Pteropus*. We used the zoogeographic realms proposed by Holt et al. (2013) to look for biogeographic patterns in fruit consumption by Old World bats. We modified the apportionment of a number of cases by looking at specific localities of observations and reduced the number of realms accordingly.

Factors that determine the distribution of an animal or plant group include geological history, climate, food resource availability, chemical environmental factors, and competition (e.g. Cox & Moore 2009). Various authors argue that the distribution pattern of plants in the southern hemisphere is better explained by events of extinction and dispersion than by the breakdown of the Gondwana continent itself (Sanmartín & Ronquist 2004) and that oceanic dispersion has a greater influence on the current distribution of taxa than vicariance (de Queiroz 2005). To explain the differences in the plants consumed by pteropodids throughout their range, one must first consider the configuration of the planet at the beginning of the Cretaceous, a period of great diversification of angiosperms (Crane & Lidgard 1989, Crane et al. 1995), in which the territories belonging today to the zoogeographic realms we examined were relatively close geographically (Afrotropical and Madagascan, and Australian, Oceanian and part of Oriental; Cox & Moore 2009). When we observe the clusters of fruit consumption formed with the data on Afrotropical, Australian, Oceanian, and Oriental realms, for example, with several genera of fruits in common, such as *Anacardium*, *Syzygium*, and *Terminalia*, this is likely a reflection of the influence of Gondwana biogeography and sea level changes in the Sunda shelf. As the rise of the Old World fruit bats occurred much later, these animals benefited from an existing feeding niche (Eriksson 2016) in these realms.

Madagascan showed a distinct pattern for both Pteropodidae and the genus *Pteropus*. Madagascar and India separated from the African continent 135 million years ago, and India then separated from Madagascar at 88 mya (Storey et al. 1995). The weak connection to other realms in the cluster in the composition of the diet of Malagasy

pteropodids as well as with the genus *Pteropus* could be related to the biogeographic scenario of the breakup of Gondwanaland 100 million years ago (Cox & Moore 2009) and the long history of isolation and the high levels of plant endemism evolved. Other studies relate the dispersal of Cenozoic fauna of African origin as the most important biogeographic force in modelling the fauna and flora of modern Madagascar (Sanmartín & Ronquist 2004, Yoder & Nowak 2006). Our data showed a separation of diet composition for Malagasy bats from other realms in the ordination, likely explained by the extreme endemism of Madagascar, where more than 80% of the plants are endemic (Myers et al. 2000, Yoder & Nowak 2006). Several species of pteropodids are endemic to the Madagascan realm (Madagascar and associated islands), including one species of *Eidolon*, two *Rousettus*, and six *Pteropus* (IUCN 2021), and several of the genera of fruits consumed by them, such as *Bakerella*, *Canephora*, *Cinnamosma*, *Fenerivia*, *Grangeria*, *Sarcolaena* and *Tambourissa* (Missouri Botanical Garden 2021) are also endemic.

The Oriental realm has the highest number of records of fruit consumption, as well as the highest diversity of species selected. This may be related to the fact that this realm (which includes the Sunda region and islands but not New Guinea - Holt et al. 2013) is near the center of the evolutionary origin of pteropodids (Teeling et al. 2005). Southeast Asia has almost twice the number of species of fruit bats per area compared to West Africa (Fleming et al. 1987). Some of the genera observed in the diet of Oriental realm pteropodids (e.g. *Adinandra*, *Chrysophyllum*, *Lannea*, *Payena*, and *Xerospermum*) do not have consumption records in the other realms. However, they are not endemic to the Oriental. Given the high species richness of pteropodids in this region, we might expect more partitioning of the available resource base and potentially more specialization in food resources among the many genera and species of bats. The studies that mention resource partitioning on pteropodids indicate that bats that coexist could forage at different heights, at different periods, consume fruit of different sizes and hardness (Thomas 1982, Francis 1994, Dumont & O'Neal 2004, Campbell et al. 2007). Some of these "adjustments" acting in this bat diverse fauna on the Oriental realm.

Our results also indicate a strong gradient in diet composition in both pteropodids and *Pteropus* across the Oriental, Oceanian, and Australian realms. These regions are distinct in a number of terrestrial groups due to past geologic history with several proposed points of separation (e.g. Wallace's line), which vary for different taxa. These barriers to dispersion are insignificant for pteropodids, and these realms are connected by the dispersion of these bats across oceanic areas as well as by the potential dispersal of a number of fruits in a stepping stone fashion from island to island by fruit bats (e.g. Docters van Leeuwen 1936, Thornton et al. 1996, Shilton et al. 1999). Even though the bats did not coevolve with the existing fruit community in some of these localities, by ecological shifting they could access these resources (Fleming & Kress 2013). The seed dispersal ability of pteropodids may contribute to the general lack of a strong distinction and a gradient in species in the diet between the Oriental, Oceanian, and Australian realms.

The Afrotropical realm (for all Pteropodidae) and the Australian realm (for both Pteropodidae and *Pteropus*) show clusters of species in the diet either endemic or largely restricted to these two continents. The diet composition of African pteropodids is heavily influenced by fruit species associated with the tropical forests and savannas of that continent. In addition, there are many species of pteropodids also endemic to and likely coevolved with these plants (eg. see Giannini 2019, and specific species accounts within, as well as information in IUCN 2021). The same is true in Australia, where the diversification and explosive radiation of the genus *Pteropus* has also occurred together with the development of a high level of plant endemism. It is not surprising that these two continents have distinct clusters of species found in the diet of fruit bats, as both continents have a long history of geographic isolation through evolutionary time.

The family Pteropodidae is well studied in several aspects of its ecology, but this is the first compilation of data on the group's frugivorous diet throughout its distribution. The data from this study confirmed the great diversity in the diet of this family and also showed frugivorous consumption with a strong predominance of the genus *Ficus*, both among most Pteropodidae genera and across the zoogeographic realms. Also, these Old World bat-plant interactions show the distinctiveness of zoogeographic realms proposed by Holt et al. (2013) based upon these observations of frugivory patterns. However, due to their flight capacity, bats have fewer barriers to dispersal and foraging, which could explain the gradients seen between some of the realms. These data help to visualize patterns and similarities in frugivory among different regions of the Old World. This database can be used as a template for additional research on the ethology and ecology of frugivorous bats and the biogeography of bats and their fruit resources.

ACKNOWLEDGEMENTS

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